Vegetation Science in retrospect and perspective – Proceedings 41st IAVS Symposium Uppsala 1998

White, P.S., Mucina, L. & Lepš, J. (eds.)

In recognition of the leadership, a career of service to vegetation science, and the many hours of toil in the production of first the Symposium and second the Proceedings, the editors hereby dedicate this volume to:
Professor Eddy van der Maarel

Eddy van der Maarel, with his wife Marijke van der Maarel-Versluys

In July, 1998, the International Association for Vegetation Science (IAVS) convened its 41st Symposium, "Vegetation Science in Retrospect and Perspective", in Uppsala, Sweden. The occasion marked several important dates: the 100th Anniversary of the Department of Ecological Botany, Uppsala University, the 75th Anniversary of the Swedish Phytogeographical Society, and what Sjögren, van der Maarel, and Pokarzhevskaya (1998) described as the 50th Anniversary of the resurrection of IAVS.

In this volume, we present the proceedings of that symposium. The 93 papers presented here encompass the diversity and breadth of vegetation science and illustrate the importance of this field in the modern world. With the increasing occupation of the earth's surface by human populations, as well as the growing human influence on the chemistry and climate of the world's ecosystems, vegetation science has never been more important. Vegetation forms the physical structure and is the basis of energy flow for almost all ecosystems. It follows that, in addition to our curiosity about the nature of vegetation, our activities also contribute to a larger understanding of the trajectory of the earth's ecosystems and the human influence and place within a changing world.

The Symposium presented 16 themes in four mainstreams. The first mainstream began with the history, methods, and theory of vegetation science, but also treated vegetation dynamics. Studies of vegetation dynamics span a huge range of temporal scales, from tens of thousands of years of soil development and climate change to the mechanisms of seedling establishment on tip-up mounds after wind disturbance. The last several decades have seen a tremendous increase in our understanding of these dynamics. We can now more easily understand that the species that make up a community have different requirements for establishment and different growth and survivorship characteristics. We also have begun to integrate local scale dynamics with the stability of larger scale community mosaics.

The second mainstream, treated classification, survey, zonation, and anthropogenic vegetation. New tools like computer mapping, geo-positioning units, and remote sensing, along with the need to understand the effect of climate change on the world's ecosystems have created a renewed vigor in efforts to classify and map vegetation. Initiatives are underway in many different parts of the globe and several of these are reported here. We must understand the composition, structure, and environmental relations of vegetation if we are to determine current human influence and predict future changes. Such information is also critical to the conservation, restoration, and management of vegetation. We are fast losing the last wild areas with low human influence and it is essential that we understand these before they are gone. It is clear that in many vegetation types there is a long history of human use and influence. In some cases, traditional landuse practices combined with low human populations produced early successional vegetation that is, to some degree, now dependent on human influence.

The third mainstream was devoted to vegetation ecology and management, including studies of restoration, grazing, fragmentation, deforestation, and long-term succession, particularly related to climate change. It is in these areas that we put our theoretical and academic studies to the test but the experimental frame that this forces upon us can also expand our basic understanding of vegetation itself.

The fourth mainstream treated the interface between plant populations and plant communities, including species interactions and effects on community diversity. Of particular importance is the understanding of ability of plant strategies and functional types to explain the general patterns of vegetation dynamics. The plant community and population ecology also reflects the width of approaches used when studying vegetation at this hierarchical level. Whereas the mechanisms of species diversity maintenance still puzzle ecologists, the approaches how to tackle the problem differ among researchers, from manipulative experiments to statistical analysis of spatial patterns. Also, the importance of the genetic structure of the populations for community dynamics is being recognized. Several studies demonstrate the importance of understanding mechanisms on population and community levels for successful nature conservation and community management.

We must acknowledge the hard work of the conveners, many of whom served as editors and reviewers of the papers: Mike P. Austin, Harmut Dierschke, and Eddy van der Maarel (History, methods, and theory of vegetation science); Jan P. Bakker and Håkan Rydin (Vegetation dynamics); Ola Engelmark, Sylvie Gauthier, and Eddy van der Maarel (Disturbance dynamics in boreal and temperate forest, long-term studies and general and short-term studies); Martin Diekmann and Francesco Spada (Vegetation survey: Large-scale approaches and case studies); Dieter Mueller-Dombois and Erik Sjögren (Succession and zonation on mountains); Stefan Klotz, Francesco Spada, and Hein van Bohemen (Anthropogenic vegetation and the role of invasive species); Julie S. Denslow and Ingvar Backéus (Ecology and management of tropical vegetation); Peter Poschlod and Eddy van der Maarel (Ecology and management of grasslands); Jörg Pfadenhauer and Håkan Rydin (Ecology and management of wetlands); Wolfgang Cramer and P. Staffan Karlsson (Long-term succession, particularly related to climate change); Johan Ehrlén and Honor Prentice (Population ecology and biosystematics in a community perspective); Deborah Goldberg and Brita Svensson (Species interactions and plant community structure); Sandra Díaz, Sandra Lavorel, and P. Staffan Karlsson (Plant functional types and plant strategy types); and Robert K. Peet and Eddy van der Maarel (Plant species diversity and internal community dynamics).

We thank Lena Lundgren and the staff at Opulus Press for handling manuscripts during the review process and the production of the volume.

Lastly, we thank our hosts at Uppsala University for all the work they did to make the meeting enjoyable and efficient for the participants.

Peter S. White
Jan Lepš
Ladislav Mucina

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Spatial application of β-diversity analysis – an iterative approach to characterize landscape heterogeneity

Beierkuhnlein, Carl

Department of Biogeography, University of Bayreuth, D-95440 Bayreuth, Germany;
Fax +49 921 552315; carl.beierkuhnlein@uni-bayreuth.de
http://www.uni-bayreuth.de/departments/biogeo/carl.htm

Abstract. In most investigations of biodiversity only α-diversity (the number of objects) is considered. β-diversity (the dissimilarity between objects) is another important way of describing diversity. In this study beta-diversity is applied to spatial distributions of samples on a landscape scale. Following an iterative process on the basis of a regular initial distribution of plots, the density of investigated plots was modified after each analysis of β-diversity between neighbouring plots. This geographical analysis of β-diversity was carried out in *Pinus sylvestris* forests of the 'Nördliche Frankenalb' (Bavaria, Germany). Three regions with high values of β-diversity were identified within this landscape. These 'hot spots' of β-diversity can be interpreted mainly as the result of small-scale geological heterogeneity. Nevertheless, sharp boundaries between different substrates were not reflected directly by narrow areas of heterogeneity. Such ecotones might be due to a lacking equilibrium of species composition close to discontinuous changes in substrate.

Keywords: Biodiversity; Euclidean distance; *Pinus sylvestris*; Spatial heterogeneity.

Introduction

The expressions α-, β- and γ-diversity were introduced and developed by Whittaker (1972, 1977) to characterize different qualities at different scales. Alpha- and gamma-diversity indicate a number of objects within a unit (initially species diversity of a certain plot or area), whereas b-diversity describes the differences in the composition of objects between units (e.g. dissimilarity in species composition between plots). Whittaker described the changes in species compositions along ecological or physiographic gradients and defined β-diversity as a rate of change. Another point of view is to do a comparison for a time series at a certain site ('species turnover', Wilson & Shmida 1984). A third way of proceeding is followed here, the comparison of spatial entities, of certain areas according to their composition of objects (in this case species). Spatial applications for the analysis of β-diversity analyses, such as the one proposed here, are rare (e.g. van der Maarel 1976). The opinions on this topic are not unanimous. Some authors link certain types of diversity with certain scales. van der Maarel (1997) adds δ- and ϖ-diversity for higher scales. Here, however, in extension of Whittakers definition, α-, β- and γ-diversity are regarded more generally as parameters for the variability of biotic objects *within* certain spatial, temporal or functional units (α) and *between* them (β) (fig. 1). γ-diversity then is the variability within the complete data set.

Compared to the mapping of homogenous vegetation types, the investigation of the variability between samples, the spatial heterogeneity reflected in patterns of dissimilarity is studied little in vegetation research. This was criticized by landscape ecologists (Turner & Gardner 1991). Of course it is more easy to cope with uniform objects than with heterogeneous ones. On the other hand we have to recognize that there is also a shortage in methodological background for the analysis of spatial heterogeneity (Rosenzweig 1995). There is not much known about spatial diversity within communities, ecosystems and landscapes (May 1994; Folke et al. 1996). Zones with high β-diversity (spatial heterogeneity) can be regarded as ecoclines (transition zones) or ecoclitos (sharp boundaries). The difference between them is dependent on the grain size (resolution) of the sampling design and on the scale of investigation.

To characterize β-diversity different resemblance indices (similarity measures, distance measures) have been developed (e.g. Euclidean Distance, Simple-Matching Index, Margalef Index). This study used such measures, especially Euclidean Distance, for the characterization of spatial heterogeneity and to identify patterns of increased values. This algorithm, being criticized as being influenced by gamma-diversity (e.g. Greig-Smith 1983; Faith et al. 1987), offers the advantage for the analysis of quantitative data as abundance values, allowing to detect patterns of diversity in species-poor forests. My goal is to present a method for the identification of areas with high values of β-diversity.

Study area

The Nördliche Frankenalb is located in Northern Bavaria, Germany and covers an area of ca. 2500 km^2. The investigation area covers an area of 1600 km^2 (40 km × 40 km). Following a regular sampling design, the data collection was performed during the vegetation period of 1997 on the basis of quadratic grid cells of 4 km^2.

The bedrock of the Frankenalb consists mainly of jurassic limestones and marls, but sandstones and clays also occur. Its altitude ranges between 300 and 700 m a.s.l. This landscape shows a mosaic of agricultural and forest land use. Forests cover ca. 30 % of the surface. Natural beech forests (*Fagus sylvatica*) are rare. Nearly everywhere in the region economically more important conifer forests, mainly dominated by Scots pine (*Pinus sylvestris*), occur and can be regarded as the typical forest type. In this preliminary study I limited samples to this forest type because of its prevalence.

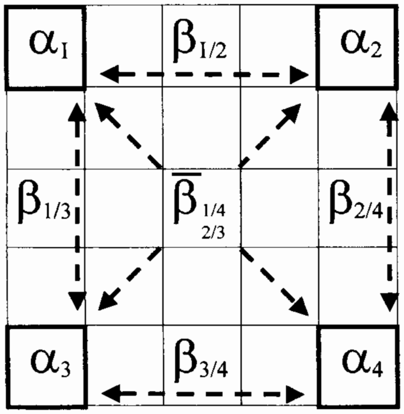

Fig. 1. Schematic illustration of α- and β-diversity for four plots representing certain values. For the central grid cell the mean value of β-diversity for the pairs 1/4 and 2/3 can be calculated.

Methods

The investigation included several steps (Fig. 2). During the initial sampling only regularly distributed grid cells were considered. Within these cells again a grid of 6 × 6 squares was installed and one of them selected by chance. This selected square was sampled only, if it was dominated by mature *Pinus sylvestris*. Further criteria for sampling were (1) the square had to have more than four trees with a DBH of more than 20 cm per 100 m^2 and (2) the square had to be more than 50 m away from forest edges, roads and forest ways.

The species composition was recorded in homogeneous parts of the forest on plots of 100 m^2. Shrubs, herbs, grasses and mosses were recorded. Their frequency was measured using 25 squares of 2 m × 2 m. Soil samples were taken. During the first iteration plots within 61 grid cells were sampled (Fig. 2). After this first phase of field work the β-diversity between neighbouring plots was calculated. The density of plots was modified afterwards. In addition to the plots of the first phase, further plots were installed in grids where the mean orthogonal dissimilarity was higher than the total mean dissimilarity of the set of all plots (Fig. 2). β-diversity (or dissimilarity) was expressed using a distance index, in this case Euclidean distance. Then again a new calculation of β-diversity was performed. This results in an iterative increase of samples.

The aim of this approach was to identify areas with high β-diversity. At the end they ought to show a dense distribution of plots, whereas homogeneous regions are quite sparsely covered with samples. Basically, with this method ecotones are detected and mapped. The transition zones between homogeneous vegetation units can be identified by showing the area and the degree of heterogeneity.

Results and Discussion

The iterative process used in this study results in the emergence of obvious patterns of diversity. The calculation of Euclidean distance (ED), after the sampling of regularly distributed plots during the first phase of field work (Fig. 3a), shows only a coarse pattern (Fig. 3b). Areas with high values cannot be clearly detected. The total mean value of ED for the data of this first phase was 76.2.

As the basis for a second phase of field work, cells that lay between the cells sampled in the first phase and showing high orthogonal dissimilarity (higher than the mean

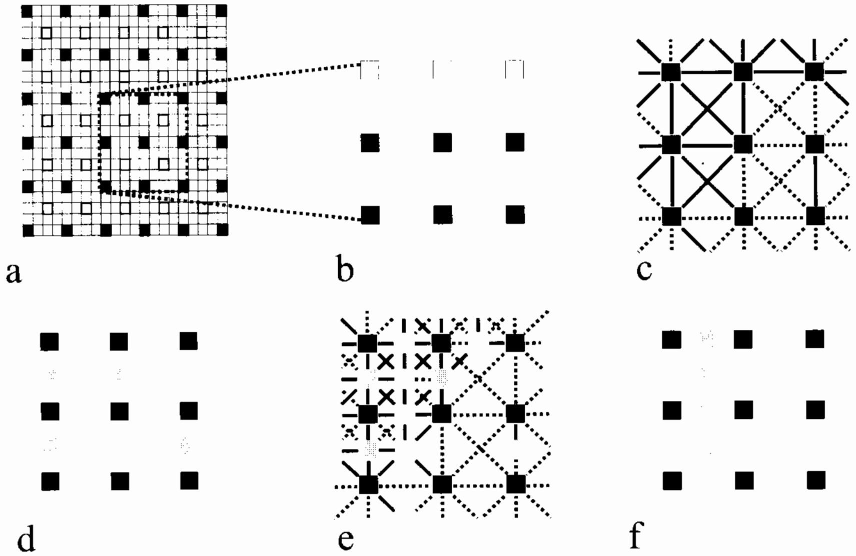

Fig. 2. a. Schematic presentation of the iterative spatial application of β-diversity analysis shown for a subset (b - f) of regularly distributed samples; **b.** Initial distribution; **c.** β-diversity values higher and lower (broken lines) than the mean; **d.** Distribution of samples in the second phase of field work; **e.** β-diversity values higher and lower (broken lines) than the mean on the basis of the second iteration; **f.** Final pattern of grid cells.

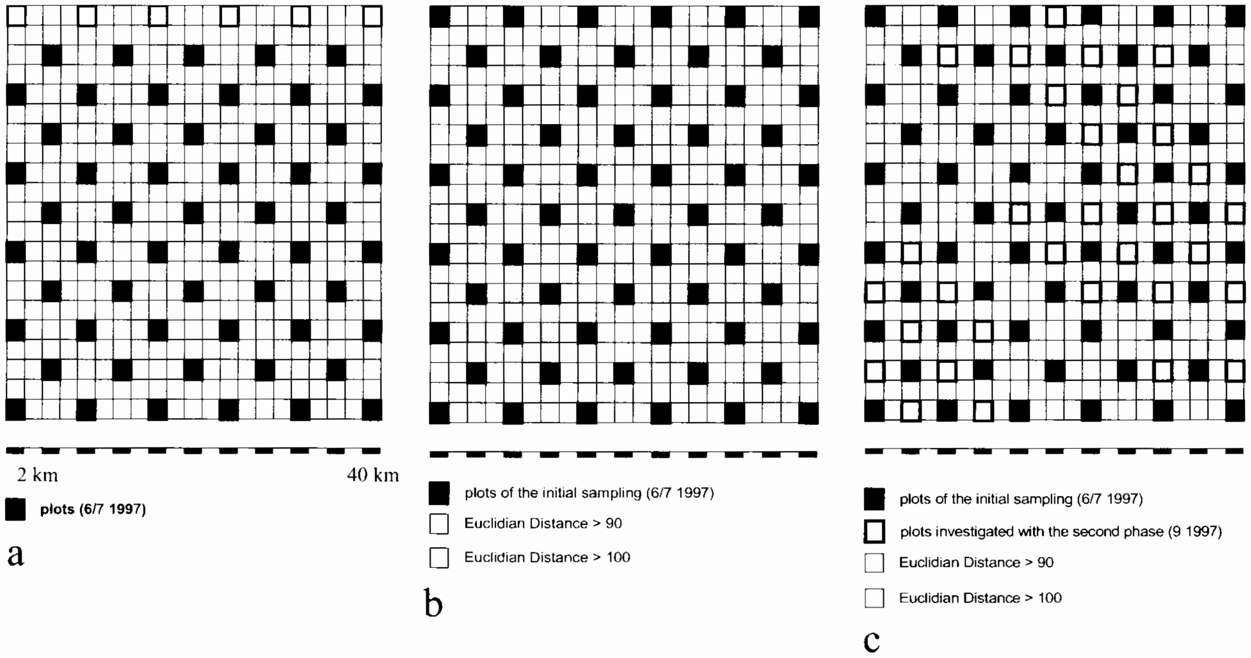

Fig. 3. Distribution of investigated grid cells with *Pinus sylvestris* forest in the landscape of Frankenalb and β-diversity between them. **a.** Initial regular distribution of cells (black); **b.** Additional indication of the higher values of mean orthogonal Euclidean distance between the plots. Values of ED higher than 90 are light grey, higher than 100 are dark grey; **c.** Distribution of investigated grid cells from the second sampling phase carried out in grid cells where the mean orthogonal ED was higher than the total mean, and again the ED between all the plots.

values of all central cells) were identified and selected. At the edge of the study area only one pair could be considered. This is a methodological restriction, because these values are not really comparable to the others. Only view grid cells could not be investigated when no *P. sylvestris* forest were found that fulfilled the criteria. This is why some grids that are grey after the first calculation were not investigated during the second phase of field work. Having calculated ED again, based on this new extended data set, the total mean of ED decreased to 72.1. This indicates the influence of the sample size and γ-diversity on the values. It could also be due to the decreasing spatial distance between the plots.

However, three distinct stripes with high values emerge in Fig. 3c. Two of these areas with high β-diversity are quite easy to interpret. The dark strip in the upper right (North-East) is located at the transition from sandstones and clays to limestones and marls that dominate in the larger central part of the landscape. The same is true for the more scattered agglomeration of dark colours in the lower left side. There the limestones from the centre are replaced by sandstones and clays again. Regarding these very sharp lines in the change of geological substrate, it is quite astonishing, that the changes in species composition, reflected by high values of ED, stretch across several km of distance. This might reflect that it needs a certain spatial range to get communities saturated and that close to abrupt changes in site conditions there is still a non-equilibrium of species composition.

The third area of high β-diversity in the centre of the landscape is ecologically not easy to interpret. Within the limestones, dolomites occur in this part of the region, perhaps this is the reason for this small-scale diversity. The site conditions according to relief, climate and land use are very much the same as they are found in other parts of the landscape.

Depending on site conditions and land use, regions with low and with high α-diversity can be detected. The latter are called 'hot spots' following a paper from Myers (1988) on tropical biodiversity (see also Hawksworth & Kalin-Arroyo 1995). Such hot spots, hot lines or hot regions can be found for β-diversity as well.

The iterative approach of the calculation of β-diversity introduced here leads to the emergence of specific spatial patterns. This is shown for the conifer forests at the landscape level of the Nördliche Frankenalb. Characteristic spatial patterns of β-diversity are identified. The investigation gives hints for the most important site conditions responsible for the development of diversity patterns. In this case substrate, effective via nutrient availability, seems to have the strongest influence. Future changes in the deposition of nutrients or toxic compounds and the acidification caused by precipitation might affect these spatial patterns via processes of soil chemistry.

The results of the application of this method are likely to be influenced by the choice of the similarity index. Therefore these results have to be compared with analyses using other indices to find out whether the detected patterns appear then, too. The similarity indices have to be scrutinized critically. ED is highly sensitive to differences in α-diversity or to dominant species.

Another problem is the spatial distance between the plots. It can be assumed that it also affects the results. The closer two plots are, the higher is the probability of that they are similar. To avoid too much influence from this, only the orthogonal distances were considered to make real distances comparable. However, with the ongoing iterations the spatial distances change and this might influence the results. But if there are still high values of dissimilarity found, even at closer distances, as it is the case in this study, it is rather sure that these areas are very heterogeneous. Nevertheless a standardization of values resulting from distance measures should be achieved by integrating spatial distance into similarity indices.

Problems of scale are closely related to the spatial limitation of vegetation units (van Leeuwen 1970; Seibert 1974). Deficits exist regarding the characterization of such borderlines or transition zones. Future approaches for the evaluation of areas have to develop methods that characterize the properties of ecotones. Generally areas with a high degree of small-scale β-diversity can be seen as transition zones. Their sharpness, and if they are considered to be ecotones or ecoclines, depends on the scale that is used. The different iterations during the investigation process of this study result in a dense distribution of samples in areas of high β-diversity. This is an unbiased tool to detect such transition zones on the basis of floristic data. The method is not scale dependent and can be applied at different levels of scale and for other objects than species.

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History of phytosociology in Europe, especially in the last 50 years

Dierschke, Hartmut

Albrecht-von-Haller-Institute of Plant Sciences, Department of Vegetation Science and Population Biology, University of Göttingen, Wilhelm-Weber-Str. 2, D-37073 Göttingen, Germany;
Fax +49551392287; E-mail hdiersc@gwdg.de

Abstract. The history of phytosociology in Europe is closely connected with the development of the International Association for Vegetation Science. Tables and comments give a short survey from the beginning in 1939 until the actual situation, concentrated on the development of the scientific organisation, international congresses and excursions, activities of working groups and commissions for special subjects of vegetation science and publications. Finally some perspectives for further development of different aspects of phytosociology are presented.

Keywords: Excursion; IAVS; Publication; Symposium.

Introduction

The development of vegetation science in Europe, especially phytosociology, is more or less congruent with the development of the International Association for Vegetation Science (IAVS). Although there are some surveys of the history of vegetation science (e.g. Westhoff & van der Maarel 1973; Dierschke 1994), the establishment phase for this scientific organisation is somewhat obscure. For later phases many reports and minutes of meetings, symposia and excursions are available. In addition, I have received some documents and correspondence of R. Tüxen. Using this basis, including own experiences since 1961, I will try to give a short survey of the development of IAVS and some perspectives of phytosociology for the future.

Scientific organisation of vegetation science in Europe

The first foundation of an international association of vegetation scientists was in 1939 as the 'Association Internationale de Phytosociologie', at a meeting of phytosociologists in Marseille (FR) (Table 1). However, the first activities ended in the turbulence of the Second World War.

The situation after 1945 was very difficult. Although personal contacts had been maintained over the years, there was no real organisation. A new beginning was discussed at a first meeting of some phytosociologists at Hilversum (NL) on 21 June 1947. This effort remained sterile, however, because of difficulty in establishing an active working committee under the bad conditions of the post-war period. There was an old Executive Committee, named in a document of 1948 to include Szafer, Nordhagen, Lebrun and Adriani (Table 1), but without any activities.

During the 7th International Botanical Congress in Stockholm in 1950 there was a meeting of the International Phytosociological Commission of the Botanical Section of the IUBS (President: C. Troll, Secretary K. Faegri), at which many of the most prominent European phytosociologists were present (Barkman 1952), but no definitive steps were taken.

Documents of R. Tüxen (DE) from 1952 show a very active correspondence, especially with W.C. de Leeuw (NL), in order to arrange a new start for an international society. The result was a meeting of a new, self-nominated Executive Board (Table 2). This meeting can be regarded as the real start of the new foundation. The International Society of Plant Geography and Ecology (also with a German and French name; see Table 2) was established with new Statutes, an Executive Board and a General Board with one representative of every country or regional section. The annual membership fee was 1 dollar. The main activities for the coming years were to be an International Symposium about the syntaxonomy of beech woods and an International Grassland Excursion in SW Central Europe.

Table 1. Foundation and first period of IAVS.

- 1939 Foundation of the Association Internationale de Phytosociologie (AIP); President: W. Szafer (PL); Vice-Presidents: P. Allorge (FR), R. Nordhagen (NO); Secretary: R. Tüxen (DE), A.S. Watt (GB), Treasurer: W. C. de Leeuw (NL); Director of the International Center in Montpellier: J. Braun-Blanquet (FR).
- Regional (national) sections with one representative in the Central Committee
- Aims:
  1. Promotion of phytosociology and geobotany
  2. Phytosociological nomenclature (rules of priority, valid publication of names)
  3. Collaboration with institutions of nature conservation
  4. Organisation of excursions
  5. Establishment of a phytosociological centre in Montpellier
- 1947 Discussions about reorganisation of AIP by some phytosociologists in Hilversum (NL)
- 1948 President: W. Szafer, Vice-President: R. Nordhagen; Secretary: J. Lebrun (BE), Treasurer: M.J. Adriani (NL)

Table 2. The Stolzenau-Rinteln period (1954-1981).

- 1954 New foundation of the International Society of Plant Geography and Ecology = Internationale Vereinigung für Vegetationskunde = Association Internationale de Phytosociologie
- Executive Board (first meeting 28.02.1954 in Utrecht): Pres.: W.C. de Leeuw, Vice-Pres.: J. Lebrun, Secr.: R.Tüxen, Treas.: M.J. Adriani
- General Board: One representative of every regional section (Membership list with 79 members from 34 countries)
- 1955 1st International Excursion: Grassland in Southwest Central Europe
- 1956 1st International Symposium at Stolzenau (DE): Phytosociology and Soil Science
- 03.09.1964 W.C. de Leeuw ✝
- 1965 9th International Symposium at Rinteln (DE); J. Lebrun (new President), Secr.: R. Tüxen
- 1974 International Society for Vegetation Science (new name)
- 16.05.1980 R.Tüxen ✝
- 20.09.1980 J. Braun-Blanquet ✝
- 1981 Meeting of 45 members of 16 countries in Rinteln: Discussion about the future of the International Society; Commission for new Statutes (Barkman, Dierschke, Ellenberg, Géhu, van der Maarel, Miyawaki, Moore, Pignatti, Wojterski)
- 25th International Symposium in Rinteln.

At the 8th International Botanical Congress in Paris 1954, the new (and old) Society got the official mandate to organize an international symposium in 1956 in central Europe. After a first excursion in 1955, the first International Symposium took place in Stolzenau (DE), organized by R. Tüxen. This was the very beginning of a more intensive cooperation and discussions amongst European phytosociologists, also with a growing number of vegetation scientists from other continents (Table 5). Stolzenau was called the 'Mecca of phytosociology', mainly based on the activities and the international reputation of R. Tüxen. After the death of W.C. de Leeuw (1964), J. Lebrun (B) became president of the Society. Secretary R. Tüxen, however, was the most important and active person for a long time.

When Tüxen moved from Stolzenau to Todenmann near Rinteln in 1965, this small town in NW Germany became a new centre of phytosociology. Every year in the week before Easter many prominent phytosociologists from all parts of the world met here during the annual symposium. In 1974 the association changed its name to the International Society for Vegetation Science (a document about this change is not available).

A turning point in the history of our association was the death of first R. Tüxen and then J. Braun-Blanquet in 1980. Already some time before, Tüxen had delegated the administration to H. Dierschke who was also responsible for the organisation of the last symposium in Rinteln 1981. Before this meeting a larger group of phytosociologists was invited for a discussion about the future of the Society. This group and the symposium participants (more than 170 from 22 countries) decided to meet in Prague the next year. A commission should elaborate new Statutes for a more democratic structure (see also Dierschke 1981).

Table 3. Reorganisation and further development of IAVS.

- 1982 Prague: Reorganisation of the International Association for Vegetation Science = IAVS = Association International pour l'Etude de la Végétation (AIEV) = Internationale Vereinigung für Vegetationskunde (IVV).
- New Statutes: Executive Committee, Advisory Council, General Assembly; Pres.: Ellenberg; Vice-Pres.: Géhu, Miyawaki, Moore, Pignatti, Wojterski; Secr.: Dierschke; Treas: Hübl; Edit: Barkman
- 26th International Symposium: Chorological phenomena in plant communities
- 1986 Halle: New Advisory Council (1986-1989); Pres.: Pignatti, Vice-Pres.: Barkman, Géhu, v.d. Maarel, Miyawaki, Neuhäusl, Westhoff, Wojterski; Secr.: Dierschke; Treas.: Hübl.
- 1990 Warsaw: New Advisory Council (1990-1993); Pres.: Pignatti, Vice-Pres.: Box, Géhu, v.d. Maarel, Miyawaki, Neuhäusl, Rivas-Martinez, Wojterski; Secr. & Treas.: Dierschke
- Spanish becomes an official language; Asociación Internacional de Ciencias de la Vegetación (AICV)
- Committee for a revision of the Statutes
- *Journal of Vegetation Science* (Official Organ of IAVS); Editors: v.d. Maarel, Neuhäusl, Peet
- 1994 Bailleul: New Advisory Council (1994-1997); Pres.: Box, Vice-Pres.: Géhu, Miyawaki, Mucina, Pignatti; Secr. & Treas.: Dierschke, Edit.: v.d. Maarel
- 1996 Lancaster / 1997 České Budějowice: Acceptance of the new Statutes.
- 1998 Uppsala: New Advisory Council (1998-2001); Pres.: Box, Vice-Pres.: Loidi, Miyawaki, Mucina; Secr.: Schaminée, Treas.: Dierschke, Edit.: v.d. Maarel
- *Applied Vegetation Science* (2nd Official Organ of IAVS)

The new Statutes were accepted by a General Assembly in Prague in 1982. H. Ellenberg was elected as new President, H. Dierschke as Secretary General (Table 3; Dierschke 1982a). Prague was the beginning of a new era, with a new (and still current) name: International Association for Vegetation Science (IAVS). It was decided that annual international symposia would take place in different countries all over the world, and further international excursions would also be organized. Besides, some Working Groups were active, regarding different special subjects of vegetation science. Every four years a new Advisory Council would be elected, with an Executive Committee (Table 3). H. Dierschke was Secretary General from 1982 to 1998. At the meeting in Uppsala 1998, J.H.J. Schaminée (NL) was elected as the new Secretary.

During the symposia in Lancaster (GB) and České Budějowice (CZ), new Statutes were discussed and accepted, based on the experiences of the past.

In summary, the development of the Association has been successful and it provides a good foundation for further development. This is also evident from the development of the membership, as is shown in Table 4.

International Congresses of Vegetation Science

Since 1956 an International Symposium has taken place almost every year, at first in Stolzenau (1956-1964), later in Rinteln (1965-1981), and afterwards in different countries all over the world (Table 5). The first official symposium was in September 1956 in Stolzenau with 82 participants from 10 European countries (see Walther 1959). However, there had already been a pioneer symposium in Stolzenau in 1953, which was later counted as number one.

The subjects of the symposia include a broad range of themes, including the main themes of vegetation science and many applications in other sciences or practical fields (e.g. Biosociology, Palynology, Landscape Ecology, Soil Science, Forestry, Agriculture, Nature Conservation) (Table 5). In connection with the symposia also meetings of smaller discussion groups took place (see Dierschke 1982b).

The International Symposia soon became the most important congresses in vegetation science. Many scientific and practical questions have been discussed. Gradually an agreement and better understanding between the different schools of vegetation science has also been achieved. Discussions of special questions stimulated the establishment of Working Groups (Table 7). Also in the future, the International Symposia will function as the most important platforms for further successful development of vegetation science.

Table 4. Membership development (members/countries).

1954	79 / 34	1989	603 / 38	1995	1388 / 75
1967	490 / 35	1990	811 / 51	1996	1430 / ??
1978	625 / 38	1991	1100 / 58	1997	1460 / ??
1982	500 / 36	1992	1161 / 66	1998	1510 / 83
1986	568 / 38	1994	1328 / 70	1999	1619 / 79

Table 5. International Symposia of the IAVS.

1953 Stolzenau (DE)
1. Phytosociology as a link between agriculture and water economy
1956 Stolzenau (DE)
2. Phytosociology and Soil Science
1959 Stolzenau (DE)
3. Vegetation mapping
1960 Stolzenau (DE)
4. Biosociology
1961 Stolzenau (DE)
5. Anthropogenous vegetation
1962 Stolzenau (DE)
6. Phytosociology and Palynology
1963 Stolzenau (DE)
7. Phytosociology and Landscape Ecology
1964 Stolzenau (DE)
8. Phytosociological Systematics
1965 Rinteln (DE)
9. Experimental Phytosociology
1966 Rinteln (DE)
10. Community Morphology (Vegetation Structure)
1967 Rinteln (DE)
11. Vegetation Dynamics
1968 Rinteln (DE)
12. Facts and Problems of Vegetational Boundaries
1969 Rinteln (DE)
13. Vegetation and Substrate
1970 Rinteln (DE)
14. Basic Problems and Methods in Phytosociology
1971 Rinteln (DE)
15. Vegetation as an Anthropo-ecological Subject
1972 Rinteln (DE)
16. Endangered Vegetation and its Protection
1973 Rinteln (DE)
17. Succession Research
1974 Rinteln (DE)
18. Landscape classification by the help of vegetation
1975 Rinteln (DE)
19. Vegetation and Climate
1976 Rinteln (DE)
20. Vegetation and Fauna
1977 Rinteln (DE)
21. Association Complexes (Sigmeta)
1978 Rinteln (DE)
22. Development and disappearance of plant communities
1979 Rinteln (DE)
23. Epharmony
1980 Rinteln (DE)
24. Syntaxonomy
1981 Rinteln (DE)
25. Structure and dynamics of forests
1982 Prague (CS)
26. Chorological phenomena in plant communities
1983 Corrientes (AR)
27. Natural and semi-natural vegetation
1984 Wageningen (NL)
28. Dependent plant communities
1985 Bailleul (FR)
29. Vegetation and geomorphology
1986 Halle (DE)
30. Recording and evaluation of anthropogenic vegetation changes
1988 Frascati (IT)
31. Spontaneous vegetation in settlements
1989 Uppsala (SE)
32. Forests of the World. Diversity and dynamics
1990 Warszawa (PL)
33. Vegetation processes as subject of geobotanical maps
1991 Eger (HU)
34. Mechanisms of vegetation dynamics
1992 Shanghai (CN)
35. Applied vegetation ecology
1993 Santa Cruz de Tenerife (ES)
36. Island and high mountain vegetation
1994 Bailleul (FR)
37. Large area vegetation surveys
1995 Houston (US)
38. Community spatial processes; Landscape and global spatial processes; Short-term temporal processes; Long-term temporal processes
1996 Lancaster (GB)
39. Vegetation science and landscape ecology
1997 České Budejovice (CZ)
40. Vegetation mapping; Experimental tests of mechanistic hypotheses of community patterns; Closely related species in plant communities
1998 Uppsala (SE)
41. Vegetation science in retrospect and perspective
1999 Bilbao (ES)
42. Vegetation and Climate
2000 Nagano (JP)
43. Global to local perspectives of vegetation science: Search for new paradigms for the 21th century

International excursions

Besides the Symposia, the International Excursions were important events of IAVS. These were not identical with the International Phytogeographic Excursions (IPE), organized by the Geobotanical Institute in Zürich. The first excursion, with 44 participants from nine countries, was directed toward grasslands in southern Germany, France and Switzerland (see Tüxen et al. 1957). This and other excursions are listed in Table 6. The excursions have always provided a unique possibility to become acquainted with the flora and vegetation of other countries, under expert local guidance, and to discuss different field methods, etc. Excursions also provide an occasion to promote international friendship and cooperation, and can be regarded as another main focus of our Association, as important as the symposia themselves.

Table 6. Excursions of IAVS.

1. 1955 Alsace, SW Germany, W-Switzerland (Berset, Lemée, Marschall, Moor, Oberdorfer)
2. 1956 Jutland (DE, DK) (Bocher, Christiansen, Sørensen, Wohlenberg)
3. 1958 Provence (FR) (Molinier, Tallon)
4. 1962. NW-France (Abbayes, Corillon, Géhu, Hocquette, Lami, Lemée)
5. 1963 NE-Poland (Falinski, Matuszkiewicz, Solinska, Wolak)
6. 1965 SE-Norway (Dahl, Kielland-Lund)
7. 1966 Abruzzi (IT) (Giacomini et al.)
8. 1967 Jura (CH, FR) (Géhu, Quantin, Richard)
9. 1968 Scotland (GB) (Bellamy, Shimwell)
10. 1970 Island
11. 1972 Portugal (Pinto da Silva, Teles)
12. 1974 Japan (Miyawaki et al.)
13. 1976 E-USA/Canada (Benninghoff, Grandtner)
14. 1978 Poland (Wojterski)
15. 1980 Ireland (Doyle, Kelly, Mitchell, Moore, O'Sullivan, Watts, Webb, White)
16. 1982 Central Italy (Pedrotti et al.)
17. 1983 Argentina (Eskuche et al.)
18. 1984 Honshu (J) (Miyawaki et al.)
19. 1986 Norway (Dahl, Kielland-Lund, Vevle)
20. 1988 California, Nevada, Utah, Arizona (USA) (Vankat et al.)
21. 1990 W-Australia (Beard et al.)
22. 1992 E-China (Song Yongchang et al.)
23. 1995 SE-USA (Box, Harcombe et al.)
24. 1996 South Africa (Bredenkamp, Lubke et al.)
25. 1997 Bohemia (CZ) (Krahulec, Prach et al.)
26. 1999 Spain, Pyrenees (Loidi, Rivaz-Martinez)
27. 2000 Japan (Fujiwara, Miyawaki)

Working groups for special topics

In addition to the main symposia, meetings of smaller working groups have discussed and elaborated special subjects of vegetation science. Table 7 lists the groups which have been mentioned in reports or/and which are still active. The most long-standing group is the Working Group for Data-Processing, now with the name Theoretical Vegetation Science. It was formed during the Rinteln symposium in 1969 and had its first meeting at Trieste in the same year (see van der Maarel et al. 1980, van der

Table 7. IAVS Working Groups and Commissions and their initiators or/and present board members.

1959 Permanent Commission for the Vegetation Map of Europe (Pres.: Tüxen; Braun-Blanquet, Emberger, Horvat, Noirfalise, Pawlowski)
1968 Commission for the Protection of Endangered Vegetation (A. Hoffmann, Hülbusch, T. Müller, Moore, Noirfalise, Preising, Westhoff)
1968 Commission for the Prodromus of European Plant Communities (Tüxen)
1969 Nomenclature Commission (Barkman, Moravec, Rauschert; Code of Phytosociological Nomenclature (1976, 1986)
1969 Working Group for Data Processing (van der Maarel, Orlóci, Pignatti) = Working Group for Theoretical Vegetation Science
1973 Working Group for Succession Research on Permanent Plots (Secr.: W. Schmidt, Willems, Bakker) = Working Group on Long-term Vegetation Dynamics
1990 European Vegetation Survey (Rodwell, Eilertsen, Mucina, Pignatti, Schaminée)

Maarel 1989). A second is the WG for Succession Research on Permanent Plots, also now with another name: Long-term Vegetation Dynamics. This group was founded during the Rinteln symposium in 1973 on Succession Research and had its first meeting after the Rinteln symposium 1974 (see Schmidt 1974, 1975; Bakker et al. 1996). Both groups have organized several further workshops, also a joint meeting in Montpellier in 1980 (see Poissonet et al. 1981), and are still active. A rather new WG, called the European Vegetation Survey, has met in Rome every year since 1992, arising out of a smaller meeting during the symposium in Warszawa in 1990 (see Mucina et al. 1993, Rodwell et al. 1995). This group took over some ideas of the Commission for the Prodromus of European Plant Communities which met several times in Rinteln (see Dierschke 1971, 1972). Important work has also been done by the Nomenclature Commission since 1969. Two versions of the Code of Phytosociological Nomenclature (which was already a task at the beginning in 1939!) have been published (1976, 1986; Barkman et al. 1986). A third version is in preparation.

Publications

There are many scientific publications in phytosociology, scattered throughout many journals and books, included in several bibliographies (e.g. Excerpta Botanica, Bibliographia Phytosociologica Syntaxonomica). There are also, however, some whole publication series which are, or were more or less directly influenced, or started by IAVS.

The first journal was *Vegetatio*, which was founded in 1948 as the so-called 'Organ officiel de l'Association Internationale de Phytosociologie'. Its history was summarized by van der Maarel & van der Maarel-Versluys (1988). For a long time the main editors (Braun-Blanquet, Tüxen, Westhoff, van der Maarel, Lieth) were indeed members of IAVS, but the ownership was by various Dutch publishers (see van der Maarel 1990). The same is true with most other series listed in Table 8, for example *Phytocoenologia* or *Excerpta Botanica*. Therefore, after some trouble with the publishers of *Vegetatio*, the Advisory Council decided at its meeting in Uppsala in 1989 to publish a new journal directly controlled by IAVS and available at a reasonable price for all members. The new *Journal of Vegetation Science* (*JVS*) has had a good start; it has developed rapidly and has significantly increased the number of members of the IAVS (see Table 4). E. van der Maarel was the main promotor of this 'journal for all vegetation scientists', with the help of Editors and later also Associate Editors, and an Editorial Board. The number of manuscripts has steadily grown over the years and has led to the establishment of a second official organ of IAVS: *Applied Vegetation Science* (*AVS*). The first volume of *AVS* was published in 1998 (see van der Maarel et al. 1998). So the IAVS has now two journals (*JVS* and *AVS*) under its ownership and responsibility. Another type of publication was the Proceedings of the International Symposia, mainly edited by R. Tüxen. The first separate volume, on Vegetation Mapping, were the Proceedings of the Stolzenau symposium in 1959. From then onwards, a new volume from the previous meeting appeared almost every year (see also Dierschke 1982b). Besides the lectures, the discussions following the talks were also included rather extensively. So every symposium volume is a valuable document on the development of vegetation science. In the last few years no real proceedings have been published, but a new series is scheduled for the coming years.

A voluminous series, the *Handbook of Vegetation Science*, was started in 1964, again upon the initiative of R. Tüxen. The first volume (No. 5, 1973) on 'Ordination and Classification of Communities' was edited by R.H. Whittaker. In the meantime 10 volumes have appeared, and 12 more are scheduled. Each volume contains contributions of experts on a specific subject of vegetation science.

Scientific outlook

This rather short survey of the history of the IAVS, as related to the history of phytosociology in Europe, shows many activities and a rather rapid development within the last 50 years. Many scientific questions have been answered, and new questions have been raised. Although there are problems for the further development of organismal and field biology in many countries (in contrast to biomolecular approaches, biogenetics etc.), vegetation science has to remain an intrinsic part of biological research and teaching. For further development and conservation of our plant cover, experts with good knowledge of the vegetation and its functioning and environment are necessary. Some perspectives for further development of different aspects of phytosociology are given in the following paragraphs:

1. Synmorphology, Symphysiology (vegetation structure and species interrelations): Fine-scale field observations and measurements as well as experimental research, gradient analysis, mapping, permanent-plot studies, etc., closely connected with population ecology and environmental sciences.
2. Syndynamics (succession, vegetation fluctuations):
   Exact short-term to long-term studies on permanent plots of natural and anthropogenic vegetation dynamics, in combination with 1 and 6.
3. Syntaxonomy (vegetation classification): Improvement of national vegetation surveys, establishment of computerized data banks (national, international), and large-scale vegetation surveys (e.g. for all of Europe).
4. Synchorology (vegetation areas): Vegetation maps of Europe and of smaller areas; grid maps showing the distribution of plant communities.
5. Sigmachorology (vegetation complexes): Further development of methods and case studies; connection with landscape ecology.
6. Synecology (environmental conditions of plant communities): Ecological measurements related to plant communities, role of plant communities in ecosystems, plant-animal interactions (biocenology), etc.
7. Applied Phytosociology: Methods of biomonitoring and bio-indication, indicator values of plants in relation to plant communities (in connection with 6), networks of global-

change monitoring stations, nature conservation, restoration of vegetation types, etc.

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The birth and infancy of vegetation science in Britain and America

Gimingham, C.H.

Department of Plant & Soil Science, University of Aberdeen, St. Machar Drive, Aberdeen AB24 3UU, Scotland, UK; Fax +441224272703

Abstract: The earliest contributions to vegetation science in Britain were made 100 years ago in Scotland, by the brothers R. and W.G. Smith. This paper argues that their influence on subsequent developments has been underestimated. Inspired by C. Flahault (Montpellier), their outlook was phytosociological and their aims were to establish a system for vegetation survey and mapping, and to understand relationships between vegetation categories and environmental factors.

After 1912 these objectives were temporarily eclipsed by the emergence of plant ecology, and the stimulus it gave to studies of plant-habitat interactions, vegetation dynamics and ecosystem processes. The convergence of approach between F.E. Clements in America and A.G. Tansley in Britain, and their influence in the two countries, will be examined. At this time little attention was paid to plant community studies, and European phytosociology was largely ignored, but this trend was reversed with the advent of quantitative methods of vegetation analysis. The effects of controversial hypotheses concerning the nature of plant communities, and the events which led to a new appreciation in Britain of the potential for and value of plant community classification, will be reviewed. As vegetation science emerges from its infancy into adulthood, the foresight of the Smith brothers a century ago can be properly evaluated.

Keywords: Association; Phytosociology; Scotland; Smith, Robert; Smith, William G.

Introduction

It is not possible in a short paper to give any comprehensive review of the early history of vegetation science in Britain and America. However, it is the intention in this contribution to offer a few glimpses into events in the past, some of which may be unfamiliar to some readers; and perhaps to introduce a rather new perspective into the origins of vegetation science in these Countries. It is hoped that examination of the sources of some of the important basic ideas of our science, and how they developed and influenced leading workers and thinkers in the subject, will lead to a better appreciation of where we stand today and the direction in which we are heading.

We look first at how vegetation science got started in Britain, by mentioning some early work which, although of considerable significance, is rather little known outside this Country. It is of interest that, in this Centenary Year of the Department of Ecological Botany in Uppsala University, early stirrings of phytosociology were also taking place almost exactly 100years ago in Scotland. Then, as we follow subsequent developments, we shall have occasion to consider how they interacted with the emergence of vegetation science in America.

Robert and William Smith

It is now widely recognized in Britain, if not elsewhere, that our earliest contributions of importance to vegetation science were made in Scotland by two brothers, R. and W. G. Smith. Robert Smith, the younger of the brothers, was a Demonstrator in Botany at the University College of Dundee from 1896 - 1900 and was the first to carry out systematic surveys and produce maps of vegetation in Britain. More than that, however, he - and subsequently also his older brother William - played major parts in a real revolution of botanical science in Britain. To understand how this came about we must take a small step back in time, and consider the influences which shaped Robert Smith's development. Already a keen field botanist, Smith became a student at Dundee in 1893 where the Professor of Botany was Patrick Geddes, an original thinker who made great changes in the teaching of Botany which he felt had fallen into a 'state of intellectual torpor'. He felt that hitherto there had been little sign of appreciation of the new ecological and physiological approach to plant geography being developed in Europe by such influential exponents as Warming in Denmark, Hult and Sernander in Sweden, Schimper in Germany, Schröter in Switzerland and Flahault in France. Geddes himself was fully in tune with these developments and was in close personal touch, especially, with Charles Flahault, the pioneer French phytogeographer and phytosociologist. [References to works by these European pioneers may be sought in Du Rietz (1921), Mueller-Dombois & Ellenberg (1974) and Sheail (1987).]

Geddes was an inspiring teacher and encouraged his students to shed the constraints of what had become an exclusively laboratory-based, descriptive study; and to turn to observing the lives of plants in their natural habitats and their social organisation – the subject matter of ecology, a term which was just then coming into general use. Geddes is not a name much remembered in botanical circles – in fact he is better remembered for his later pioneering work in what we now call human ecology, especially the built environment and town planning – all deriving from his broadly sociological outlook. This led him to move away from natural science, but not before he had recognised the potential of his student, Robert Smith, by appointing him to his teaching staff, following his graduation in 1896, and (most significantly) arranging for him to spend the winter of 1896-1897 working in Montpellier with Flahault.

Robert Smith, already strongly disposed towards the interpretation of vegetation as composed of plant communities, was much impressed by Flahault's aim of mapping the vegetation of France on the basis of groups of tree species characteristic of each region, and identifying 'associations végétales', consisting of sets of species with similar habitat requirements. Smith came back to Scotland keen to apply Flahault's methods, in a modified form, to an ambitious project on which he had already embarked, to classify and map the vegetation of his native country. Modification was necessary because Flahault's survey was based largely on tree vegetation, of which there was relatively little left in Scotland where the vegetation was a mosaic of types all much modified by human uses; and Smith developed his own classification based on plant associations – their physiognomy and characteristic species, especially the dominants. Joined by his brother William, surveys of several areas in south and central Scotland were conducted and vegetation maps at a scale of 1:126 729 (2 English miles to 1 inch) prepared for publication (R. Smith 1900a, b). Tragically, however, Robert died in 1900 following an attack of appendicitis, at the age of 26. The work he had initiated was completed by William (W. G. Smith 1904, 1905) who not only continued with similar surveys and mapping in N. England from his base in Leeds, but also drew the attention of a much wider scientific audience to the achievements and potential of the new approach, in lectures and papers (W.G. Smith 1902).

Vegetation science in Britain

It is thus evident that the first stirrings of vegetation science in Britain were strongly influenced by the phytosociological outlook which was taking shape in Europe. Some historians of ecology in Britain have labelled the work of the Smith brothers and the small group of field botanists which gathered round them as 'the approach of the phytogeographer'. If by that they mean an approach centred exclusively on the geographical distribution of individual species, they are wrong: Smith himself commented in 1899 that while this had been the case in the earlier years of the 19th Century when 'the biological element was hardly touched on', his own new view (1898) was that "The study of vegetation has now become a study of plant associations – the life-forms which constitute them, the conditions which determine them and the relations between them", and he goes on: "such a community, made up of chief species, subordinate species, and dependent species, constitutes a Plant Association". Written exactly 100 years ago, that was a remarkably far-sighted statement. Furthermore, he was an enthusiastic advocate of the practical value of vegetation maps, emphasising their importance as a record of the vegetation of Scotland at the time, and as vehicles for further research of an ecological nature. His list of items needed for the proper description of the vegetation of an area is interesting:

1. The chief associations into which it may be divided;
2. The particular conditions of heat, light, moisture and food distinguishing the associations;
3. The particular adaptations or life-forms of the species of each association;
4. The relations between the species:
   (1) dominant social forms;
   (2) secondary social forms;
   (3) dependent species;
5. The influence of man and animals;
6. The general conditions of climate and of vegetation of the region compared with other regions.

Robert Smith's untimely death regrettably destroyed plans for the survey and mapping of the vegetation of the whole of Scotland. However, his influence had spread and a small group of like-minded botanists had gathered around W. G. Smith, and continued, for a time, the work of survey and mapping in N. England and Ireland. This group became, in 1904, 'The Central Committee for the Survey and Study of British Vegetation' – the forerunner of the British Ecological Society (founded in 1913).

However, although the vision of the Smith brothers was still actively stimulating the development of British vegetation science for the first decade of the twentieth Century, the survey and mapping project rather quickly came to an end, partly because of the increasing cost of producing maps, but also because the widening horizons of ecological science were drawing interest away from primary survey and plant community classification. In this change of direction, a major part was played by A.G. Tansley, a scientist of great strength of character, a founder member and leading light of the 'Central Committee'. Under his influence and that of his associates on the Committee, the whole centre of gravity of developing vegetation science moved south to Cambridge and London, and its focus turned more to the investigations of interactions between plants and their environment, ecological processes and vegetation dynamics.

Clearly, Tansley was very much a 'vegetation scientist' because his main aim and achievement was to study and describe British vegetation (Tansley 1911, 1939a), and he was much impressed with the enthusiasm of the new Central Committee, mentioning that even 'those who were initially sceptical about the existence of plant communities were convinced by their experiences of the study of vegetation in the field'. However his outlook was not that of a phytosociologist and he moved away from the approach of the Smith brothers, though later he described them as "the original pioneers of modern ecology in Britain" (1939b). It was the interaction between plants and their environment - all aspects of it – and the dynamics of processes taking place in vegetation that really motivated him and those around him.

Vegetation science in America

In this he aligned himself with some of the ideas of one of the pioneers of vegetation science in America, F.E. Clements, whom he described as "the greatest individual creator of the modern science of vegetation". So we should now turn our attention briefly to the infancy of vegetation science in America and consider where it was leading. Clements, like the others already mentioned, was starting to publish his ideas almost exactly 100 years ago. While he certainly had a profound influence on vegetation science in America and Britain, it is important to recognise the influence of another American pioneer, H.C. Cowles, who was perhaps really the first to undertake a detailed study of a particular example of vegetation (plant succession in the inland sand dunes of Lake Michigan) published in 1899, in which he applied the concept of vegetation dynamics to the understanding of an actual field situation. Later in his life, Tansley acclaimed

Cowles as "the great pioneer of the subject", thus giving him the accolade he had previously accorded to Clements. Certainly, Cowles had a great influence on Tansley himself and others of the early Committee for the study of British vegetation, who were greatly taken with his dynamic view of vegetation. However, although Cowles' work was, and is, regarded as a classic, it was Clements whose ideas became most influential in the early years of the 20th Century. This was chiefly because of the way he deliberately set out to create a general theory of vegetation based on his studies of plant succession (1916), vegetation dynamics and development, elaborated into his famous theory of the plant formation. "As an organism the formation arises, grows, matures and dies. The plant formation is the adult organism of which all the initial and medial stages are but stages of development."

This is not the place to go into all the repercussions of this theory, or of the controversy it created in America when it was challenged by Gleason's later (1926) individualistic concept of the plant community: "The vegetation of an area is merely the resultant of the fluctuating and fortuitous immigration of plants and the equally fluctuating and variable environment".

That argument is now largely of historical interest, and probably did not have nearly as much lasting influence on the progress of vegetation science as did Clements' early work on the development and structure of vegetation, and on research methods for the practical analysis of vegetation using quadrats and transects. It was this approach to vegetation science, and Clements' ability to draw together the results of much work in America and elsewhere, that appealed to Tansley, rather than the theoretical superstructure of which he became increasingly critical. But for a time the two were closely in touch, and greatly admired each other's ideas, and as both were strong leaders this had the effect of diverting attention away from primary survey, mapping and universal systems of classification towards intensive studies of particular examples of vegetation – still vegetation science, but with a different orientation, concentrating more on ecological processes and on physiological and experimental ecology.

Relations with phytosociology

This happened at precisely the time when the phytosociological approach to vegetation classification and mapping was gaining ground and becoming widely applied in Europe and Scandinavia, for example by J. Braun-Blanquet who developed the tradition established by Flahault in Montpellier, and by G.E. du Rietz in Uppsala, and R. Tüxen in Germany. It has to be admitted that the preoccupations of British and American vegetation scientists led them for a considerable time to ignore, or even to express scepticism regarding the methods and theoretical basis of Continental phytosociology, despite the fact that Tansley urged (in 1922) that British workers would benefit from the perception of plant associations as social units. However, he wrote later (1939a) "I am unable to form an opinion as to the validity or usefulness of the terminology of plant communities invented by Dr. J. Braun-Blanquet, and have therefore had to forego any attempt to consider its possible application to British vegetation".

Nevertheless, in America and a little later in Britain, a sociological approach to vegetation science was reviving from around the 1920s with the introduction of quantitative and statistical methods for the analysis of community composition. In America in the 1950s this took the form of the development of graphical methods of ordination of vegetation samples to display variation in floristic composition; while in Britain statistical and computer based methods of community classification were pioneered at about the same time.

Although on the whole vegetation scientists in Britain and America, many of them engaged on quantitative and statistical vegetation analysis, still held aloof from European and Scandinavian phytosociology, they did rekindle interest in the floristic composition of plant communities and the factors controlling it. Furthermore, as early as 1949 the methods of Braun-Blanquet had been applied to Irish vegetation by Braun-Blanquet and Tüxen during an International Phytosociological Excursion; to be followed in the decade from 1952 by J.J. Moore who had become a disciple of R. Tüxen and applied his approach extensively in Ireland. However, it was, in fact, one of Tansley's former pupils, H. Godwin, who felt the time was ripe in the early 1950s to re-examine the possibility of applying the methods of European phytosociology systematically to British vegetation.

Godwin arranged for one of his research students, M.E.D. Poore, to spend some months in Montpellier, thus creating a close parallel with Geddes' earlier promotion of Robert Smith. This time the purpose of the visit was for Poore to familiarize himself with the theory and methodology of Braun-Blanquet.

Like Robert Smith, Poore returned to his native Scotland and began to apply a modified version of this methodology to the recognition and classification of plant communities of the uplands at the level of the Association (Poore 1955). This marked a renaissance of interest in the survey and classification of British plant communities which has continued ever since, and has produced such classic works as 'The Plant Communities of the Highlands' (McVean & Ratcliffe 1962), 'Plant Communities of Scotland, a preliminary Phytocoenonia' (Birse 1980) and the series of five volumes of 'British Plant Communities', which were the culmination of a National Vegetation Classification project, edited by J. Rodwell (1992a, b; 1993a, b).

The last-mentioned work is a good example of the recent rapprochement between the aims and approach of European phytosociology and the use of quantitative, statistical techniques for handling large amounts of relevé data and generating computer-based classifications – a rapprochment which, it should be added, has been greatly promoted by the work and activity of Eddy van der Maarel. But here we get beyond the infancy of vegetation science to its more mature development.

Conclusion

In summing up, mention may be made of the comment that vegetation science has a 'polytopic origin', springing up almost independently in numerous different centres under the leadership of major figures, themselves much influenced in their several approaches by the nature of the vegetation around them. Examples are the 'schools' of vegetation science in Switzerland, France, Denmark, Scandinavia, Britain, America, to name a few.

There is certainly a good deal of truth in this, but it is an incomplete analysis. I suggest that each of the major figures was profoundly influenced by the thinking of those who preceded them, in whatever country, and the pioneers were enthusiasts, often crusaders, anxious to pass their enthusiasms to students and others who worked with them – who then developed the individual approaches into distinctive schools which only now are coming together.

Looking back over the present Century in Britain, it is evident that Robert Smith, himself much influenced by Flahault, lit a flame of vegetation science, which flared briefly and then seemed to flicker and almost die. The Anglo-American approach spear-headed by Tansley and Clements took over and then gave place to quantitative, statistical methods, but now the flame lit by the Smith brothers is very much alive again. It brought a breath of fresh air into British botany and launched the subject of vegetation science into a proper scientific study of the outcome of the interplay between environment and the available flora. The influence of the Smith brothers on subsequent developments has, I believe, been underestimated but is now being given more of the recognition it deserves. As vegetation science emerges from its infancy into adulthood, the foresight of these two brothers a Century ago can be properly evaluated.

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Change soil properties by alpine plant species: a monoculture experiment

Onipchenko, V.G.[1]*, Makarov, M.I.[2] & van der Maarel, E.[3]

[1]*Department of Geobotany, Biology Faculty, Moscow State University, 119899 Moscow, Russia;* [2]*Department of Soil Science, Moscow State University, 119899 Moscow, Russia;* [3]*Department of Ecological Botany, Uppsala University, Villavägen 14, S-752 36 UPPSALA, Sweden;*
**Fax +7959394309;*
E-mail vonipchenko@vonipchenko.home.bio.msu.ru

Abstract. The ability of different alpine species to change soil nutrient concentrations was estimated through monocultures of 17 species grown on an homogenized acid alpine soil mixture. The experiment was carried out at 2750 m a.s.l. in the Teberda Reserve, Northwest Caucasus. Soil nutrient contents (NH_4, NO_3, P, Ca, Mg, K) and pH were analysed after 6 yr. The same soil mixture but without plants was used as a control. Alpine species changed soil properties in different ways. For each soil property there was a different species which had lowered the concentration more than any other species, e.g. *Matricaria caucasica* for NO_3 and *Festuca ovina* for P. Many species increased the cation content (Ca, Mg, K) in the soil in comparison with the control. All species, except *Sibbaldia procumbens*, increased soil pH.

Keywords: Alpine grassland; Alpine heath; Alpine soil; Caucasus; Snowbed community; Soil nutrient.

Nomenclature: Onipchenko 1994, except *Campanula tridentata* Schreb.

Introduction

According to resource competition theory, the ability of a plant to decrease soil nutrient concentrations is one of the most important properties for competitive success (Tilman 1982). There are few studies dealing with soil property changes in monocultures (e.g. Wedin & Tilman 1993). Virtually nothing is known about plants and communities from high mountains.

Alpine communities in the Caucasus are species-rich (Onipchenko & Semenova 1995). Several community types can be recognized on the basis of their floristic composition. They vary in ecological conditions, notably winter snow depth and range from snow-free alpine lichen heaths to snowbed communities (Onipchenko 1994). They differ significantly in soil properties (Grishina et al. 1993). Different species from these communities are able to change soil nutrient concentrations and acidity in the soil they root in. We wished to investigate this through growing them for several years in monoculture on initially homogeneous soil under semi-natural conditions. In total 17 species from different systematic groups were tested in this way.

Material and Methods

Study area

The study area is situated in the Teberda State Reserve, a part of the Karachaevo-Cherkessian Republic, Northwestern Caucasus, Russia (43° 27' N, 41° 41' E). The study sites are located on Mount Malaya Khatipara, in the alpine belt at 2700-2800 m a.s.l. The study species are typical of four widespread alpine communities:

1. Alpine lichen heath (ALH) with dominance of fruticose lichens;
2. *Festuca varia* grassland (FVG);
3. *Geranium gymnocaulon-Hedysarum caucasicum* meadow (GHM);
4. Snowbed vegetation (SBC). (See further Onipchenko 1994.)

Study species

17 typical and/or dominant species (six monocots and 11 dicots) were chosen, belonging to eight families (Table 1).

Field experiment

A soil mixture from the upper layer (0 - 25 cm) of native alpine soils (Umbric Leptosol) and pure sand was prepared and homogenized by repeated sieving. Large roots and stones (> 7 mm) were deleted. The mixture was put in 1-l plastic boxes. Boxes were situated in alpine meadows at ground level. Drainage holes in the bottom of the boxes allowed down water flow and prevented anaerobic conditions. Each plant species was grown from seeds in 10 replicates (boxes). 10 boxes with the same soil mixture but without plants were used as a control. Experimental and control boxes were situated within five 36-box blocks in random manner. Plants were grown for six years (1991-1996); we applied some irrigation during dry periods to prevent strong desiccation.

Table 1. List of study species, their taxonomic position and their community preference.

Species	Family	Community
Anemone speciosa	*Ranunculaceae*	ALH
Antennaria dioica	*Asteraceae*	ALH
Campanula tridentata	*Campanulaceae*	ALH, SBC
Carex sempervirens	*Cyperaceae*	ALH
Carex umbrosa	*Cyperaceae*	ALH
Festuca ovina	*Poaceae*	ALH, FVG
Festuca varia	*Poaceae*	FVG
Geranium gymnocaulon	*Geraniaceae*	GHM
Hedysarum caucasicum	*Fabaceae*	GHM
Leontodon hispidus	*Asteraceae*	FVG, GHM
Matricaria caucasica	*Asteraceae*	GHM
Nardus stricta	*Poaceae*	FVG, GHM, SBC
Phleum alpinum	*Poaceae*	GHM
Scorzonera cana	*Asteraceae*	FVG
Sibbaldia procumbens	*Rosaceae*	SBC, GHM
Taraxacum stevenii	*Asteraceae*	SBC
Trifolium polyphyllum	*Fabaceae*	ALH

Soil analysis

Soil samples were collected from each box and air-dried. The fine soil fraction (< 1 mm) was separated for chemical analysis by dry sieving. Samples with damaged plants (roots or shoots damaged by herbivores) were excluded from the analysis; the final number of replicates was less than 10 for several species - and down to two for *Trifolium polyphyllum*. Chemical soil analysis included water soluble NO_3, NH_4, Ca, Mg, K, exchangeable Ca, Mg, K (1 M $CH3COONH_4$), NH_4 (2% KCl), mobile (0.5 M CH_3COOH) and low mobile (0.1 M HCl) P, and pH (H_2O and 2% KCl).

Data analysis

One way analysis of variance (ANOVA) was used to estimate the significance of the difference between different variants for each of the soil properties.

Results

All species in monoculture changed the concentration of all soil properties except low-mobile P (Tables 2 and 3). Significant differences were found for most soil properties, at least for species differing much. For each lowest values another species was responsible (Table 3). Many species increased cation content (Ca, Mg, K). All species, except *Sibbaldia procumbens*, increased the pH of the soil.

Four plant families were represented with two or more species. Significant differences among families were found for all nutrients, except low mobile P and water-soluble K (Table 2, 4). *Fabaceae* decreased cation contents (Ca, Mg, K), but increased nitrogen (NH_4, NO_3). *Cyperaceae* (*Carex* spp.) decreased ammonium content, both *Asteraceae* and *Cyperaceae* decreased nitrate concentrations greatly; phosphorus content was decreased by grasses. So we can observe some kind of specialization between taxonomic groups.

When we combined the species according to their community preference (Tables 1, 2; community level), only small differences were found. Only the species of the *Festuca varia* grassland (mainly grasses) increased K and Mg concentrations and pH.

Table 2. Results of One-Way ANOVA for testing the significance of influence on soil properties for different species, families and community-wise species groups: *** = $p < 0.001$; ** = $p<0.01$; * = $p<0.05$; n.s. = not significant.

	Species	Families	Community groups
NH_4 (exch.)	***	***	n.s.
NH_4 (H_2O)	***	***	n.s.
$NO_2 + NO_3$	***	**	n.s.
P (mobile)	**	**	n.s.
P (low mobile)	n.s.	n.s.	n.s.
K (exch.)	***	*	*
K (H_2O)	***	n.s.	***
Ca (exch.)	***	***	n.s.
Ca (H_2O)	***	**	n.s.
Mg (exch.)	***	***	*
Mg (H_2O)	***	***	**
pH (H_2O)	***	***	n.s.
pH (KCl)	***	***	*

Discussion

Our results support Tilman's (1982) ideas of geochemical specialization among plants within communities. Wedin & Tilman (1993) showed that grasses of the climax prairie decreased the soil nitrate concentration much stronger than early successional grasses. In our experiments *Matricaria caucasica* lowered nitrate concentration better than other species. It is of interest to note that *M. caucasica* occupied mainly open areas (gaps) after disturbance in alpine zone and is a weak competitor in closed communities (Onipchenko & Rabotnova 1994).

It is well-known, also for alpine communities, that *Fabaceae* increase the soil N concentration through nitrogen fixation (Carr et al. 1980; Bowman et al. 1996). However, among the *Fabaceae* only *Hedysarum caucasicum* had *Rhizobium* nodules while these were practically absent on *Trifolium polyphyllum* roots. Most of the species increased cation (Ca, Mg, K) contents and pH values. This seems to be related to the prevention of cation leaching and to nitrification – which leads to soil acidification after any disturbance. Both the soil in monocultures and in the control contained less Ca and Mg than the initial soil

Table 3. Species which created the lowest and highest soil nutrient concentrations in the experiment, respectively. Dimensions for average values (AV): NH_4, P, K, Ca, Mg - mg/kg; NO_2+NO_3-µg/kg.

Soil properties	Species creating the lowest concentration	AV	Species creating the highest concentration	AV	Control
NH_4 (exch.)	*Taraxacum stevenii* *Sibbaldia procumbens*	10.1	*Hedysarum caucasicum*	21.7	13.7
NH_4(H_2O)	*Carex sempervirens*	7.1	*Hedysarum caucasicum*	20.8	9.8
N(NO_2+NO_3)	*Matricaria caucasica*	210	*Trifolium polyphyllum*	767	1466
P(mobile)	*Festuca ovina*	0.65	*Hedysarum caucasicum*	1.02	0.74
K(exch.)	*Antennaria dioica*	67	*Festuca varia*	90	82
K(H_2O)	*Antennaria dioica*	29	*Scorzonera cana*	43	37
Ca(exch.)	*Trifolium polyphyllum*	318	*Festuca ovina*	442	370
Ca(H_2O)	*Hedysarum caucasicum*	81	*Festuca ovina*	93	81
Mg(exch.)	*Trifolium polyphyllum*	27	*Festuca varia*	40	27
Mg(H_2O)	*Trifolium polyphyllum*	10.9	*Festuca varia*	13.6	11.8
pH(H_2O)	*Sibbaldia procumbens*	4.69	*Phleum alpinum*	4.99	4.75
pH(KCl)	*Antennaria dioica*	4.27	*Festuca ovina*	4.43	4.27

Table 4. Soil nutrient concentrations under plants from different families (for dimensions see Table 3); AST = *Asteraceae*; CYP = *Cyperaceae*; FAB = *Fabaceae*; POA = *Poaceae*.

	FAB	AST	POA	CYP	Control
Ca(H_2O)	86	87	91	90	81
Ca(exch.)	330	386	429	367	370
K(exch.)	74	79	85	76	82
Mg(H_2O)	114	121	129	118	118
Mg(exch.)	277	298	358	285	268
NH_4(exch.)	168	112	116	106	137
NH_4(H_2O)	14.8	8.6	8.2	7.4	9.8
N(NO_2+NO_3)	560	280	440	290	1466
P(mobile)	0.89	0.77	0.70	0.74	0.74
pH(KCl)	4.33	4.30	4.38	4.34	4.27
pH(H_2O)	4.78	4.77	4.88	4.82	4.75

mixture. The more acid control soil contained 2-7 times more nitrate than soil under monocultures. Acidification and intensive nitrification are typical of disturbed soils without plants (Bormann & Likens 1979).

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Retrogressive succession in old landscapes

Walker, J.[1]*, Thompson, C.H.[2], Olley, J.[1] & Reddell, P.[3]

[1]*CSIRO Land and Water, PO Box 1666, Canberra, ACT 2601, Australia;* [2]*CSIRO Tropical Agriculture, St. Lucia Qld 4067, Australia;* [3]*CSIRO Land and Water, Centre for Rainforest Ecology, Atherton, Qld 4883, Australia;*
**Fax +6162465856; E-mail joe.walker@cbr.clw.csiro.au*

Abstract. A podzol chronosequence on freely-drained coastal dunes is used to illustrate a natural soil and landscape ageing process and the vegetation response over a time period of some 120 000 yr. Six dune ages were established using pedological and geomorphic evidence. Ages were estimated using optically stimulated luminescence techniques. On young dunes (dunes 1-4, with a maximum age of 40000 yr for dune system 4) progressive plant succession to a 'climax' was observed. On the older dunes a run-down of vegetation biomass and system function was observed. The hypothesis developed is that old landscapes will show an accelerated run-down when disturbed. Examples from four old landscapes in Australia support the view that old landscapes tend not to fully recover following disturbance. Since old landscapes are common in many parts of the world these observations have implications for system resilience and rehabilitation.

Keywords: Coastal dune; Cooloola; Disturbance; Parabolic dune; Podzol; Progressive succession; Retrogressive succession.

Introduction

A podzol chronosequence on coastal parabolic dunes at Cooloola (subtropical, ca. 150 km north of Brisbane) has been shown to be closely associated with vegetation structure and species composition (Walker et al. 1980; Thompson 1981; Harrold et al. 1987). The chronosequence provides nine windows in time (three in dune system 1 and two in dune system 6), from the present back to before the last interglacial period, some 120000 years BP. The first three windows represent plant colonization from bare sand to sufficient vegetation to form a protective cover. The vegetation succession through the younger dunes is characterised by progressive increases in species richness, community structure and biomass. The older dunes exhibit retrogressive succession where structure and biomass are greatly reduced, and species change from those characteristic of forests, to those of heath. From field observations we have inferred that changes to the plant assemblages on the freely drained dunes are associated with changes in access to soil nutrients. In the younger systems all the plant growth-forms can access the nutrients and progressive succession occurs. As the depth of nutrients in the Bhs horizon (Soil horizon which has humic deposits) increases (beyond 8-10 m) access to nutrients decreases and regressive succession follows. Detailed dating using optically stimulated luminescence (OSL) dating techniques (Aitken 1998; Olley et al. in press) suggests that retrogression begins after ca. 40000 yr in these dune systems.

In this paper we develop the hypothesis that retrogressive successions are a common feature of old landscapes and provide some examples to support this view. The implications for management or rehabilitation of old landscapes could be important since they may not return to their pre-disturbance state.

Disturbance and recovery in progressive and retrogressive systems – a hypothesis

Looking beyond Cooloola, and dune systems, what evidence exists to support the view that the pedological age of landscapes can be a major determinant of the range of landscape or ecosystem responses to disturbance and land-use. The link between vegetation structure and function to pedogenesis and landscape age, was recognized and described by early soil scientists, especially Jenny (1941). It is generally recognized that system instability may arise for many different reasons, including the type and intensity of disturbance impacts. Likewise different rates of recovery from disturbance can be expected from different soil and vegetation systems. Trudgell (1977) gives many examples of these kinds of responses. Here we focus on the difference between pedologically old systems vs. young systems, an area apparently little considered in ecological theory and in landscape management.

Understanding vegetation responses in ancient landscapes is particularly relevant to Australia. Like many areas of the tropics Australia escaped the direct effects of the Pleistocene glaciations which destroyed the Tertiary landscapes and weathering mantles over much of the northern hemisphere. In these ancient landscapes where the rates of weathering have continued to exceed the rates of erosion, the residual products of weathering have formed thick soil mantles that generally lack weatherable minerals and have very low concentrations of available plant nutrients. The extensive areas of lateritic soils in Australia, and in the tropics generally are examples. As secondary minerals form in the weathering zone, there is an initial increase in the availability of plant nutrients, but this rapidly decreases as the supply of weatherable minerals is depleted (Stark 1978). The vegetation response to such weathering is to initially show no direct selection pressure for nutrient conservation mechanisms in species mixes that characterize this stage. As weathering increases, availability of nutrients to plants decreases, and a trend towards those species with more efficient mechanisms for nutrient capture and retention, and lower vegetation biomass follows. The new system state may be stable, often due to tight nutrient cycling within the phytomass, and morphological and physiological adaptations of the species. However, such systems on old, nutrient-limited landscapes may be particularly vulnerable to the effects of disturbance, perhaps even to the extent of system collapse. For example, the failure of many rainfor-

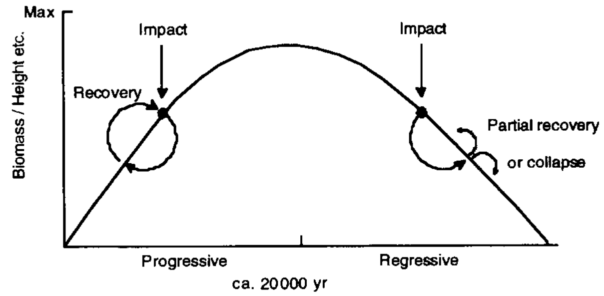

Fig. 1. In younger landscapes, after an impact such as clearing, the vegetation will return to the original state, whereas in an old landscape vegetation will only partially recover or collapse.

ests on lateritic soils to regenerate following clearing and burning. Similarly, questions as to the probable adverse effects of log removal on the sustainability of both native and plantation forests on old landscapes in the humid tropics are gaining prominence.

The hypothesis (see Fig. 1) is: a pedologically young system if disturbed, will tend to return to something similar to its previous state fairly quickly (multiple states could exist). An old system is unlikely to return to its pre-disturbance state, or a functionally similar variant, but will most likely regress. Responses to disturbance also change with progressive ageing and this is illustrated in Fig. 1.

The mechanisms controlling retrogression will vary from place to place. Some could have nutrient leakage problems similar to those at Cooloola, but on a different time scale. Others, due for example, to changes in soil physical properties which affect water entry and storage (e.g. soil compaction, surface crusting etc.) will show different degrees of retrogressive responses to disturbance.

The following are some Australian examples of what we consider to be retrogressive systems.

A regression in old tropical rainforest systems in North Queensland

In this example, some soil properties associated with biological productivity and rates of nutrient cycling are compared across a series of stages of rainforest succession (in this case, succession that follow the abandonment of land that was cleared for agriculture). This study in lower montane tropical rain-forest systems on the Atherton Tableland in north Queensland, is more fully described by Reddell et al. (in press). The data are for two soil types that are strongly contrasting in their inherent fertility, and that originally supported two very different rainforest structural types. One rainforest type (complex notophyll vine forest) dominates on soils developed from recent Quaternary basalt flows (nutrient-rich, comparatively young soils), the other is a simple notophyll vine forest typical of much older Palaeozoic meta-sediments (lower nutrient status, especially P) in the area. Trends in microbial biomass, organic matter and soil bulk density (note that lower values represent better bulk density, hence the data are inverted in 2c) are shown for the two forest types in Figs. 2 a-c. These measures of system state suggest that the younger system on basaltic soils is recovering towards the original state, but on the older soils derived from metasediments the rainforest succession does not indicate a full recovery and regressive succession is evident. The lack of recovery in this case is reflected in a limited ability to conserve soil carbon.

Lack of recovery of hydraulic properties in a grazed Eucalyptus populnea woodland

The soils in this extensive semi-arid woodland system in eastern Australia are solonized red-brown earths, solonized solonetz and solodic soils (Paleustalfs, Natrustalfs and Torrerts), and are derived from undifferentiated quartz sands, silts and gravels. For ca. 100 yr this ancient landscape has been used for widespread grazing of cattle and sheep, and more recently for wheat production. A decline in surface soil properties, including crusting is evident in many areas. As part of an experiment in plant population dynamics, started in 1966, some grazed areas were permanently fenced off from domestic livestock. Braunack & Walker (1985) investigated the recovery of the surface soil from compaction after fencing off for a period of 16 years. They used thin sections of the top 1 cm of the soil and quantified pore and particle sizes. The data indicated that the duplex red-brown earth soil showed little evidence of recovery from the compacted state. The changes to the

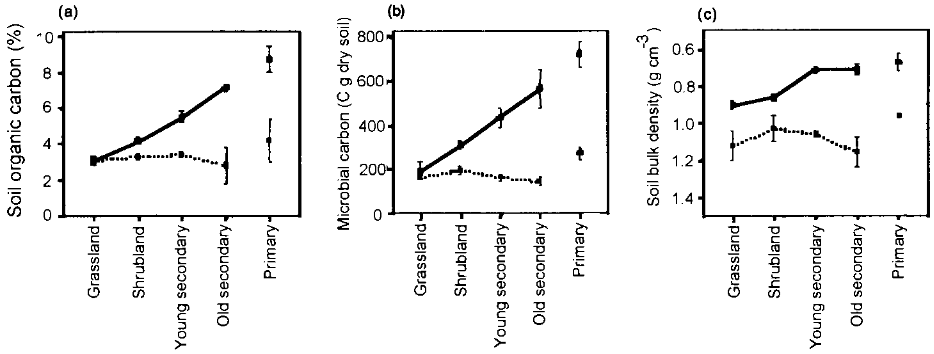

Fig. 2. Measures of soil organic carbon (**a**), microbial biomass (**b**) and soil bulk density (**c**) during secondary succession. Solid lines are for a young landscape, dotted for an old landscape. In young landscapes a recovery trend is towards the primary state, but not for old landscapes.

hydraulic properties (e.g. infiltration rates) favour woody species rather than the grasses present in the original woodlands, and structural and functional changes follow.

Remobilization of salt stored below the rooting zone in semi-arid ecosystems

In arid and semi-arid areas of Australia, evaporation exceeds rainfall inputs by a large margin. These areas are also characterized by low slopes and hence low hydraulic gradients. Salts brought onto landscapes, either by accession from rainfall or by wind, are leached vertically below the rooting zones of the native perennial vegetation. The lack of lateral movement results in a store of salt in the subsoils. The salt hazard becomes a problem when land-use practices mobilize the salt laterally or vertically. Tree clearing since European settlement of Australia has induced a major change in recharge and hydraulic gradients in many landscapes. The resultant rises in the water tables brings salt upwards to within the rooting zone or in many cases to the soil surface. Salinization has a pronounced impact on the survival of the vegetation. If left alone retrogression goes towards a collapse of vegetation and bare salinized soil. Even if areas contributing to recharge and salt mobilisation are planted with trees now, it is estimated that it will take centuries to re-establish a new equilibrium in the regional groundwater systems (Bari & Boyd 1994).

Dieback in eucalypts as a regressive response to change in system state

Dieback of isolated and small clumps of trees (seen as a reduction in leafiness of eucalypts and usually followed by death), is widespread in the New England tablelands of New South Wales. Dieback is often attributed to the massive and repeated defoliation of trees by leaf-eating insects, particularly leaf beetles (chrysomelids) and christmas beetles (scarabs). Walker et al. (1983) interpreted the phenomenon as a predictable response of an old landscape to disturbance. The argument presented was that most soils on the tablelands are highly weathered, and the forests and woodlands under these conditions are highly dependent on recycling of nutrients. Most of the nutrients are associated with the organic matter in the A_1 soil horizon. Tree clearing, pasture improvements and subsequent domestic livestock grazing have changed the soil water balance, nutrient cycling and the soil biota. Accelerated decomposition of the organic material and subsequent loss of nutrients have placed the existing eucalypts under additional stress. The fact that dieback is generally absent from areas with younger soils away from the tablelands, lends support to the retrogression hypothesis.

Conclusion

The Cooloola chronosequence implies that retrogressive succession is a natural ageing process. The examples quoted from other systems suggest that retrogressive mechanisms other than nutrition can operate. These include long term damage to soil structure and hence hydraulic properties, declining soil carbon fluxes and storage, rising water tables leading to the mobilisation of stored salt, and stresses caused by the interruption of tight nutrient cycling systems. Collapses in system function can occur to any system if it is impacted in a massive way. We are suggesting that lesser impacts are required in old systems to produce an irreversible decline in system function. Retrogressive trends in ecosystems that occur on old landscapes may be common, but have received little attention in the ecological literature. The practical implications are that old landscapes have limited resilience to agricultural exploitation. Limited production potential of old landscapes has of course been recognised for many years. Less obvious is the possibility that rehabilitation of old landscapes may require establishing plant species that are not typical of the pre-disturbed state. They may even function quite differently. Changing vegetation structure in this way changes habitat and there are implications for conserving endangered fauna or attracting back the original fauna – it may not be possible.

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Comparison of ordination methods for investigating vegetation/ environment relationships

Wentworth, Thomas R. & Ulrey, Christopher J.

Department of Botany, North Carolina State University, Box 7612, Raleigh, NC 27695-7612, USA;
Fax +19195153436; E-mail tom_wentworth@ncsu.edu

Abstract. The Thompson River drains a forested watershed in the southeastern escarpment region of the Blue Ridge Mountains in the states of North and South Carolina, USA. Data from 0.1-ha plots provided the basis for analysis of vegetation pattern within this watershed. We employed three types of vegetation data: cover classes for all vascular plant taxa, midpoints of the cover classes and midpoints of the cover classes standardized by species maxima. These data were analysed by two ordination methods, Detrended Correspondence Analysis (DCA) and Non-metric Multidimensional Scaling (NMDS). The similarities between ordinations generated by these methods, as evaluated by Procrustes analysis, varied with the type of data used. We also compared ordinations to determine how effectively each method identified outliers. Because the underlying structure of these data was unknown, such comparisons were of limited utility for evaluation of the effectiveness of the methods used. To address this problem, we created simulated data with attributes matching those of the real data, then we tested the ability of the ordination methods to capture patterns inherent within the simulated data. Ordinations using NMDS proved significantly better than those using DCA in recovering the underlying structure of the simulated data; both methods performed best with the original cover class data and worst with the midpoint transformation.

Keywords: Data transformation; Detrended Correspondence Analysis; Non-metric Multidimensional Scaling; Ordination; Procrustes analysis; Simulation; Thompson River watershed.

Introduction

Quantitative vegetation analysis aims to reveal and summarize trends and relationships in complex, multivariate data describing community composition and environment. Such analysis should lead to better understanding of the natural systems that the data represent and may lead to the generation of hypotheses about causal relationships. Among quantitative approaches, indirect ordination methods are widely used to detect compositional trends in vegetation data. The aim of these methods is to present in relatively few dimensions the dominant or latent patterns present in highly dimensional data representing the abundances of species across an array of sampling units. Indirect ordination methods create spatial arrangements (ordinations) of sampling units in one or more dimensions, in which the distances between sampling units in the ordinations are related to their compositional dissimilarity.

Detrended Correspondence Analysis (DCA; Hill & Gauch 1980) and Non-metric Multidimensional Scaling (NMDS) are presently the two most popular methods for indirect ordination. The widespread use of DCA is partly due to its ease of use, computational efficiency and extensive distribution of the program DECORANA (Hill 1979). NMDS, although developed in the early 1960s (Shepard 1962; Kruskal 1964a, b), has been less commonly applied in ecological studies (Minchin 1987), possibly because it has been less widely available in software packages, requires considerable training or experience to use correctly, and is computationally intensive. However, NMDS has become increasingly well-represented in the plant ecology literature (e.g., Oksanen 1983; Kantvilas & Minchin 1989; Tueller et al. 1991).

Our goal was to compare the efficacy of DCA and NMDS as evidenced by their abilities to capture patterns inherent in vegetation data. We wished to first compare the results of applying the two ordination methods to a familiar real data set. However, ordinations of real data are difficult to evaluate objectively because the underlying structure of the data is unknown (Minchin 1987). Indeed, few published papers have compared ordination methods using real data for this reason. Thus we also wished to compare the results of these methods using simulated data. Objective comparison of ordination methods applied to simulated data (e.g., Swan 1970; Austin 1976; Kenkel & Orlóci 1986; Minchin 1987) is relatively straightforward because the underlying structure of the simulated data is known. However, vegetation scientists may be uneasy about adopting an ordination method simply because of its outstanding performance with simulated data. Simulated data may fail to capture structures inherent in real data. For this reason, we attempted to create simulated data with properties matching those of real data for use in our ordination comparisons. Our final objective was to compare the results of using various data transformations on the outcome of ordinations performed on both real and simulated data.

Study area

The original data used in this study come from the Thompson River watershed, a 35000 ha forested area in the southern Blue Ridge mountains, in the states of North and South Carolina, USA. The typical forest cover in this region consists of broad-leaved winter-deciduous species, with oaks (genus *Quercus*) the most dominant and widespread. The landscape is characterized by high annual precipitation (> 200 cm/yr), and moderate elevations (averaging ca. 800 m). The entire watershed has experienced moderate to high levels of anthropogenic disturbance, mostly the result of logging.

Field methods

Data were collected from 101 0.1-ha plots located by a stratified-random procedure throughout the Thompson River watershed. A 0.25 km × 0.25 km grid was established on a map of the study area. Each of the ca. 700 points in this grid was placed into one of 48 strata defined by combinations of three elevation classes, four aspect classes and four topographic position classes. Two points were drawn at random from each of the strata and plots were established at these points unless they were found to be disturbed by recent (within 40 yr) human activity; when a point was rejected, it was replaced by another selected at random from the same stratum. A few additional plots were also established to represent topographic situations not readily fitting into the stratification scheme. Abundance data for 247 vascular plant species were converted to a 10-class estimated cover scale (similar to that used by Peet et al. 1998), as follows:

1=0-0.5%; 2=0.5-1%; 3=1-2%; 4=2-5%; 5=5-10%; 6=10-25%; 7 =25-50%; 8=50-75%; 9=75-95%; 10=95-100%.

Because the cover classes approximate a geometric series, these data were, in effect, a transformation of actual cover measurements in which the dominant species are de-emphasized. The cover class data were also transformed to create two additional data sets. One transformation involved substituting the percentage midpoint of each cover class for the cover class itself (hereafter referred to as midpoint data), re-emphasizing the importance of dominant species. The other transformation involved standardization of the percentage midpoint data to species maxima (i.e., all abundances for a given species across sampling units were divided by the maximum abundance for the species, hereafter referred to as standardized data). This transformation permitted all species to contribute in a similar fashion to the ordination outcome.

Simulated data

Simulation was accomplished using the program COMPAS v. 3.40 (Minchin 1997, public domain software). The approach taken by COMPAS in simulating vegetation data amounts to creating a Gleasonian universe (i.e., one in which species respond individualistically to environment) of specified dimensionality and then overlaying a sampling design within this universe. Species response curves are allowed to extend beyond the sampling region. This is an important feature to consider when simulating vegetation data, since in real data species are often represented only by the tails of their response curves. We attempted to create simulated data with properties similar to those of the real data from the Thompson River watershed. Although many properties were available, we chose to focus on distributions of species frequency and abundance, β-diversity (compositional turnover) and species richness. Arriving at a simulated data set with properties matching those of the original data required a trial-and-error approach. COMPAS allows the user to specify response curves for a species group, which is a set of species with similar responses. We opted to define species groups based on maximum abundance and range as observed in the real data. A direct gradient is required to describe the range of a species. We selected three dominant and orthogonal environmental variables that had been previously identified as important in this watershed. All response functions were unimodal and symmetrical and contained neither quantitative nor qualitative noise. Other options in COMPAS were manipulated to create data sets with characteristics matching those of the real data. As an example, the modes for all species in a group could be assigned to a random, normal, exponential, gamma, or lognormal distribution as we attempted to match properties between simulated and real data. Our sampling pattern was a uniform 3-dimensional grid of 100 sampling units, nearly identical in size to the original data set (101 plots). Because the simulation procedure used has stochastic elements, we created 10 simulated data sets for analysis. Only the cover class data were simulated; the two transformations of the cover class data were derived directly from the cover class simulations. Readers interested in further details regarding COMPAS options used to create simulated data are encouraged to contact the authors.

We used several analytical tools to evaluate differences among ordination results. Procrustes analysis was used to determine the true difference between any two ordination results by eliminating trivial differences related to rigid rotation of the axis system, inversion, dilation or contraction of the ordination space, or shifting of the origin. The residual mean square (RMS) statistic quantified the residual, non-trivial differences between two ordinations as the mean of squared distances between corresponding sampling units in the two ordinations after Procrustes fitting. RMS-values below 0.1 are considered to represent situations where the ordinations could be considered essentially identical. We were also interested in the way in which the ordination methods handled outlier plots in the real data. Outliers were identified by determining the average distance of each sampling unit to all others. Sampling units lying more than two standard deviations from the average of such distances for all sampling units were considered outliers.

Ordinations

DECODA v. 2.05 (Minchin 1994) was used for implementation of NMDS and Procrustes analysis. DECORANA (Hill 1979) as corrected by Oksanen & Minchin (1997) was used for implementation of DCA. Previous work with the Thompson River data, combined with experience gained from work with NMDS ordination, indicated that the latent structure of these data could be summarized in three dimensions. Thus we compared in all cases the first three dimensions of DCA ordination with the results of a three-dimensional NMDS ordination. DCA was performed with detrending by segments. Downweighting of rare species was performed to reduce distortions in DCA due to the inherent properties of its χ^2 distance measure. The Bray-Curtis measure of dissimilarity (Bray & Curtis 1957) was used with NMDS. Starting configurations for NMDS were determined randomly. Since NMDS solutions can become trapped in local minima, 10 random configurations were generated. The NMDS solutions resulting from each of these 10 starting configurations were compared to one another

Table 1. Root mean square (RMS) statistics for comparisons of ordinations using Non-metric Multidimensional Scaling (NMDS) and Detrended Correspondence Analysis (DCA). For each analysis using real data, the DCA ordination was Procrustes fitted to the NMDS ordination and the RMS-value represents the non-trivial difference between the two ordinations. For the analyses with simulated data, 10 different simulated data sets were created; the DCA ordination for each was Procrustes fitted to the corresponding NMDS ordination and the mean RMS-values (± SE) are presented.

	NMDS vs. DCA ordinations	
	Real data (n = 1)	Simulated data (n = 10)
Transformation	RMS	RMS ±SE
Cover class	0.182	0.117 ±0.023
Standardized	0.268	0.227 ±0.029
Midpoint	0.277	0.286 ±0.021

(with Procrustes analysis) to detect differences indicating aberrant solutions. The Procrustes analyses indicated insignificantly small differences among the 10 solutions, so we chose one of these at random for use in our analyses.

Results

Analyses of real data

The NMDS and DCA ordinations of the cover class data were moderately different, with an RMS-value of 0.182 (Table 1). Both ordinations placed the outlier stands previously identified in marginal positions, a desirable outcome. The two ordinations of standardized data differed substantially; the RMS-value for this pair was 0.268, appreciably higher than the RMS-value for the untransformed cover class pair (Table 1). However, both ordinations appeared to have identified the outliers well. The two ordinations of the midpoint data were also quite different from one another, with an RMS-value of 0.277, similar to that for the two ordinations of standardized data. Both ordination methods placed outliers on the peripheries of their respective ordinations, but separation of outliers from other stands was not as evident as it was in ordinations of the other data types.

Analyses of simulated data

The simulated cover class data compared favorably with the real data from the Thompson River watershed. The simulated data had essentially the same number of plots (100) and total species (259) as did the real data (101 and 247, respectively). We also obtained what we believed to be good matches for the rank-distributions of both frequencies and abundances, based on inspection of frequency vs. rank and abundance vs. rank graphs. However, the two data sets differed in other respects. The mean species richness per plot of the simulated data (86.3 species) was nearly twice that of the real data (47.0 species). Beta diversity, computed as total species divided by the mean species richness per plot minus one (Whittaker 1960), was considerably higher in the real data (5.36) than in the simulated data (3.04).

In evaluation of the ordinations of simulated data, the original sampling grid served as a known reference to the inherent structure of the data. Ordination success was evaluated by determining how well this known structure was recovered. Accordingly, RMS-values were computed, following Procrustes fitting to the known structure.

With cover class data, both ordinations captured the underlying structure of the simulated data without serious distortion. Indeed, the mean RMS-value of 0.112 for the NMDS ordinations of cover class data (Table 2) approached the value of 0.10 generally considered to represent two ordinations that are essentially identical. The mean RMS-value of 0.166 for the DCA ordinations indicated that this method was somewhat less successful in capturing underlying structure.

With the standardized data, the NMDS method was somewhat less successful in capturing the underlying data structure, with the mean RMS-value increasing by ca. 20% to 0.134 (Table 2). However, the DCA ordinations of these data substantially distorted the underlying structure (mean RMS = 0.267). The DCA ordinations of the standardized data compared unfavorably with the DCA ordination of the cover class data and were clearly much poorer than the NMDS ordinations of either the cover class data or the standardized data. The midpoint data challenged both ordination methods. Nonetheless, NMDS, with a mean RMS-value of 0.216 (Table 2), in this case performed much better than did DCA, which delivered a highly distorted product (mean RMS = 0.360).

In summary, mean RMS-values for NMDS ordinations were significantly lower than those for DCA conducted on the same data sets, as evaluated with t-tests (Table 2), indicating better performance of NMDS. Across data types, both methods performed best with the original cover class data, more poorly with the standardized data and most poorly with the midpoint data. As ordination performance declined, the difference between results of the two ordination methods also increased (Table 1).

Table 2. Root mean square (RMS) statistics for comparisons of ordinations using Non-metric Multidimensional Scaling (NMDS) and Detrended Correspondence Analysis (DCA) applied to simulated data. 10 different simulated data sets were created; the NMDS or DCA ordination for each was Procrustes fitted to the known sampling distribution and the RMS value represents the nontrivial difference between the ordination and the sampling distribution. All RMS values presented are means (± SE) (n = 10).

Transformation	NMDS vs. Distribution RMS ±SE	DCA vs. Distribution RMS ±SE	Comparison of RMS Means t-value	p-value
Cover class	0.112 ±0.004	0.166 ±0.022	2.34	0.0419
Standardized	0.134 ±0.004	0.267 ±0.025	5.31	0.0004
Midpoint	0.216 ±0.009	0.360 ±0.018	7.29	< 0.0001

Discussion

We were struck by the difficulty of arriving at objective criteria for assessing efficacy of ordinations conducted on real data. Although it was possible to determine how different two ordinations were from one another, the lack of an objective benchmark made such comparisons difficult to interpret. However, we did find that the ordinations on the real data varied from being quite similar to one another (the case with cover class data) to being more dissimilar (the case with the two transformed data sets). Although outliers appeared to be reasonably well delineated in most ordinations, it was difficult to determine from visual inspection whether one ordination or another performed better in this respect.

Simulated data offered the potential for evaluating ordination success in recovering known structures. We found that NMDS was superior to DCA when used with the simulated cover class data or either of its transformations. This work complements a growing body of results from Minchin (1987) and others suggesting that NMDS is indeed a method superior to DCA for ordination analysis of community data. In addition, both methods performed poorly with the midpoint data and both performed much better with the original cover class data. Superior performance with this popular approach to assessment of vegetation abundance is encouraging, while the poorer performances with transformed versions of the cover data suggest that these data types are less useful, at least in ordination analyses.

Construction of simulated data with properties matching those of real data proved challenging. While we were successful in matching certain properties well (number of plots, total number of species, rank-distributions of frequencies and abundances), this matching could only be achieved by allowing other properties (average species richness per plot, β-diversity) to differ substantially. Introduction of qualitative error (stochastic conversion of expected abundances to zero) into the simulated data would have permitted better matching of the richness and beta diversity measures, but would have reduced our ability to match the other properties. Our simulated data thus represented a compromise among desired attributes.

An interesting parallel emerged in our comparison of the results of ordinations on both real and simulated data. The transformation (midpoint) that proved most challenging for the ordination methods when applied to simulated data (Table 2) also resulted in the greatest disparities of results when the two ordinations were applied to either real or simulated data (Table 1). It would be of interest to determine if this is a general rule that can be applied to all ordinations.

We continue to work with ordination comparisons using both real and simulated data. We are examining other data sets and, in the case of simulations, we are exploring use of skewed (as opposed to symmetric) response curves, introduction of noise, and other properties that may be matched with properties of real data sets. In any comparison or testing of analytical methods, we believe that it is particularly important to create simulated data with structure emulating that of real data, and to conduct parallel analyses of both real and simulated data.

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Separation of subspecies along a temperature gradient

Vetaas, Ole R.

Botanical Institute, University of Bergen, Allegt. 41,
N-5007 Bergen Norway;
Fax +4755589892; E-mail ole.vetaas@bot.uib.no

Abstract. The conceptual niche model is implicit in several theories in vegetation science, population ecology, biosystematics and speciation. Whittaker and Austin have demonstrated that the response of a single species to environmental gradients can explicitly link the conceptual models of a vegetation continuum and the realized niche of a species. Whittaker has suggested that a bimodal response may indicate segregation in subpopulations with distinct genetics (ecotypes). This study used General Additive Models (GAM) and Generalized Linear Models (GLM) to evaluate if two interbreeding taxa (*Rhododendron arboreum* ssp. *arboreum* and ssp. *cinnamomeum*) had two distinct realized niches with respect to temperature. The species *Rhododendron arboreum* did not have a bimodal response to temperature. The two subspecies increased from either end of the temperature gradient towards the middle, when plots in which the taxa were actually growing were analysed. Only ssp. *arboreum* showed a weak unimodal response to temperature. Both subspecies showed unimodal responses to temperature when plots where the target taxa did not occur were included in GLM and GAM. The ecological or biosystematic interpretation depend on the numerical approach, which illustrate the problem of formalizing the conceptual niche concept. This demonstrates that the development of vegetation theory is lagging behind the rapid advances in numerical techniques.

Keywords: Elevation gradient, Himalaya, Nepal, Niche separation, *Rhododendron arboreum.*

Introduction

The bell-shaped response curve for species along environmental variables is a well- excepted model in vegetation theory (Whittaker 1956; Gauch & Whittaker 1972; Jongman et al. 1987). Whittaker (1956, 1967) and Austin (1985) have argued that such response curves can be viewed as a unidimensional realized niche of a species. This may bridge the conceptual models of a vegetation continuum with biosystematics theory. A proper ecological niche is one of the characteristics of a biologically defined species (*sensu* Mayr 1982), and is the main criterion for the ecological species concept (*sensu* van Valen 1976; Andersson 1990).

The Gaussian optimum curve is, however, an idealized model, and asymmetric and bimodal curves have been demonstrated by several authors (Whittaker 1967; Werger et al. 1983; Austin et al. 1990; Bio et al. 1998). Whittaker (1967) has suggested that deviation from a unimodal bell-shaped response, such as bimodal, may indicate segregation in subpopulations with distinct genetics, (ecotypes or subspecies). Bimodality is, however, not so easy to detect with the curve fitting procedure currently applied, such as Generalized Linear Models (GLM: Nelder & Wedderburn 1972; Austin et al. 1990). In this respect the non-parametric extension of GLM, Generalized Additive Models (GAM: Hastie & Tibshirani 1990) is an improvement since it allows the data to determine the shape of the response curve. Thus bimodality or asymmetry can easily be detected.

This study aims to evaluate if two subspecies of *Rhododendron arboreum* have distinct realized niches with respect to temperature. This was done by checking for (1) a bimodal structure in *R. arboreum* and (2) a bell-shaped unimodal response in the two subspecies. The effect of including plots where the target taxa do not occur is discussed in relation to the ecological and biosystematical interpretation.

Material and Methods

Area and taxa

The sampling took place along an elevation gradient from 1500 m a.s.l. up to 3600 m following the Dudh Kkoshi river in the Solu-Khumbu District in East Nepal (27° 30' -50' N and 86° 40' -50' E). The upper part of the gradient (> 3200 m a.s.l.) is within the Mt. Everest National park and has a cool temperate climate, whereas a warm temperate climate is found at lower elevation. The area has a monsoon climate where 80% of the precipitation falls during the summer season (May to October) (ca. 1000 - 2000 mm/yr). However, short showers are common during winter, falling as snow above 2300 m a.s.l.

The climate station closest to the lowest sampling point (Okladunga at 1720 m a.s.l.) has a mean annual temperature of 16.4°C, and average minimum and maximum temperatures of 5.4 °C (January) and 23.1 °C (July) respectively. The highest station (Tengboche at 3800 m a.s.l.) has an annual mean of 3.9 °C, and average minimum and maximum temperatures of –10.1 °C and 14.3 °C respectively.

The forests along the gradient from 1500 m a.s.l. to 2900 can be classified as 'Low to Mid-Montane Hemi-Sclerophyllous Broadleaf Forest' (Singh & Singh 1987). The canopy dominants are evergreen oak trees, such as *Quercus glauca*, *Q. lanata*, *O. lamellosa* and *Q. semecarpifolia*, with a subcanopy layer of *Rhododendron arboreum* Sm. and phanerophytes belonging to the *Lauraceae* (cf. Dobremez 1976; Vetaas & Chaudhary 1997). Above 2900 m a.s.l. there is woodland dominated by *Abies spectabilis*, *Rhodendron arboreum*, *R. wallichi* and shrubs mainly *Juniperus* spp. (Dobremez 1976).

The area can be regarded as a cultural landscape where the forests are often 'islands' in a matrix of fields and grasslands. The forest patches sampled were of varying size and often situated adjacent to vegetation modified by human activity.

Rhododendron arboreum is a large tree-forming *Rhododendron* in the subgenus *Hymenanthes*. The two target subspecies, *R. arboreum* ssp. *arboreum* and ssp. *cinnamomeum*, have different indumentum on the lower surface of the leaves. Spp. *arboreum* has a silvery to grey compacted indumentum and ssp. *cinnamomeum* has a loose indumentum with a brown to dark rusty brown colour (Chamberlain 1982). Biogeographically the subspecies differ: ssp. *arboreum* is most common in the western Himalaya and ssp. *cinnamomeum*, in the eastern. Their distributions overlap in East Nepal and adjacent India and Bhutan, where ssp. *arboreum* is more common at lower elevations and ssp. *cinnamomeum* higher up.

Sampling and analyses

A total of 103 plots of 0.1 ha were sampled in the spring of 1997 in the valley which leads to Mt. Everest base camp. Due to topography and the cultural activity it was not possible to sample all 100 m intervals systematically along one transect (slope). Thus a sequence of 100 m intervals may not necessarily be geographically close, which breaks the continuous relation between geographical space and elevation/temperature as in classical direct gradient analyses (Whittaker 1967). Five plots were sampled at each 100-m interval according to the following scheme: a mature *Rhododendron arboreum* in the forest adjacent to a well-established footpath was used as the middle point of the first plot at a pre-defined elevation interval (e.g. 1500-1600 m, etc.). This plot was used as the starting point for the subsequent four plots, which should be at the same elevation with a minimum horizontal distance of 30 m between. Due to inaccessible terrain (e.g. inclination > 50 %) the distance between the plots varied from 30 to 200 m. The number of individuals were counted in each plot, and the altitude noted. A local temperature lapse rate was estimated (five stations) to be 0.56 °C per 100 m – the national lapse rate for annual mean temperature is 0.51 °C (cf. Dobremez 1976).

Numbers of individuals were square-root transformed prior to regression analysis in order to reduce overdispersion. Two analyses were made for each taxon; with and without plots where the target taxon did not occur. General Additive Models (GAM: Hastie Tibshirani 1990) were used to determine whether *R. arboreum* has a bimodal response to temperature. The same method was used to check if the two subspecies have a unimodal (bell-shaped) response. A cubic spline smoother (4 df) was used in GAM, which allows the data to determine the shape of the response curve instead of being limited by shapes available in parametric regression.

Table 1. Smoothed temperature predictor in GAM for **(A)** *Rhododendron aboreum*, **(B)** *R. aboreum* ssp. *cinnamoeum*, and **(C)** *R. aboreum* ssp. *arboreum*. $p < 0.001$ in all cases.

	Deviance explained	F-value	Absence values
A	39.94	17.61	Excluded
	40.72	18.50	Included
B	47.15	11.71	Excluded
	51.40	27.96	Included
C	40.41	9.87	Excluded
	66.67	52.00	Included

If bimodal or unimodal responses were detected parametric tests were made using Generalized Linear Models (GLM; McCullagh & Nelder 1989). Unimodality was evaluated by testing the significance of a model including a second order term against a linear model. Bimodality was evaluated by testing the significance of a model including a third and fourth order term against a unimodal model. Overdispersion was generally high; this means that an *F*-test (Chambers & Hastie 1993) is required.

All GAM and GLM analyses were made with both an assumed Gaussian and a Poisson error distribution. The Anscombe residual from each test was compared by drawing a diagnostic Q-Q-plot (Chambers & Hastie 1993). This indicated that the Poisson model was best for GLM and the Gaussian for GAM, although the differences were not large in either analysis. All analyses were performed using the S-plus program version 3.3 (Anon. 1993).

Results and Discussion

There was no sign of a bimodal structure in the response curve to temperature when the two subspecies were analysed together with GAM (*R. arboreum*) (Fig. 1). A clear unimodal response was confirmed in GLM by a highly significant second-order polynomial and a nonsignificant third order polynomial. A slight skewness (not significant) will appear in Fig. 1 if the data were not square-root transformed and analysed with a log-link function (Poisson error).

Subspecies *arboreum* has a unimodal response to temperature in the GAM analyses where absence values were excluded, but subspecies *cinnamomeum* has a positive log-linear trend (Fig. 2a, c). The significance of the unimodal response in GAM of ssp. *arboreum* (Fig 2c) was confirmed by a significant second order term in GLM, but this relied solely on the two samples with low values (at 2650 m a.s.l.

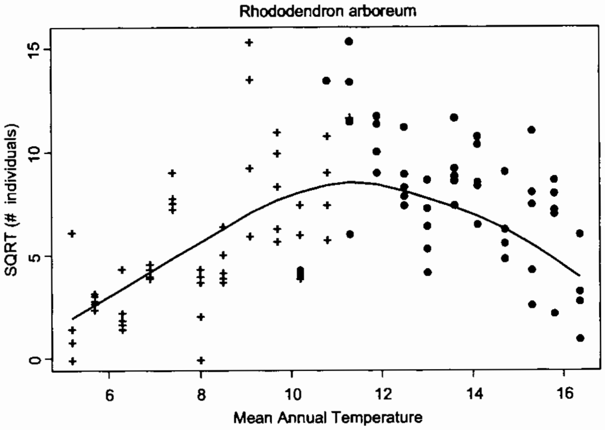

Fig. 1. Response model for *Rhododendron arboreum* with smoothed annual mean temperature as predictor in GAM (cf. Table 1).

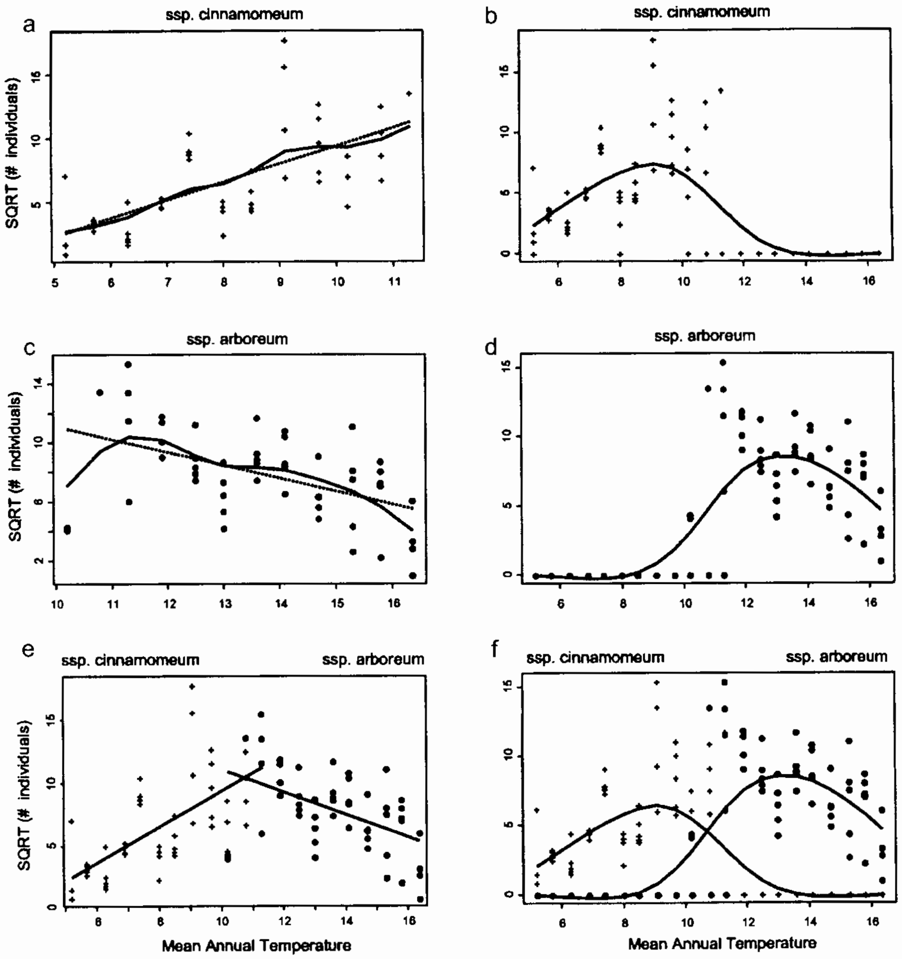

Fig. 2. GAM analyses with smoothed annual temperature as predictor and subspecies *cinnamomeum* (**a** and **b**) and *arboreum* (**c** and **d**) as responses. (**e**) is based on the combination of (**a**) and (**c**) without absence values; (**f**) is based on the combination of (**b**) and (**d**) combined with absence values (cf. Table 1). Interrupted lines (**a** and **c**) are linear models (GLM).

= 10.2 °C). However, this may be the result of a too low sampling intensity in the zone of overlap (2500-2800 m). Both subspecies have pronounced bell-shaped responses in the GAM analyses where absence values were included (Figs. 2b, d). A significant second-order polynomial in GLM confirmed this pattern.

The ambiguous niche concept (cf. Smith 1990) is to some extent clarified when the unidimensional niche is linked to the unimodal response model. Accordingly, two subspecies with distinct realized temperature niches should have a differentiated unimodal response to temperature. Although segregation in temperature was not revealed by a bimodal pattern at the species level, the two subspecies showed clear differentiation with a small overlap along the temperature gradient when analysed separately. By combining the graphs where absence values are included (Fig. 2b and 2d) two distinct temperature niches are found (Fig. 2f). The analyses without absence values, however, indicate that the subspecies do not show a proper unimodal response (Fig. 2e).

It makes sense to include plots where the target taxa do not occur in analyses of species-environment responses as the species response curve along a given ecological variable may simply appear as the frequency distribution of that particular ecological variable if only plots where the species occur are included (Kershaw & Looney 1985: 29). A normal or skewed frequency distribution is common for environmental variables (Jongman et al. 1987), but temperature in this study is uniformly distributed.

The species *R. arboreum* has a clear unimodal response to temperature and a very long temperature range (12°C) (Fig. 1). It is quite natural that different morphological attributes (i.e. leave indumentum) have evolved in a species which grows from the warm temperate zone up to the sub-alpine zone, which justifies the splitting of the species into two subspecies. The fact that the subspecies have distinct realized niches (if we except the inclusion of absence values), may also be used as a guide to judge the taxonomic status of the subspecies. A proper ecological niche is an important characteristics of the species concept, defined biologically (*sensu* Mayr 1982) and ecologically (*sensu* van Valen 1976; Andersson 1990). Following this rationale one may argue that the two subspecies are actually two genuine species. Absence values in systematics, however, have a totally different meaning than in ecological analyses (cf. above). The ecological condition at the site of an individual should be regarded as a character of the individual in the same way as a morphological character. Accordingly, it does not make sense to include a character value for an individual that is not present.

In this respect the potential of the niche concept to link theory in vegetation science and systematics is not straight forward. Those who advocate an ecological species concept (van Valen 1977; Andersson 1990) should also be aware of the difficulties in defining a niche. The shape of the response curve, i.e. the niche, will depend on subjective choices by the investigator, e.g. number of plots where the target taxa do not occur. Although a niche for a taxon can be easily estimated by regression techniques, such as GLM and GAM (Austin et al. 1990, 1997; Yee & Mitchell 1991; Bio et al. 1998), the above interpretations illustrate the problems of formalizing the conceptual niche model into a more graphical or mathematical model valid within different biological disciplines. Since the results in this case depend on the numerical approach it demonstrates that the development of vegetation theory is lagging behind the rapid advances in numerical regression techniques.

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Long term changes in the ground flora of English woodland and some implications for nature conservation

Kirby, Keith J.

English Nature, Northminster House, Peterborough, PE1 1UA, UK;
Fax +441733568834; E-mail keith.kirby@english-nature.org.uk

Abstract. Selected changes in the vascular plants of the forest floor over periods of 15 to 30 yr are described from four sites in southern England. Examples are presented of changes in species-richness driven by stand dynamics, recently-felled stands having a high richness; richness may also increase after thinning and decrease if a dense understorey develops. Changes in ground flora composition, decreases of formerly common species and increases of formerly rare species are described for other woods following increased deer grazing. For two woods data are presented showing high species turnover at the stand level, but relatively little change when the results for the whole set of quadrats were combined. Implications for the managers of nature reserves include the desirability of monitoring the ground flora as well as tree and shrub dynamics; the need to consider common as well as rare species if only selected species are to be used as possible indicators of change; and the need to monitor at both stand and whole-site levels because different sorts of change are detected at each.

Keywords: Monitoring; Deer grazing; Woodland ground flora.

Nomenclature: Stace (1991).

Introduction

Considerable effort has gone into studying the growth and turnover of tree populations, as illustrated by the number of long-term plots in unmanaged woodland, in which the fate of individual trees can be followed (e.g. Peterken & Jones 1987; Peterken & Backmeroff 1988). Variations over time in the woodland ground flora (all vascular plants less than 2 m high, except regeneration of trees and shrubs) have been less studied in England. The ground flora may change at different temporal and spatial scales to the trees; for example high turnover rates have been recorded for the ground flora from permanent plots and small-scale patterning is found around tree bases and root-plates (e.g. Barkham 1992; Buckley et al. 1994).

From a nature conservation perspective such long-term changes must be appreciated. We may wish to maintain the characteristic flora of a particular site, but did the species have the same abundances twenty years ago; if species abundances change over the next ten years is this part of a cyclical fluctuation on the site or is the composition of the wood changing irreversibly? Data collected by myself, colleagues and predecessors from four woods in southern England illustrate issues that need to be considered by reserve managers.

Sites and Methods

The field data presented illustrate the response of the ground flora to different treatments and impacts over periods ranging from 15 to 30 years. The data, consisting of species lists and cover-abundance for the ground flora, are from the following sites.

1. Orlestone Forest (Kent) (ca. 20 ha sampled) – a mixed wood of *Carpinus betulus* and *Quercus robur*, partially replanted with even-aged stands of *Pinus* spp., *Picea abies* and *Fagus sylvatica*. Five 200 m^2 quadrats were recorded at random positions within each of seven stands on three occasions, 1983, 1991, 1998 (Kirby 1990; 1993).
2. Monks Wood (Cambridgeshire) (157 ha) – a mixed wood of *Fraxinus excelsior*, *Acer campestre* and *Corylus avellana*, coppiced until the beginning of this century, but subsequently allowed to grow-up as unmanaged high forest. The abundance of eight ground flora species was compared using separate samples of thirty-six 400 m^2 quadrats recorded in 1966 and 1996 (Crampton et al. 1998).
3. Wytham Woods (Oxfordshire) (320 ha) – a mixed wood, predominantly of *Fraxinus excelsior*, *Acer campestre*, and *Corylus avellana*, but with a varied structure and management history. One hundred and sixty -three 100 m^2 permanent quadrats were recorded in 1973/4 and 1991 (Dawkins & Field 1978; Thomas & Kirby 1992; Kirby et al. 1996; Kirby & Thomas 1999).
4. The Warburg Reserve (Oxfordshire) (100 ha) – a mixed wood of *Fagus sylvatica* and *Fraxinus excelsior* with a varied structure and management history. 96 100-m^2 permanent quadrats were recorded in 1974 and 1992 (K.J. Kirby & R.C. Thomas unpubl. data).

Results

Orlestone Forest

Mean species richness varied between stands and over time depending on the stage in the growth cycle that each stand was at, at each recording time (Table 1). Species-richness increased after felling and then declined as the canopy closed; but thinning of stands or development of a woody understorey also tended to increase or decrease richness respectively.

Monks Wood

Between 1966 and 1996 six of the eight ground flora species showed large changes in frequency, most notably the decline in *Mercurialis perennis* and increases in *Poa trivialis* and *Brachypodium sylvaticum* (Table 2). The change in frequency in *Rubus fruticosus* was not significant, but it had declined in abundance: at least up until 1973 it formed thickets 0.5 - 1.0 m high in much of the wood. In the 1996 quadrats *Rubus* was present only as individual stems less than 10 cm high.

Wytham Woods and The Warburg Reserve

There was a high turnover of species in individual quadrats (Table 3), as indicated by the high number of species in

Table 1. Changes in the mean species-richness (vascular plants) over a 15-yr period for different stands in Orlestone Forest, Kent.

Tree crop	Age in 1983 (yr)	Mean species no per 25 m² quadrat (n = 5)(SE in brackets) 1983	1991	1998
Quercus-Carpinus	70	6.2 (1.0)	7.0 (1.6)	3.6 (0.9)[a]
Pinus spp.	34	10.0 (1.1)	8.2 (0.7)	5.0 (0.7)[b]
Pinus spp.	20	7.6 (1.3)	3.6 (0.4)[c]	5.8 (1.6)
Pinus spp.	3	14.0 (0.4)	11.4 (1.7)[d]	5.6 (0.8)
Picea spp.	32	8.6 (1.3)	14.4 (1.0)[e]	5.6 (1.0)
Picea-Tsuga spp.	21	1.2 (0.2)	3.2 (1.7)	12.0 (1.0)[f]
Quercus-Fagus	66	2.6 (0.2)	3.4 (0.5)	2.6 (0.6)[g]

Notes on stands:
(a) Fewer gaps were recorded in the canopy and understorey in 1998 in this stand than previously; (b) Between 1983 and 1998 the understorey of *Carpinus* in this stand increased considerably; (c) This stand was row-thinned between 1991 (when canopy closure was complete) and 1998; (d) In 1991 the canopy here was still open, but it closed rapidly in the following seven years; (e) The change in species number follows clear-felling in 1988, followed by rapid canopy regrowth between 1991 and 1998; (f) This stand was clear-felled in c.1995; hence the increase in species richness by 1998; (g) No apparent changes in canopy or understorey over the period concerned.

each permanent quadrat that were recorded at only one of the two dates. There were also changes in the overall abundance of some species, such as *Brachypodium sylvaticum* in Wytham Woods that were comparable to those seen at Monks Wood (Table 2). *Rubus fruticosus* also declined in cover in Wytham Woods, even though it remained frequent. However *Carex pendula* which had increased at Monks Wood, did not change in frequency at Wytham Woods over a similar period. Neither *Poa trivialis* nor *Brachypodium sylvaticum* showed changes in frequency at the Warburg Reserve, in contrast to the other two sites. The mean ground flora cover increased slightly at the Warburg Reserve, but declined significantly at Wytham Woods (no comparable data are available for Monks Wood).

Other measures that might be used to assess biodiversity such as mean species number or the total number of species present in the whole set of quadrats showed very little difference between the two recording times (Table 3).

Discussion

Most ancient woods in England are very small (less than 20 ha), with a history of coppicing up until the beginning of this century, followed by neglect (Spencer & Kirby 1992; Peterken 1981). Many more-or-less even-aged stands are now being brought back into management (felling, thinning, cutting of the understorey). Their ground flora will tend to follow the pattern illustrated by the results from Orlestone Forest, whereby the relative and absolute richness of different stands changes over quite short time-scales.

The ground flora changes at Monks Wood, which happened across the whole of a large site, do not appear to be related to stand growth (as at Orlestone). Rather they reflect the impact of a new factor, increased grazing pressure by the introduced deer *Muntiacus reevesii*, as has been demonstrated through study of exclosures in the wood (Cooke et al. 1995). Increased nitrogen deposition had also been suggested as a possible cause of this change, but neither here nor in Wytham Woods could clear evidence to support this be found.

In the Wytham Woods and Warburg Reserve high levels of turnover at quadrat or stand level took place, as at Orlestone, but were evened out in indices that combined the results for the whole site. Even so changes in the frequency of common species (e.g. *Brachypodium sylvaticum*) did occur, whereas previous work (e.g. Barkham 1992) had tended to emphasise the contribution of the uncommon species to turnover rates.

Implications for nature conservation managers

The woodland ground flora is highly dynamic over periods of a decade or more: change should be expected. Over quite short time-scales, the relative and absolute species-richness of different areas may change greatly. Decisions on nature conservation value and management of stands are often based (at least in part) on assessment of the ground flora. Allowance must therefore be made for the sorts of changes illustrated here.

While some ground flora changes reflect internal stand dynamics and are cyclical, others are largely independent

Table 2. Changes in the frequency of selected ground flora species in three woods.

	Number of quadrats in which a species was recorded at: Monks Wood[a]		WythamWoods[b]		The Warburg Reserve[b]	
Date	1966	1996	1974	1991	1974	1992
No of quadrats	36	36	163	163	96	96
Glechoma hederacea	20	29	99	110	24	21
Mercurialis perennis	18	7	137	132[c]	85	85
Rubus fruticosus	15	21[c]	142	127[c]	82	75
Hyacinthoides non-scriptus	9	11	62	63	6	9
Brachypodium sylvaticum	1	32	63	136	66	60
Urtica dioica	1	9	122	129[c]	48	57
Poa trivialis	0	35	110	140	35	34
Carex pendula	0	18	43	41	0	0

(a) The quadrats were temporary, each 400m^2 (Crampton et al. 1998); (b) The quadrats were permanent quadrats, each 100m^2 (Kirby et al. 1996); (c) Associated cover estimates for these species at these sites indicated a decline in the cover of *Mercurialis perennis* at Wytham, declines in the abundance of *Rubus* at both Monks Wood and Wytham Woods, and an increase in the abundance of *Urtica* at Wytham Woods.

Table 3. Changes in overall species cover and composition of Wytham Woods and The Warburg Reserve, 1974 - 1991/2.

	Wytham Woods		The Warburg Reserve	
No of quadrats	163		96	
Date	1974	1991	1974	1992
% ground flora cover*	80 (2)	64 (2)	62 (3)	73 (3)
No of species per quadrat*	16.7 (0.8)	17.2 (0.7)	18.7 (1.2)	16.7 (1.1)
No recorded only on one occasion*	7.2 (0.5)	7.7 (0.5)	9.0 (0.7)	6.9 (0.6)
Total no of species in full quadrat set	173	167	161	145
Sorensen's similarity index	85%		81%	

* standard errors in brackets.

of what is happening to the tree and shrub layer and may be directional. Changes at stand level may not reflect those for the wood as a whole and *vice versa*. Therefore woodland monitoring programmes for nature conservation purposes should include ground flora as well as the woody layers and provide results that can be used at the site as well as the stand level.

Change in the frequency and abundance of common ground flora dominants have occurred over the last thirty years in woods in England. These can have a major significance for the functioning of other parts of the ecosystem: e.g. loss of thickets of *Rubus fruticosus* may eliminate nesting sites for nightingales *Luscinia megarhyncha* (Gosler 1990), but allow an increase in lower-growing ground flora species (Kirby & Woodell 1998). Indicator species for monitoring programmes should not be selected only from among the rare and unusual species, or those thought to have a narrow ecological range.

The results presented here are from a narrow range of sites. The nature conservation agencies are planning to expand both the number of sites where long-term ground flora studies are done and are exploring the use of plant attributes (Grime et al 1988; Ellenberg 1988) to improve the analysis and interpretation of the results.

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17 years of change in a dune slack community in the Eastern Cape

Lubke, Roy A.[1*] & Avis, A.M.[1,2]

[1]*Department of Botany, Rhodes University, Grahamstown, 6140 South Africa; [2]Present address: Coastal and Environmental Services, P. O. Box 934, Grahamstown, 6140 South Africa; E-mail ces@imaginet.com.za;*
[*]Fax +27466225524; E-mail borl@rhobot.ru.ac.za

Abstract. In 1980 we observed the colonization of a wet bare dune slack with many seedlings of *Scirpus nodosus*. In an investigation on the salt tolerance of this species, observations were made on the soil and environmental characteristics of the site and a detailed map of the vegetation was produced. Subsequent observations have been made on species recruitment and vegetational changes recorded annually. After 17 yr, a detailed quantitative analysis of these data revealed the species dynamics within the system and changes in species diversity, cover and abundance. This has provided a unique opportunity to test an earlier model for succession produced by the authors in 1984. The rigorous quantitative analysis shows that these early predictions were correct. Shrub density remained low until 1991 and has now increased rapidly, while sedges and rushes increased initially to peak in 1983 and then to drop to near zero by 1998. Species richness increased to peak at 23 species in 1985 and 1987 and has subsequently decreased. Vegetative cover increased to 40-50% from 1985 to 1992 and has now increased to about 80%. The development of the slack vegetation, from pioneers to climax dune thicket, is dependent on the prevailing climate, particularly rainfall, of the region.

Keywords: Colonization; Dune thicket; Kleinemonde; *Scirpus nodosus*; South Africa; Species richness.

Introduction

The Eastern Cape Coastline is well endowed with extensive dune systems similar to the Pacific Northwest Coast of North America (Wiedemann, 1984; Wiedemann & Pickart 1996) and unlike the North Sea Coasts of Europe (but similar to the Wadden Sea Islands (Dijkema & Wolff 1983; Westhoff & van Oosten 1991). The vegetation of these dune fields is often confined to pioneer foredune communities, dune slacks which are sparsely vegetated, and bush pockets which may represent select patches of more extensive thicket (Parker-Nance et al. 1991; Avis 1992; Lubke et al. 1997).

Lubke (1983) gave a brief account of the dune vegetation, and studies on the effects of the harsh climate on the growth and succession of plant communities has followed (Avis & Lubke 1982; McLachlan et al. 1987). In a synthesis paper on the dune slack communities, we hypothesised that the slack vegetation follows a rapid succession from pioneers to a woody scrub community, but is limited by the prevailing climate, particularly rainfall, wind and consequently sand movement (Lubke & Avis 1988). This model of dune succession, drawn from our studies and those of McLachlan et al. (1987) on the Alexandria dune fields, is largely untested temporally although spatial analysis of the communities does confirm these changes (Avis 1992).

Fortunately, a site in the dune slack established to study the effect of salt spray and other conditions on the pioneer sedge, *Scirpus nodosus* (Lubke & Avis 1982; Avis & Lubke 1984), was sampled annually. Now, 17 yr later, these data have been analysed using quantitative methods. The aim of this paper is to show how the temporal data confirms the autogenic succession of plants in the Eastern Cape dune slacks and dune systems.

Study area

The coastal strip between the Kleinemonde and Riet Rivers, ca. 12 km east of Port Alfred, is 4 km long and covers an area of ca. 350 ha. This portion of the 1820 Settler farm, Tharfield bounded by the Port Alfred/East London road in the north and the sea in the south has been proclaimed a private nature reserve. The dune cordon consists of ca. 100 ha of eastwardly migrating transverse sand dunes reaching ca. 50 m above sea level (Tinley 1985). The dune and dune slacks are sparsely vegetated in parts and the permanent vegetation begins with dune thicket from 100 to 700 m from the shore. In protected areas the thicket becomes well established coastal forest with trees up to 10 m tall (Lubke 1983). The foredunes are vegetated in part by pioneer grasses and shrubs and the moist dune slacks are invaded by sedges, rushes, herbs and grasses. The study area is situated at the eastern side of the nature reserve and was first studied by Lubke & Avis (1982). The wet site was stabilized by *Juncus krausii* with *Scirpus nodosus* plants in a protected hollow, with large dunes to the south, east and west. The site was chosen for study because of the abundance of *S. nodosus* which was the dominant pioneer in the moist slack (Lubke & Avis 1982).

Methods

Vegetation sampling

The study area was triangular in shape and to facilitate mapping of the vegetation, the area of 220.5 m^2 was divided into quadrats of 2.5 m × 2.5 m or 3 m × 3 m. A scale map of the study area was produced on which the vegetation in each quadrat was plotted. Initially, only the triangular shape was sampled and mapped as the site to the north of the hypotenuse of the triangle was bare sand. By 1984 this area had become colonized and the square area of 441 m^2 was sampled. In order to calculate density and percentage frequency of the dune slack species, quadrats of 1 m^2 each were taken from the bottom left of each large marked quadrat (Lubke & Avis 1982). The number and aerial cover of individuals of each species was recorded for each quadrat. The site was mapped and sampled annually from 1981, initially in September and then subsequently in the summer months, January, February or March. In 1982, 1993, 1994, 1996 and 1997 no sampling was carried out (Fig. 1).

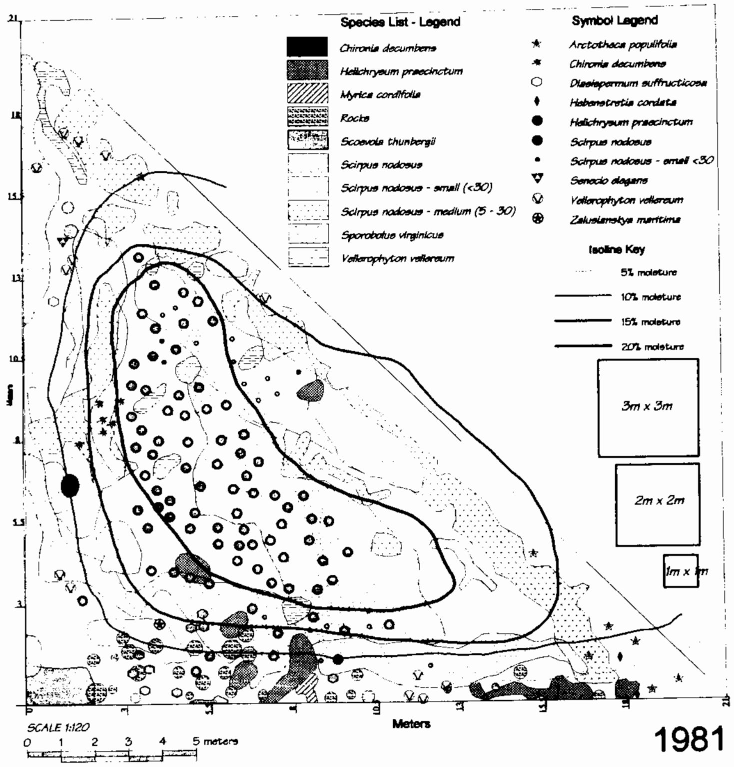

Fig. 1. Initial sampling in the dune slack in 1981 showing the map of the vegetation and the size of the quadrats for mapping. After 1981 vegetation in the upper triangle was also sampled. Smaller 1-m^2 quadrats were used for density and cover determination (see text). The isolines show the original soil moisture values in the hollow in the centre of the triangular area.

Data analysis

The species of the dune slack were divided into major functional types, viz, pioneers, sedges and rushes, herbs or forbs and shrubs. The mean density and percentage cover of each species for the quadrats was calculated for each annual sample and the change over time was plotted. These data were also used to show the distribution of the quadrats relative to one another on ordination scatter diagrams using Correspondence Analysis (Hill 1979). The field maps of the cover of the species was digitised and subjected to the TNT mips system. This made it possible to calculate the change in vegetated area of the different species and species groups with time.

Results

Changes in species composition in the study slack

The mapping of the vegetation at almost annual intervals revealed changes in frequency, density and cover of the species and functional types over a 17-yr period. These changes are best shown graphically from the GIS maps but cannot be reproduced here. The wet slack was first colonized in about September 1979 and by the time of the first map in 1981 was well covered with *Scirpus nodosus* plants and seedlings while in drier areas *Sporobolus virginicus*, *Scaevola plumeri* and *Myrica cordifolia* occurred.

A wet slack phase followed during which time many common slack herbs, sedges and rushes appeared (up until

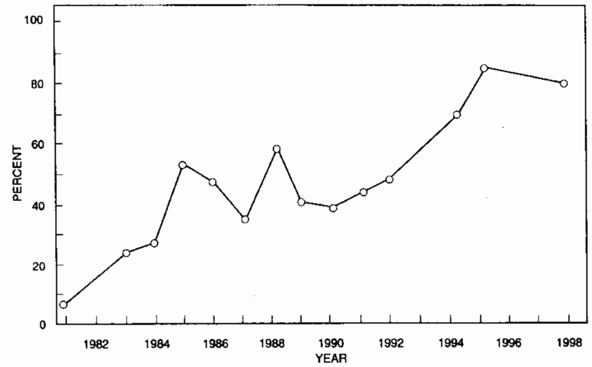

Fig. 3. Change in total percentage cover of the vegetation over 17 years in the dune slack.

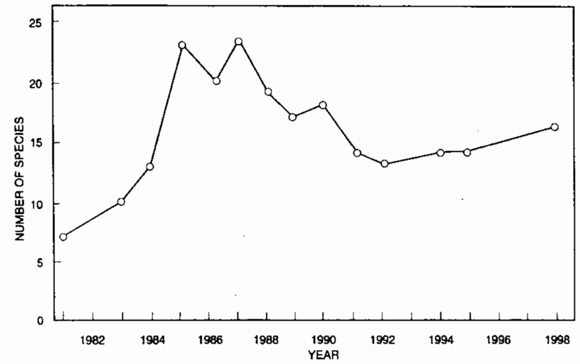

Fig. 2. The change in plant species number over 17 years in the dune slack.

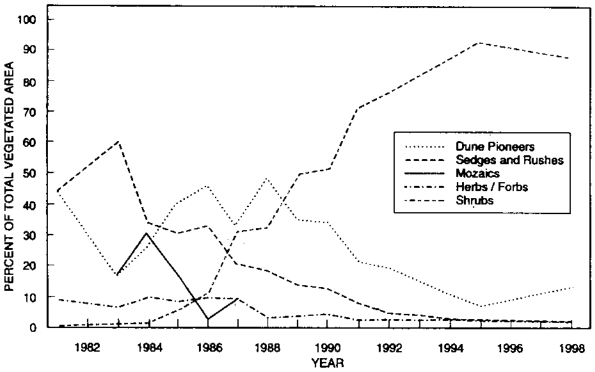

Fig. 4. The percentage cover of the major plant species groups over the 17 years in the dune slack.

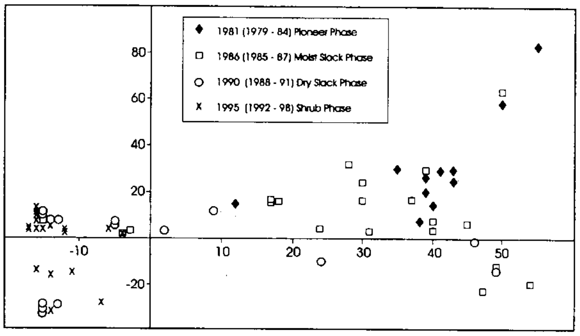

Fig. 5. The Correspondence Analysis scatter plot of the quadrats sampled in the major phases over the 17-year period.

1985 and 1987), when the species richness was the greatest (Fig. 2). The number of species subsequently decreased although in this dry slack phase (1988-1991) a number of other shrub species, typical of the dune scrub stage of succession were already present. These included *Chrysanthemoides monilifera, Rhus crenata, Metalasia muricata, Passerina rigida, Stoebe plumosa.* The former two are bird-dispersed while the latter are wind-dispersed species. *Passerina rigida* is one of the early colonizers which provides perch sites for frugivorous birds. *Myrica cordifolia*, was already present and would have advanced into the slack from the southern extreme of the dune region. It grows as a creeping shrub from stems at, or just below, the soil level.

Total percentage cover slowly increased to fluctuate from 40 to 80% between 1985 and 1992, then increasing rapidly to about 80% in 1995 (Fig. 3). The percentage cover can be allocated to pioneers, shrubs, etc. and a summary of these data showed how the pioneers (sedges and rushes) decreased slowly from the initial pioneer period between 1979 and 1984 and then dropped to almost zero by 1998 as they were shaded out by the shrubs, and the slack dried out. (Fig. 4). In contrast shrubs only slowly become more abundant and higher in number and density up to 1991 and are only now increasing rapidly to consist of over 80% of the vegetation cover. The dune pioneers increased in the dune slack phase of 1985 to 1988 as much of the bare sand in the northern region of the slack was colonised but they have now decreased in cover to about 10% as they are replaced by shrub species (Fig. 4).

Ordination of the quadrats in the different community phases

The Correspondence Analysis plot of the quadrats in different phases of succession is shown in Fig. 5. Because of the large number of quadrats when the total set would be analysed, only four years representing the different phases are presented. The quadrats of the pioneer phase are in the top right, in moving through the moist slack phase (1986) quadrats are scattered throughout the region, to the dry slack phase (1990) when the quadrats are found more predominantly to the left. Finally in the shrub phase (1995) the quadrats are all clustered on the left.

Discussion

Our earliest model of succession was based on observations of the region (Lubke 1983; McLachlan et al. 1987) and a short temporal study of a dune slack community exposed to a changing local environment (Lubke & Avis 1988). Further studies of spatial sequences within the Tharfield Nature Reserve supported this model (Avis 1992). Changes from either foredune, but usually dune slack, to a dune scrub community dominated by shrubs and finally a thicket community were evident from these ordination studies (Avis 1992). Predicted change in species composition in our model was also evident in this study.

The results accumulated over a longer period of 17 yr give added support to the successional model. Pioneer slack sedges and rushes initially occurred densely in the moist areas (Lubke & Avis 1988) although supporting a low cover (Figs. 2 and 4). Species richness increased over time to a maximum when there were many herbaceous, slack species along with the dune pioneers and shrubs in the slack phase of the succession. The species number decreased as shrubs became abundant, a common phenomenon in successional changes where species interactions become less marked in the 'stable' vegetation (Greig-Smith 1952). In our earlier study (Avis 1992) we found that the diversity index deceased marginally from young slacks to old slacks, but then increased in the dune thicket.

Passerina rigida is the first woody species to invade the dune slack and initially became very common and is a major 'linking species' of dune scrub, between the old dune slacks and thicket communities (Avis 1992). Other shrubs such as *Stoebe plumosa* and *Anthospermum littoreum* were probably wind-dispersed into the slack, but *Rhus crenata* and *Chrysanthemoides monilifera* are bird-dispersed (Castley 1992) and these species were found to arrive after *Passerina rigida,* which forms suitable perch sites for birds.

The Correspondence Analysis ordination (Fig. 5) supports the earlier evidence (Lubke & Avis 1988) that the succession has now reached a bush clump stage (Avis 1992). The directional change in individual quadrats has not been indicated by arrows, as was done in a successional study of dune slacks on Schiermonnikoog by Grootjans et al. (1991), but the change of all quadrats in different years is shown in this figure. *Myrcia cordifolia* which is often dominant in bush clumps is the most abundant shrub at the present time (1998). This species is dispersed by birds and bushpigs (Castley 1992), but in this case migration into the area was vegetative from the southern area of the study site. It appears that these bush clumps, also found in large dune fields (Talbot & Bate 1991), are newly established woody communities able to survive sand burial and are not remnant forest pockets. The bush clumps in these dune fields (Avis 1992) have been shown to be different from the inland thicket (Turner 1992; Turner et al. in prep) and this supports the view of the successional changes from slack to bush clumps. The remnant theory of bush clumps being isolated remnants of a more extensive thicket vegetation (Bate & Dobkins 1992; Castley 1992), as originally proposed by Tinley (1985), does not appear to hold in this case.

The migration of dune sand from the west to the east in this particular slack is resulting in the loss of total vegetative cover across the study site in the last three years (Fig. 2). Previous estimates show that these transverse dunes move at the rate of ca. 3 m/yr (Lubke & Avis 1988). Should the shrubs be able to migrate ahead of the sand at this rate the bush clump will survive although the present sample site will once again be covered by bare sand. Climatic or soil data have not been recorded for the site except in the earlier studies (Lubke & Avis 1982; Avis & Lubke 1984). Our predictions are that the major controlling factors are climate, especially rainfall. Data from the last 25 yr shows that the rainfall was higher in the 1970s, allowing the sedges to become established in the wet slack. Throughout the 1980s and 1990s the rainfall has been somewhat lower, enabling the shrubs to become established while the sedges and herbaceous plants have disappeared. Thus, the pioneer sedges and rushes only become established in wet cycles. This substantiates our prediction that with an erratic and variable rainfall of less than 1000mm/yr the dune fields in the region will not be colonized and covered with climax coastal thicket (Lubke & Avis 1988). Although the migrating bush clump stage has been reached, the plant communities cannot move past this stage in the succession, as the drift sands smother the more stable trees and thicket species as sand dunes migrate eastwards as a consequence of the strong winds that occur in the region. The shrubs of the dune scrub stage, such as *Myrica cordifolia* and *Rhus crenata* can survive sand burial whereas trees of climax dune thicket, such as *Sideroxylon inerme* and *Minusops cafra,* would be buried as they are slower growing species.

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Long-term experiments in ecological restoration

Marrs, Robert H., Le Duc, Michael G., Johnson, Stephen W. & Mitchell, Ruth J.

Applied Vegetation Dynamics Laboratory, School of Biological Sciences, University of Liverpool, P.O. Box 147, Liverpool L69 3BX, England;
Fax+441517944940; E-mail calluna@liverpool.ac.uk.

Abstract. Experiments on land restoration offer a unique opportunity to investigate ecological processes in developing or heavily managed ecosystems using well planned experiments. In spite of this, many reported experiments are of relatively short-term duration, and often stopping 'when the management objectives have been achieved'. Here we argue that long-term studies of experiments designed to manipulate successions and or/restore targeted ecosystems can provide important insights into the functioning of ecosystems generally.

Introduction

The applied restoration ecologist has many advantages over colleagues interested in understanding ecosystems and ecosystems processes; the applied scientist can deliberately manipulate a given ecosystem towards defined objectives and this can in itself be a tool for investigating ecological concepts. Let us assume that the generalized model developed for explaining ecological succession by Odum (1969) is a good starting point, and there is a general increase in complexity and stability in succession time (Fig. 1a). From an applied ecologists viewpoint this successional model can be viewed from a range of perspectives. First, the very act of defining a restoration objective means that a defined target or goal can be set on this trajectory. Second, the ecosystems can be manipulated either to encourage and increase successional development towards this target, or the succession may have to be reversed in order to achieve the goal (Fig. 1b). Examples of the former include restoring new ecosystems on raw mineral wastes, where essentially a primary succession is being mimicked (Marrs & Bradshaw 1993), and the latter where a late-successional ecosystem is being reversed to an earlier stage so that a sub-seral community can be maintained, for example a grassland or heathland (Mitchell et al. 1997).

Another advantage that applied ecologists have over ecologists working in more pristine habitats is that they are often able to apply perturbation treatments that are more severe than would be considered suitable in semi-natural or natural vegetation. Applied ecologists routinely use severe disturbance regimes (Snow & Marrs 1997), addition of fertilisers and even sewage sludge (Marrs & Bradshaw 1993) and herbicides (Marrs & Griffith 1986; Lowday & Marrs 1992). An important objective of applied restoration work is that the target should be achieved, and hence the ecologist is in control. By being in control, and being able to predict the outcome of the treatments in a successional context accurately, the applied ecologist will be acting in a thoroughly professional manner.

In this paper the results of a long-term experiment (18 yr) designed to reverse succession on lowland heath invaded by *Pteridium aquilinum* (bracken) will be reviewed. The aim of the study was to derive techniques which would reduce the bracken infestation and allow a *Calluna vulgaris* dominated heathland to develop. Initially this experiment was very successful with some treatments being very effective at reducing bracken and allowing *Calluna* to establish. However, over the longer-time scale, i.e. after 12 yr, *Calluna* died out and a grass heath developed. Here, we use variation partitioning (Borcard et al. 1992; Legendre 1993; Økland & Eilertsen 1994) to attempt to elucidate the likely causes.

Methods

Experimental treatments and design

Detailed methods are given in Marrs et al. (1998a); thus only a brief summary is given here. 24 combinations of bracken control and heath restoration treatments were applied to dense bracken stands at Cavenham Heath (National Grid reference TL755725) a *Calluna*-dominated heath in Breckland UK, over an 18-yr period in two phases. In Phase I (1978-1984) there were six bracken control and two seeding treatments in factorial combination in four replicate blocks. The bracken control treatments were (1) untreated, (2) cutting yearly in July, (3) cutting twice yearly in June and July, (4) asulam applied in 1978 (5) asulam applied in both 1978 and 1979, and (6) asulam applied in 1978 plus yearly cutting in July thereafter. Fronds were cut by mechanical scythe and left on the plots.

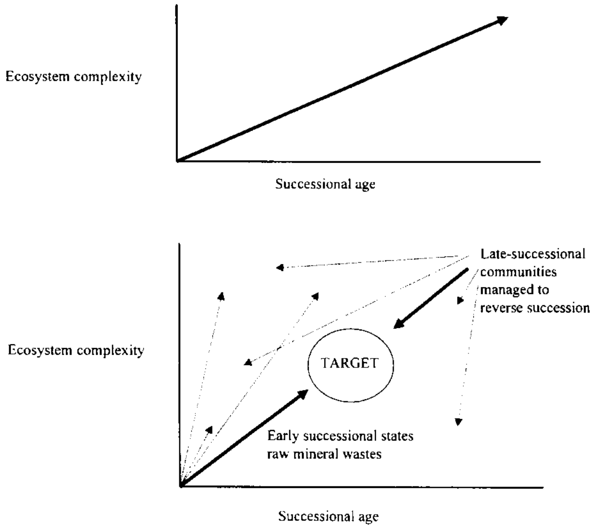

Fig. 1. Hypothetical models of (**a**) Odum's (1969) view of increasing ecological complexity with successional age, and (**b**) how this can be viewed in terms of targets for ecological restoration from two directions - bold lines show the preferred result and dashed lines ones that miss the target.

Asulam (4.4kg active ingedient/ha) was applied in 400 litres water/ha using a motorized mistblower or a knapsack sprayer. The two seeding treatments were (1) unseeded, and (2) seeded with *Calluna* (20 000 seeds/m^2). In Phase II (1985-1996) the four blocks were pooled into two, each containing a pair of plots with similar treatment history. Within each of the pooled blocks bracken control was continued/reapplied to one of the pair and stopped on the other (Marrs et al. 1998a).

In Phase I, the aim was to assess the initial success of vegetation establishment and biomass samples were collected from each plot and dry mass measured. In Phase II, species cover was measured (Marrs et al. 1998b).

Environmental data sets

Climatic data were obtained for 1966 to 1996 from the nearest Meteorological Station (Broom's Barn, National Grid reference TL746756, 7 km to the south of Cavenham Heath). Amongst the important factors influencing *Calluna* growth are temperature and moisture availability (Marrs 1986), and seasonal means for maximum and minimum air temperature and rainfall were calculated.

Spatial location of each plot was located using grid coordinates x and y (accurate to the nearest half m), and all quadratic and cubic combinations of x and y were computed to allow for recognition of complex spatial trends (Borcard et al. 1992).

Estimates of atmospheric nitrogen deposition total annual wet deposition (kg N ha^{-1} yr^{-1}) between 1986 and 1993 were obtained for three sites in the southeast of England and weighted-averages based on the distances from Cavenham used to predict the annual nitrogen deposition on the experimental site.

Multivariate analysis

Species-environment and sample (experimental plots in this case)-environment relationships were investigated by Canonical Correspondence Analysis (CCA) using CANOCO (ter Braak 1988a,b, 1990). Here, the species data (biomass or cover), was used without the down-weighting option. The environmental variables included control treatments relevant to each time period as nominal variables, and climatic, spatial effects and elapsed time since treatment, as continuous variables. The 'forward selection' procedure within CANOCO was used to select those environmental variables which add significantly to the explanation of the observed species variance. There can only be as many constrained axes as there are environmental variables and CCA analysis with less than four variables are thus hybrid, being partially unconstrained. Eliminating variables from the data that did not add significantly to the explanation of the variation in species abundance gave more realistic estimates of the variation explained (Borcard et al. 1992).

Within each Phase a separate CCA analysis was done for each environmental variable to determine the fraction of variation explained by that variable alone. The ratio of the eigenvalue of the constrained axis and the total inertia (which is the sum of all eigenvalues in a correspondence analysis) gave the variation explained by the individual variable in question. The significance of each variable was tested with a Monte Carlo test (with 99 unrestricted permutations). The variation partitioning was then analysed using combinations of data sets for each Phase (Borcard et al. 1992; Økland & Eilertsen 1994).

Results

The effects of treatment on the bracken biomass has been reported by Marrs et al. (1998a). All bracken control treatments had some effect although the persistence and overall impact differed (Fig. 2). Cutting had the most effect overall, but took longer to produce a sustained effect, whereas spraying asulam had an instant effect, but there was relatively rapid recovery. Where treatments were continued or repeated the control was sustained, but where control treatments ceased after 6 yr there was a relatively rapid recovery.

The success of the treatments on *Calluna* after 10 yr showed that all were successful to some degree, but best cover was obtained where bracken had been well controlled with the cut twice yearly treatment and *Calluna* seed had been applied (Fig. 3). The results showed clearly that a late-successional bracken invasion could at least be severely reduced and *Calluna* re-established.

However, in 1991 it was noticed that almost all of the *Calluna* had died out and there was a change in vegetation towards a grass heath. The multivariate analysis of the Phase I data gave a reasonably good model with eigenvalues of 0.35, 0.15, 0.11 and 0.05 for the first four axes respectively. In Phase II the model fitted explained much less of the variation, with eigenvalues of 0.18, 0.12, 0,.071 and 0.04 for the first four axes. As the experiment progressed the effects of management became less important, and the effects of climate, bare ground (a surrogate measure of rabbit activity which had increased during the 1980s) and spatial position became much more important (Marrs et al. 1998b; Marrs & Le Duc in press).

Discussion

The results from this study showed that success or failure occurred depending on the time scale over which success was judged. In the short term, we were able to demonstrate that the initial objectives could be achieved relatively easily. There was reasonable and in some cases good bracken control, which could be sustained over the 18-yr period. There is no reason to believe that this success could be sustained indefinitely assuming that the management effort is continued. Moreover, it was possible to establish *Calluna* in reasonable amounts and certainly sufficient to meet the desired conservation objectives.

However, over the longer time scale of 18 yr the restoration objectives *sensu stricto* have not been achieved because of the large scale *Calluna* dieback noted in 1991. As a result there has been a shift in the community from one dominated by *Calluna* to a typical Breck grass flora (Watt 1940, 1981a, b; Dolman & Sutherland 1992). Whilst this

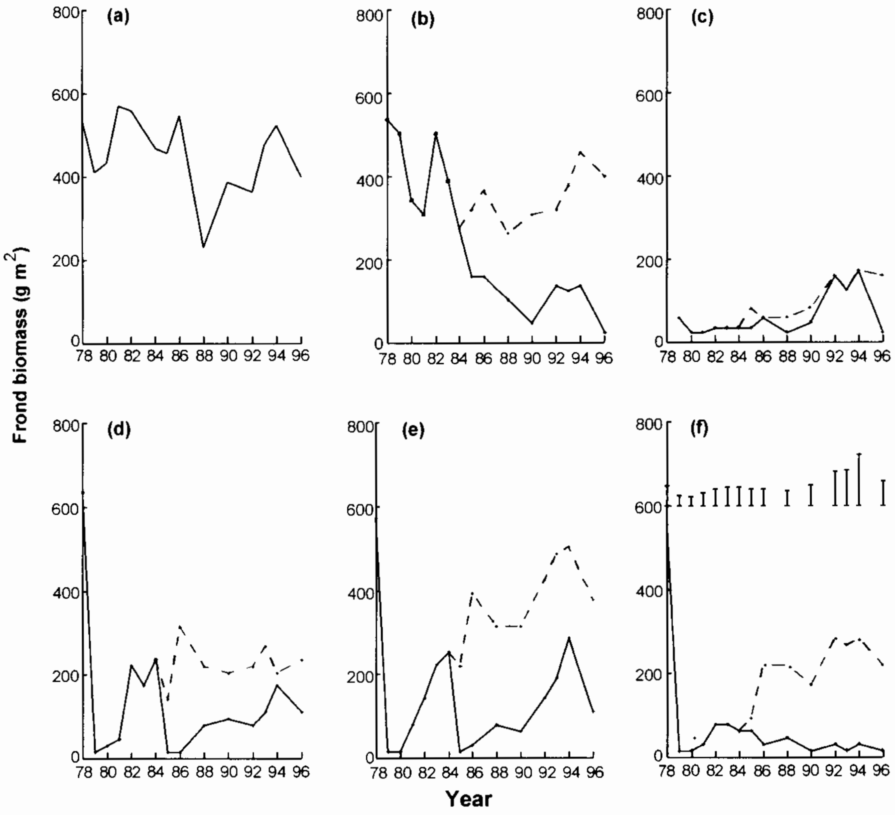

Fig. 2. Changes in bracken biomass over an 18-yr period at Cavenham Heath: (**a**) untreated, (**b**) cut once yearly, (**c**) cut twice yearly, (**d**) asulam 1978, 1984, 1990, (**e**) asulam 1978, 1979, 1984 and 1990, (**f**) asulam 1978 plus cutting once yearly. Dashed line indicates treatments stopped after 1984. Vertical bars (**f**) show LSD-values for each year.

objective is not the desired one it is deemed of more conservation value than the original bracken-dominated ecosystem. Thus, from a management point of view this secondary target can be deemed semi-successful.

However, it is worth speculating on the reasons why *Calluna* died out and there was a change towards grass heath. The variation partitioning suggests that in Phase I the management treatments applied by the experimenter were the major factors controlling the vegetation, and time and space were perhaps secondary. It was noted that after 6 yr that there was substantial development of clonal species in certain plots (Marrs & Lowday 1992), especially in unseeded treatment and this might have a 'founder effect' on subsequent vegetation trajectories. In Phase II the applied management treatments had very little effect on the vegetation trajectories with the main factors controlling vegetation being climate, effects of rabbit grazing and spatial effects. The spatial effects reflect those noted in Phase I. Inspection of the climate and nitrogen deposition data show that immediately before the *Calluna* dieback the site experience greater than average inputs of atmospheric nitrogen deposition and winter minimum temperatures, and lower than average spring rainfalls. Moreover, the summers of 1990 and 1991 experienced greater than average summer temperatures. It is postulated that the elevated nitrogen and lower rainfall perhaps allowed the *Calluna* to grow well over winter, but it could not survive extreme spring drought and summer heat. *Calluna* is well known to exhibit such dieback events in Breckland (Pickworth-Farrow 1925; Marrs 1986, 1993).

This study highlights the danger of extrapolating from short-term experiments to making longer-term predictions. It also indicated that even when applying management treatments the applied restoration ecologist can 'lose control' and the vegetation can start responding to factors outside the experimenters control. However, it also indicates that even when this occurs the data can be used to elucidate and refine ideas on succession.

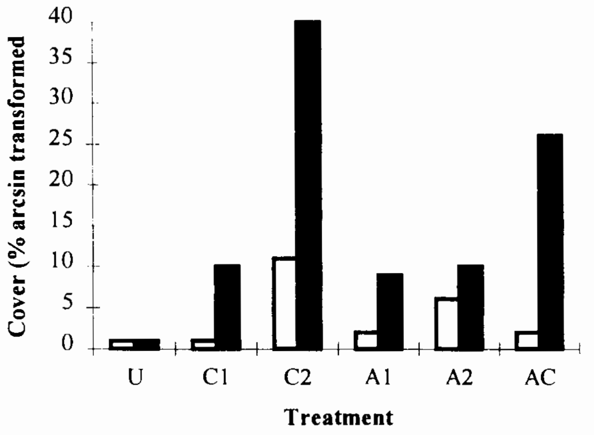

Fig. 3. *Calluna* cover in 1988 in the bracken treated plots at Cavenham Heath: U = untreated; C1 = cut once yearly; C2 = cut twice yearly; A1 = asulam 1978, 1984, 1990; A2 = asulam 1978, 1979, 1984 and 1990; AC = asulam 1978 plus cutting once yearly; open bars = unseeded; shaded bars = seeded.

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Vegetation succession in a salt-water lagoon in the polder Beltringharder Koog, German Wadden Sea

Wolfram, Ch.*, Hörcher, U., Lorenzen, D., Neuhaus, R., Aegerter, E. & Dierßen, K.

Institute of Botany, Department of Vegetation Science, Kiel University, Olshausenstraße 40, D-24098 Kiel, Germany;
**Fax +494318801522; cwolfram@bot.uni-kiel.de*

Abstract. In 1987 a salt-water lagoon system of 846 ha was created as part of the polder Beltringharder Koog (3342 ha). The main nature conservation target was to restore tidal flats and salt marshes comparable to Wadden Sea habitats in order to compensate for the embanked area. Permanent plots and vegetation mapping were used to study vegetation succession. After the embankment a lowered groundwater level, the presence of large unflooded tidal flats and desalination of the soil had led to changes of the salt-marsh vegetation. Former salt marshes had changed to glycophytic grasslands with *Cirsium arvense* and *Epilobium hirsutum* stands. Former tidal flats were covered with *Suaeda maritima, Spergularia maritima, S. salina* and *Salicornia ramosissima.* After the introduction of a simulated tidal flooding regime the invasion of glycophytes stopped. A typical salt-marsh zonation with a *Salicornia* zone, *Puccinellia* zone and *Elytrigia atherica* zone established. Newly found red list plant species were *Atriplex pedunculata* and *Bassia hirsuta.*

The 10-yr-old semi-natural salt-water lagoon could not compensate for the loss of former Wadden Sea habitats, for example as feeding area for wetland birds. Nevertheless the newly developed salt marshes became a habitat for endangered halophytes and an important resting area for wetland birds during high tides.

Keywords: Embankment; GIS; Halophyte; Nature conservation; Restoration; Salt marsh; Semi-natural.

Nomenclature: Stace (1997) for vascular plants; Oberdorfer (1994) for syntaxonomy.

Introduction

Over the last few centuries large areas of salt marshes and mud-flats of the German Wadden Sea have been embanked. In the past, new polders were used as farmland (Bantelmann 1966; Behre 1994). During the last decades, the ecological system of the Wadden Sea has been recognized as an extraordinary and highly specific and endangered habitat for many plant and animal species. Effects of the embankments for coastal protection, land use and new settlements have been weighed against nature conservation. In 1987 the embankment of 33.4 km^2 of the Nordstrand Bay – part of the Schleswig-Holstein Wadden Sea – was finished and became the new polder Beltringharder Koog (54°33' N, 8°54' E). The main purposes were to reduce erosion processes of tidal creeks and shorelines and to shorten the dikeline for coastal protection (Anon. 1981). When the bay was embanked 845 ha of intensively grazed salt marshes and 2450 ha of mud flats were disconnected from tidal flooding (Neuhaus 1997; Wolfram et al. 1998). Before the embankment the Nordstrand Bay had been one of the largest unfragmented salt marsh areas and one of the most important feeding areas for wetland birds migrating along the East Atlantic Flyway on the northern German Wadden Sea coast (Hötker & Kölsch 1993; Hötker 1994). To compensate for the loss of these habitats the new polder Beltringharder Koog was preserved as a nature reserve area. One of the main targets of nature conservation was to restore tidal flats and salt marshes comparable to Wadden Sea habitats in a semi-natural salt-water lagoon system. To establish this lagoon system ca. 846 ha were separated from the rest of the polder by dams. The salt water of the lagoon is connected with the Wadden Sea by two sluices. This paper will focus on vegetation succession and management problems of this semi-natural salt-water lagoon system.

The following questions will be answered: Is it possible to restore a wadden-like habitat in a polder? How will the vegetation succession continue? Are there differences between the vegetation of the semi-natural salt-water lagoon and other salt marshes? Is the vegetation comparable to other semi-natural salt-water systems in polders?

Methods of documentation of succession

Vegetation changes were studied every year on permanent plots of 4 m^2. Vegetation mapping was carried out in 1987, 1992 and 1996 (Wolfram et al. 1998). A GIS (Geographic Information System) analysis was used to discover vegetation replacement in the salt-water lagoon area. The water-level of the lagoon was measured by a tide-gauge.

Results

Hydrology and tidal regime of the salt-water lagoon

Shortly after the embankment the tidal range was lowered from 3.4 m to zero. This led to large areas of unflooded mud flats. The soil of the former salt marshes and the mud flats dried out. During the first three years, the water level of the lagoon was not regulated and varied, sometimes more than 2 m per month. Since 1990 a tidal range of 0.2 to 0.4 m has been tested. The tidal range generally had to be restricted to 0.2 m because of the erosion near the sluice gates. After rebuilding of the sluice gates in 1994 it was possible to have a controlled tidal in- and outflow during the natural tides of the Wadden Sea. It was possible to get a tidal range of ca. 0.4 m but the most frequent tidal range was ca. 0.3 m or less. To promote inundation of the higher salt marshes comparable to stormfloods, an artificial buildup of salt water during three tides with a range of 0.8 m was introduced about twice a month. These stormflood simulations were restricted to the non-breeding period of birds between the 1st of August and the 14th of April every year. The minimum water level of the lagoon was at 0.2 m above sea level and the maximum at 1.0 m above sea level. An area of 378 ha was permanently covered with salt water. In 1996 about 228 ha belonged to mud flats without vegetation.

Vegetation succession

In 1987, the salt-water lagoon system was established on former tidal flats. Only 11.7 % of the area were covered with vegetation: 10.5% *Salicornia dolichostachya* stands, 0.9% *Spartina anglica* stands and only 0.3% *Puccinellia maritima* salt marshes. In the following years vegetation cover and plant species composition changed dramatically. The largest part of former mud flats dried out. Benthic organisms died which led to a high decomposition of organic material. A thick layer of cyanobacteria and algae mats developed. Therefore the invasion of vascular plants was delayed within the first four years. On former salt marshes a species replacement from halophytic to glycophytic vegetation took place during the first five years after the embankment. This process was comparable to the vegetation development in other new polders (cf. Joenje 1978; Brehm 1979). The succession is documented by the species dominance diagrams of two representative permanent plots (Fig. 1). Both plots were placed in the *Salicornia* zone of 1987. Permanent plot A-1 is located 0.89 m above sea level and permanent plot A-3 ca. 1.44 m. Both plots were not flooded during the first 6 yr. In permanent plot A-1 the cover of *Salicornia* increased to a high cover in 1988 (Fig. 1A). In 1989 *Salicornia* was replaced by the perennial salt-marsh grass *Puccinellia maritima*. In the following years desalination of the soil due to rainfall and drought during summer led to increasing cover of glycophytic grassland species. In this case *Poa trivialis* and *Holcus lanatus* could be found – but on other plots, e.g. A-3 (Fig. 1B), also *Cirsium* species occurred. In 1994 stormflood simulations were carried out in order to force the regeneration of upper salt marsh communities on higher elevations and to counterbalance the desalination of the soil. This actually influenced the vegetation up to a level of 1.0 m above sea level. Since the permanent plot A-1 was flooded about twice a month non-halophytic grassland species have been replaced by salt marsh species – mainly *Elytrigia atherica, Juncus gerardii* and *Festuca rubra.* At higher elevations, e.g. permanent plot A-3, glycophytes such as *Epilobium hirsutum, Cirsium arvense* and *Poa* species could persist (Fig. 1B).

The GIS analysis of the vegetation maps from 1987 and 1996 demonstrates a vegetation replacement in space and time. In 1996 ca. 142 ha open mud flats of 1987 were additionally covered with vegetation (Fig. 2A). Almost 70 % of this area was dominated by the halophytic annual vegetation of the *Salicornia* zone forming the new lower salt-marsh vegetation of the lagoon system. 18 ha developed to glycophytic and upper salt-marsh vegetation on artificial sand-islands and dams which had been built in 1988. The development of the old *Salicornia* zone (1987: 89 ha *Salicornetum strictae*, 8 ha *Spartinetum anglicae*) is shown in Fig. 2B. In 1996 only 3.8 % of this area still belonged to the *Salicornietum strictae.* About 34 % was covered by the annual *Salicornietum ramosissimae* (with *Suaeda maritima, Spergularia maritima, Sp. salina, Salicornia ramosissima*) which is typical of summer-dry mud-flats.

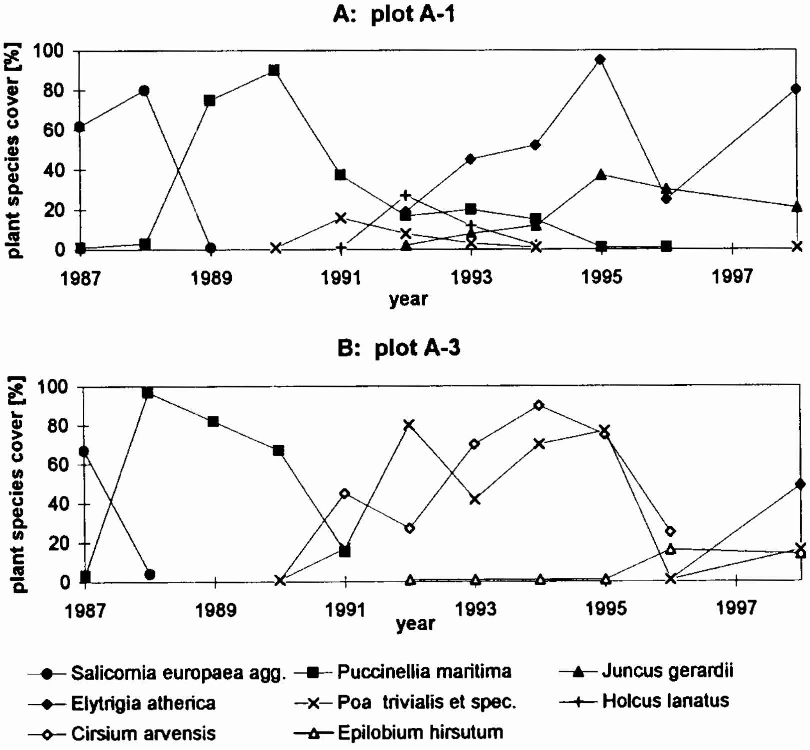
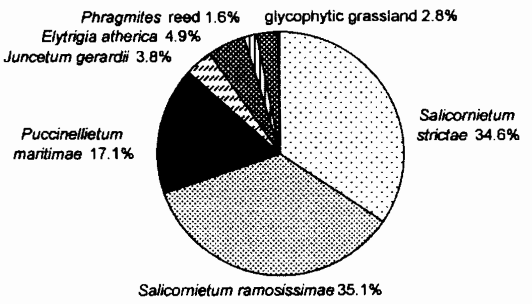


Fig. 1: Succession of plant species in permanent plots on low (**A**) and high (**B**) elevation in salt marshes of the salt-water lagoon Beltringharder Koog/Germany in the years 1987-1998.


A: 142.3 ha open mud-flats of 1987 covered with vegetation in 1996:

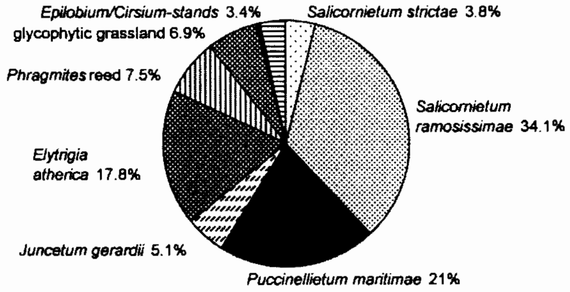

B: The area of the *Salicornia* zone 1987 (96.6 ha) was covered in 1996 with:

Fig. 2. Vegetation types on (**A**) former mud-flats and (**B**) the former *Salicornia* zone in the salt-water lagoon of the Beltringharder Koog 10 yr after the embankment (1996).

44 % of the area developed to perennial salt-marsh vegetation with *Puccinellietum maritimae* in the lower parts and *Juncetum gerardii* and *Elytrigia atherica* stands at higher elevations. About 10% of the area changed to glycophytic grassland or to *Cirsium arvense* and *Epilobium hirsutum* stands. The small *Puccinellia* zone of 1987 was replaced completely by glycophytic vegetation in 1996.

Until 1996 a new typical salt-marsh zonation had established with open mud flats and an annual halophytic *Salicornia* zone (136 ha) within the area of the daily tidal range. Also a perennial *Puccinellia maritima* zone (45 ha) occurred between 0.3 and 0.5 m above sea level. Vegetation which is typical of high salt marshes (35 ha) with *Juncus gerardii* and *Elytrigia atherica* developed on areas above 0.5 m above sea level. Only 15 ha of the unflooded part of the lagoon were covered by glycophytic grasslands, *Cirsium* spp. and *Epilobium* spp. stands, including first shrubs of *Salix cinerea, S.* × *multinervis, Sambucus nigra* and *Crataegus monogyna*. From 1992 onwards *Phragmites australis* expanded into the areas of the *Puccinellia* and *Juncus gerardii* zone. Within 5 yr this species has occupied an area of 9 ha and it is still spreading. The invasion of *Phragmites australis* and *Elytrigia atherica* (5 ha in 1992 to 24 ha in 1996) has changed the structure of the upper salt-marsh vegetation. The cover of vegetation types with a low canopy like the *Juncetum gerardii* and the *Puccinellietum maritimae* was reduced. These processes will continue because the salt marshes are not grazed.

Flora of the salt-water lagoon

Atriplex pedunculata and *Bassia hirsuta* are the newly found highly endangered halophytic Red Data Book species (Mierwald & Beller 1990) of the Beltringharder Koog. In 1998, *Atriplex pedunculata* had its largest population in Schleswig-Holstein in the *Puccinellietum maritimae* of the semi-natural salt-water lagoon system with more than a million individuals. Other protected and rare species were *Atriplex longipes* ssp. *longipes, A. portulacoides, Carex distans, C. extensa, Centaurium littorale, C. pulchellum, Parapholis strigosa, Sagina maritima, S. nodosa* and the moss *Didymodon tophaceus.*

Discussion

Vegetation changes and tidal management

10 yr after the embankment it was possible to restore a typical salt marsh zonation in the salt-water lagoon system by a semi-natural tidal management. But the salt marsh development of the lagoon is still in a dynamic state and further succession will change the proportions of plant communities soon. The invasion of *Phragmites* into the halophytic *Puccinellia maritima* and *Juncus gerardii* zone may cause a replacement of salt marshes by brack water reeds due to biotic interaction. This has also happened in other polders with semi-natural salt-water lagoons in Germany such as the Rantum-Becken, or the Dithmarscher Speicherkoog (Petersen 1987; Lütke Twenhöven unpubl.). The Beltringharder Koog is the only one with a semi-natural tidal system. This could be the chance to establish a permanent salt marsh vegetation within a polder. The salinity of the lagoon water of ca. 21 - 28 ‰ is comparable to the Wadden Sea (Hagge et al. unpubl.). If the growth of *Phragmites* under brack water conditions is restricted to a maximum of soil salinity of ca. 17 or 19 ‰ (Schmeisky 1974; Richter 1987) it should be possible to establish a *Salicornia* zone and a part of the *Puccinellia maritima* zone without *Phragmites* within the area of the tidal range. At a higher elevation *Phragmites* may occur on salt marshes in its terrestrial form. A comparable situation can be found in long-term ungrazed salt marshes on sandy soils, e.g. on the islands Sylt and Amrum and the Eiderstedt peninsula (Hobohm 1986; Neckermann 1987). In the past, most areas of the mainland salt marshes in Schleswig-Holstein have been intensively grazed by sheep (Kiehl 1997) and the salt marsh vegetation was dominated by short grass communities of *Puccinellietum maritimae* and *Juncetum gerardii.* Grazing may be the most important factor to keep away high *Phragmites* reeds from the salt marshes (Raabe 1981). The ungrazed salt marshes of the salt-water lagoon are not comparable to the large area of intensively grazed salt marshes of the former Nordstrand Bay. This means that it was not possible to replace the important former feeding areas for many Wadden Sea birds either (Hötker & Kölsch 1993; Hötker 1997). Nevertheless, the semi-natural salt-water lagoon has become a new but different habitat. Firstly new endangered halophytes occurred and secondly it has become an important resting area for Wadden Sea birds during high tides. In total it was not possible to

compensate for all functions of salt marshes and mud flats of the former Nordstrand Bay by a rather small semi-natural salt-water lagoon.

The value of the salt-water lagoon for nature conservation can be seen in a historical framework. Before embankments were started in the Middle Ages, the Wadden Sea coast had a more dynamic coastline (Behre 1994). Natural salt-water lagoons occurred behind barrier islands, spits or peninsulas. Low surf and water dynamics will have had similar conditions comparable to the semi-natural salt-water lagoon system of the polder. The vegetation with *Salicornia* and *Puccinellia* zones on lower and *Elytrigia atherica* and *Phragmites australis* on higher salt marshes could have been similar. With a high technical expenditure of the tidal management of the lagoon an extraordinary habitat relating to former time coastal habitats may grow. Nowadays no comparable system to the polder Beltringharder Koog exists. A continuous monitoring of permanent plots and repeated vegetation mapping until the vegetation will be in a stable state should give an answer, whether a replacement of wadden-like habitats in polders as a compensation of embankments is acceptable or not.

Conclusion

10 yr after the embankment, restoration management with controlled tidal ranges has created a semi-natural salt-water lagoon system with salt marsh vegetation. The succession of salt marsh vegetation is still going on. In the future the invasion of *Phragmites australis* into the ungrazed salt marsh will probably change large areas into brackish water reeds. This process is comparable to other Dutch and German polders. In general the development of new habitats in the semi-natural salt-water lagoon cannot compensate for the loss of natural Wadden Sea salt marshes. Nevertheless, the newly developed salt-water lagoon has become a habitat for endangered halophytes and an important resting area for wetland birds during high tides. The function of this man-made system is vulnerable and depends on nature conservation management.

Acknowledgements. This work was supported by the local Government of Schleswig-Holstein as part of the coastal protection project 'Ecological Investigation of the Embankment of the Nordstrand Bay'. The project was supported by the Office of Land- and Water Management ALW-Husum, which put the hydrological and elevation data to our disposal. Kathrin Kiehl and Klaus Westensee gave helpful comments on earlier versions of this manuscript.

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Changes in two Minnesota forests during 14 years following catastrophic windthrow

Arévalo, J.R.[1,2*], **DeCoster, J.K**[3], **McAlister, S.**[1] **& Palmer, M.W.**[1]

[1]*Department of Botany, Oklahoma State University, Stillwater, OK 78078, USA;* [2]*Departamento de Ecología, Universidad de La Laguna, 38206, La Laguna, Islas Canarias;* [3]*Department of Biological Sciences, Louisiana State University, Baton Rouge, LA 70803, USA*
[*]*Fax +34922318311; E-mail jarevalo@ull.es*

Abstract. We monitored damage, forest structure and tree species composition following a catastrophic windthrow in permanent plots in an oak forest and a white pine forest in central Minnesota. *Quercus borealis* and *Populus grandidentata* dominated the oak forest, and *Pinus strobus* and *Betula papyrifera* dominated the white pine forest prior to the storm. The storm removed 60% of the basal area and 40% of the density of trees in the oak forest, against 80% of the basal area and 60% of the density in the white pine forest. 14 yr after the storm, the basal area of the oak forest was 80% of the basal area before the storm and density increased 65%. At the same time, the white pine forest's basal area was just 43% of that before the storm and the density increased 5%. The number of tree species remained the same in the oak forest, but increased in the white pine forest. Ordination of tree species composition revealed a shift from earlier successional species to later successional species, both as a direct effect of the storm as well as during recovery following the storm. The net effect of the disturbance was to accelerate the successional processes, removing earlier successional species and providing few opportunities for other tree species to become established.

Keywords: Basal area; Convergence; Density; Disturbance; LTER; Succession

Introduction

Windstorms are an important kind of disturbance in forests (Perry 1994). Catastrophic winds are increasingly under investigation because global climate models predict an increase of severe winds in mid and high latitudes (thunderstorms and tornadoes) and in the tropics (hurricanes) (Overpeck et al. 1990). Wind disturbances offer opportunities to study regeneration of devastated areas as well as effects on forest dynamics (Webb 1988, 1989; Glitzenstein & Harcombe 1988; Abrams & Scott 1989).

Disturbances are reported in general as accelerators of successional processes due to the elimination of earlier successional species and creating new open spaces for other species to become established (Abrams & Scott 1989). In more advanced successional forests, medium-high frequency level of disturbance creates a mosaic of patches of different and successional status, resulting in an increase of vegetation diversity (Pickett & White 1985).

The NE USA have a low rate of extremely strong winds, where return interval of catastrophic winds (hurricanes and tornadoes) is between ca. 1200 (Canham & Loucks 1984) and 1500 yr (Thom 1963). Due to that, windthrows, with a rate of once every 100-150 yr (Moore 1988), represent a basic element in the understanding of forest structure and dynamics (Foster 1988).

We monitored changes in basal area, density and tree species composition in two Minnesota forests. The objectives of the study are to document trends in forest structure, composition, and diversity, and to interpret these trends in light of the successional status of the forests.

Material and Methods

Study site

We conducted our study in the Cedar Creek Natural History Area (CCNHA), which is one of the U.S. National Science Foundation's Long Term Ecological Research (LTER) sites, located in Anoka and Isanti Counties, Minnesota. CCNHA is located on the Anoka sand plain. On July 3, 1983, straight-line winds caused substantial mortality in a number of forests throughout CCNHA. We established permanent plots in two different sites: an oak forest dominated by *Quercus borealis*, *Q. alba*, *Q. macrocarpa* and *Populus grandidenta*, and a pine forest dominated by *Pinus strobus*. Since *P. strobus* typically colonizes oldfields, and since the white pine forest has the appearance of an even-age structure, we believe this site is of an earlier successional stage than the oak forest. Neither of the sites had any clear signs of cutting or other major recent anthropogenic disturbance.

Sampling

Two weeks after the storm, we established a 50 m × 50 m plot in the oak forest, and a 60 m × 50 m plot in the pine forest. We mapped the locations of all living and dead stems > 2.5 cm DBH, by species. We also counted, but did not map, saplings (individuals > 1.3 m in height but < 2.5 cm DBH) in each quadrat. Since it was usually obvious when the dead trees were killed during the windstorm, we were able to reconstruct pre-storm, as well as post-storm, forest structure. We remapped the plots in 1990, 1993 and 1997.

Data analysis

We used Detrended Correspondence Analysis (DCA, Hill & Gauch 1980) to examine whether species composition changed through time, whether the two sites behaved similarly, whether the initial effect of the disturbance was to accelerate succession, and whether the two sites converged in composition through time. We performed separate analyses for the two sites using tree basal area.

We performed all multivariate analyses with CANOCO (ter Braak 1987). Except where otherwise noted, statistical methods followed Zar (1984).

Table 1. Basal area (m^2/ha) and densities (ind/ha) of trees in the Oak forest along 14 yr of succession. Total values are also indicated.

	1983 before storm		1983 after storm		1990		1993		1997	
	B.a.	Dens.	B.a.	Dens.	B.a.	Dens.	B.a.	Dens.	B.a.	Dens.
Acer negundo	0.0137	8.00	0.0137	8.00	0.0944	48.00	0.1539	48.00	0.1646	28.00
Acer rubrum	0.1513	56.00	0.1430	48.00	0.8200	360.00	1.5777	600.00	2.5384	708.00
Amelanchier spec.	0.1088	64.00	0.0835	48.00	0.1166	64.00	0.1056	60.00	0.0516	16.00
Betula papyrifera	2.4433	128.00	0.7307	48.00	0.8997	64.00	0.5844	64.00	0.6832	64.00
Cornus alternifolia	-	-	-	-	0.0049	8.00	0.0053	8.00	-	-
Corylus americana	-	-	-	-	-	-	0.0036	4.00	-	-
Fraxinus nigra	0.8024	172.00	0.6828	148.00	1.3811	292.00	1.9584	384.00	2.3362	376.00
Ilex verticillata	-	-	-	-	-	-	-	-	0.0023	4.00
Pinus banksiana	4.6468	64.00	-	-	-	-	-	-	-	-
Pinus resinosa	0.6448	8.00	-	-	-	-	-	-	-	-
Pinus strobus	1.5808	24.00	0.1606	8.00	0.4344	8.00	0.5504	8.00	0.7285	8.00
Populus grandidentata	4.0061	120.00	0.2314	36.00	0.4505	132.00	0.6892	128.00	0.8368	92.00
Prunus serotina	0.4184	68.00	0.3188	56.00	0.8222	236.00	0.8775	212.00	1.1066	180.00
Prunus virginiana	0.0388	36.00	0.0164	16.00	0.0337	20.00	0.0257	16.00	0.0247	16.00
Quercus alba	0.2238	40.00	0.2238	40.00	0.3700	44.00	0.4895	60.00	0.5881	60.00
Quercus ellipsoidalis	12.9681	248.00	8.7360	160.00	10.9118	164.00	11.9369	188.00	13.5847	172.00
Quercus macrocarpa	0.8755	64.00	0.8755	64.00	1.0485	92.00	0.6762	96.00	0.7602	92.00
Vitis riparia	-	-	-	-	-	-	-	-	0.0076	12.00
Ulmus americana	0.0491	4.00	0.0491	4.00	0.0725	4.00	-	-	-	-

Results

The pre-storm basal area and the density of the oak forest were 28.97 m^2/ha and 1104.00 ind/ha respectively. In the oak forest the dominant species were *Quercus borealis*, *Populus grandidentata* and *Pinus banksiana*. The pre-storm basal area and density of the white pine forest was 41.94 m^2/ha and 1069.20 ind/ha. The dominant species was *Pinus strobus*, and with much less importance (Tables 1 and 2).

The two forests differed in their initial response to disturbance, and their recovery following disturbance (Fig. 1). The oak forest lost 60% of the basal area and recovered 40% during the succession, while the pine forest lost 80% of the basal area and recovered only 20% (Fig. 1a). Tree density in the oak forest quickly increased to well above the initial values, and experienced a slight decline from 1993 to 1997. In contrast, in the pine forest, tree density approximately returned to pre-storm levels by 1993 (Fig. 1b). The sapling density decreased after 6 yr of succession in the oak forest, due to mortality as well as recruitment to tree size classes; we did not observe this pattern in the pine forest (Fig. 1c).

The two forests also differed in how species richness changed through time. Tree species richness following the storm was unchanged in the oak forest while it increased by five species in the pine forest (Table 1 and 2). Prior to the storm, *Q. borealis* was the dominant species of the oak forest and it remained dominant immediately after the storm and after 14 yr of succession. The basal area of *Q. borealis* was reduced by 37% in the oak forest with similar basal area in the 1997 sampling compared to before the storm. The most numerous species in the oak forest prior to the storm

Table 2. Basal area (m^2/ha) and densities (ind/ha) of trees in the Pine forest along 14 yr of succession. Total values are also indicated.

	1983 before storm		1983 after storm		1990		1993		1997	
	B.a.	Dens.	B.a.	Dens.	B.a.	Dens.	B.a.	Dens.	B.a.	Dens.
Acer negundo	0.0202	9.90	0.0202	9.90	0.1679	42.90	0.2810	49.50	0.4544	49.50
Acer rubrum	0.0540	13.20	0.0330	9.90	0.1664	49.50	0.3248	62.70	0.6053	62.70
Amelanchier sp.	-	-	-	-	0.0020	3.30	0.0052	6.60	0.0039	3.30
Betula papyrifera	5.1361	128.70	1.5327	39.60	1.5672	39.60	0.6404	56.10	0.8339	85.80
Cornus alternifolia	0.0146	9.90	-	-	0.0022	3.30	0.0114	13.20	0.0120	9.90
Fraxinus nigra	0.1902	89.10	0.1623	79.20	0.6029	155.10	0.9235	165.00	1.2070	161.70
Ilex verticillata	0.0034	3.30	-	-	0.0058	9.90	0.0080	13.20	0.0048	6.60
Pinus strobus	36.2622	640.20	10.1999	178.20	11.5766	204.60	12.8287	214.50	12.8419	207.90
Populus grandidentata	0.0354	9.90	0.0317	6.60	0.0573	9.90	0.0756	6.60	0.0630	3.30
Prunus pensilvanica	0.0134	3.30	0.0134	3.30	0.0325	3.30	0.0496	6.60	0.0545	3.30
Prunus serotina	0.1851	135.30	0.1067	85.80	0.4652	184.80	0.7511	194.70	0.9240	141.90
Prunus virginiana	0.0068	6.60	0.0041	3.30	0.0117	6.60	0.0127	3.30	0.0228	6.60
Quercus alba	-	0.00	-	-	0.0313	26.40	0.0721	36.30	0.1284	36.30
Quercus ellipsoidalis	0.0027	3.30	0.0027	3.30	0.0727	56.10	0.2016	135.30	0.5283	231.00
Quercus macrocarpa	0.0062	3.30	0.0062	3.30	0.0342	13.20	0.0530	19.80	0.0876	19.80
Rhamnus cathartica	-	-	-	-	-	-	0.0062	6.60	0.0145	9.90
Rhamnus frangula	-	-	-	-	-	-	0.0022	3.30	0.0062	6.60
Rhus typhina	-	-	-	-	0.0251	26.40	0.0565	33.00	0.0668	23.10
Ulmus americana	0.0152	9.90	0.0059	6.60	0.1360	42.90	0.3382	49.50	0.3423	33.00
Vitis riparia	-	-	-	-	-	-	0.0128	19.80	0.0157	16.50
Zanthoxylum americanum	0.0018	3.30	0.0018	3.30	0.0043	6.60	0.0071	9.90	0.0114	13.20
Total	41.94	1069.20	12.12	432.30	14.96	884.40	16.66	1105.50	18.22	1131.90

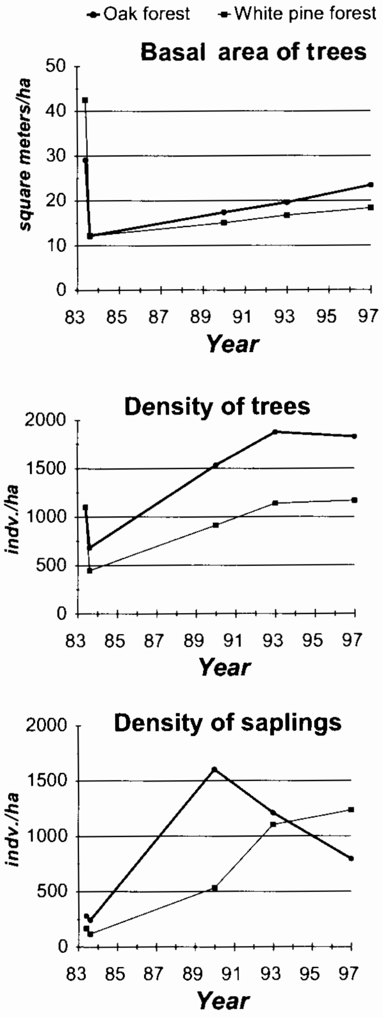


Fig. 1. Tree basal area (**a**), tree density (**b**) and sapling density (**c**) as a function of time since the windstorm. The initial decline in 1983 represents the direct effects of the storm.

were *Q. borealis* and *P. grandidentata*. *Acer rubrum* and *Fraxinus nigra* have replaced them after the storm (Table 1).

In the pine forest *P. strobus* was the dominant species in terms of basal area. It also remained dominant immediately after the storm and throughout the study. *P. strobus* lost 60% of its basal area during the storm. After 15 yr the basal area of *P. strobus* did not recover its pre-storm levels. *P. strobus* remained numerous, but *Prunus serotina* and *Q. borealis* had similar densities (Table 2).

Codominant species (*B. payrifera*, *P. grandidentata* and *P. strobus* in the oak forest and *B. papyrifera* in the pine forest) were more affected and did not recover their codominance after 15 yr.

Ordination of both sites through time (based on basal area) showed a strong site effect on the first axis, with species typical of the pine forest on the left, and species typical of the oak forest on the right (Fig. 2). The second axis appeared to be a temporal effect, with species that increased through time at the top, and those which decreased at the bottom. Note that the initial effects of the disturbance (i.e. comparing the 1983 site scores before and after the storm) are in the same direction as the change in later years. This means that the best-surviving species also grew well following the storm.

Discussion

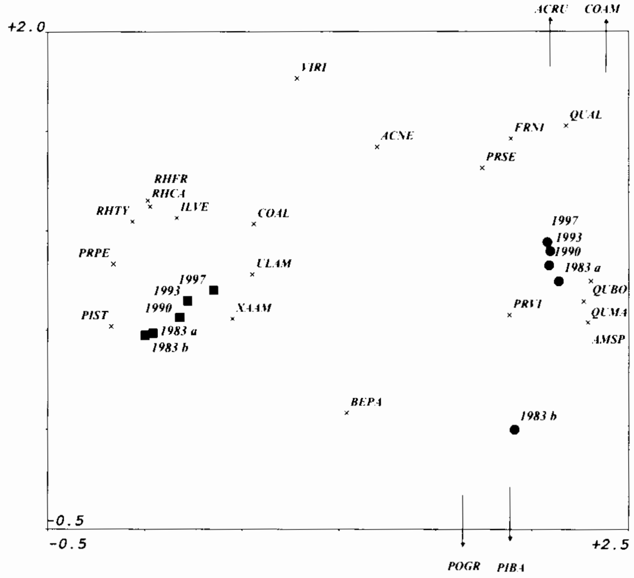
Although tree species richness did not change much in the oak forest, it increased in the secondary pine forest. Tree richness tends to reach a low point in the middle of secondary forest succession, and then increase as the forest enters a steady-state (Bormann & Likens 1978, but see Perry 1994). It is possible that by releasing juveniles that were competitively suppressed by the canopy, the windstorm accelerated the inevitable increase in diversity.

In the oak forest, the two most shade-tolerant species, *Quercus borealis* and *Acer rubrum* almost recovered or even increased their basal area after 14 yr, and also *A. rubrum* has the greatest basal area after 14 yr. *A. rubrum* has

Fig. 2. Species and site scores for the DCA axes based on tree basal area (eigenvalues 0.731 and 0.053; cumulative % variance of species data of both axes was 82.7%). Circles indicate the oak forest and squares the white pine forest (indicating the sampling year; b = before the storm; a = after). Axis 3 (not shown) did not reveal interpretable patterns for species of sites; its eigenvalue = 0.009.

Abbreviations for species names:

ACNE	*Acer negundo*	ACRU	*Acer rubrum*
AMSP	*Amelanchier* spec.	BEPA	*Betula papyrifera*
COAL	*Cornus alternifolia*	COAM	*Corylus americana*
FRNI	*Fraxinus nigra*	ILVE	*Ilex verticillata*
PIBA	*Pinus banksiana*	PIST	*P. strobus*
PRPE	*Prunus pensylvanica*	PRSE	*P. serotina*
PRVI	*P. virginiana*	POGR	*Populus grandidentata*
QUAL	*Quercus alba*	QUBO	*Q. ellipsoidalis*
QUMA	*Q. macrocarpa*	RHCA	*Rhamnus cathartica*
RHTY	*Rhus typhina*	ULAM	*Ulmus americana*
VIRI	*Vitis riparia*	XAAM	*Zanthoxylum americanum.*



a high rate of asexual regeneration that may explain its high density. Canham & Marks (1985) considered *A. rubrum* to be a climax species that depends on pulses of resources produced by small-scale disturbance.

Although *Pinus strobus* decreased dramatically after the storm in the white pine forest, and recovered very little, it continued being the dominant species in the pine forest. However, the current rapid increase in *Prunus serotina*, *Q. borealis*, and other more shade-tolerant species, implies that *P. strobus* will soon be replaced.

In the late successional oak forest, disturbance did not cause an extreme change in the structure. In the white pine forest, however, changes are more dramatic and the recovery of basal area and density is slower. Physiognomy, structure (age, height and density), and compositional characteristics of the vegetation mosaic explains the difference between the later and earlier successional stand.

The net effect of the disturbance was to accelerate succession by removing large early successional trees, at least in the white pine forest. Windthrows could provide establishment opportunities for other tree species, especially in earlier successional stands. This point of view has been strongly supported in various studies (Dyer & Bair 1997; Glitzenstein & Harcombe 1988; Abrams & Scott 1989; Glitzenstein et al. 1986), and is contradictory to Clements' (1916) paradigm, according to which disturbance largely interrupts and reinitiates seral development.

The study of successional convergence is greatly affected by temporal and spatial scale as well as the sampling design (Lepš 1991). It is therefore difficult to know whether our observation of a slight successional convergence between the two forests is a general phenomenon. It is not possible to untangle whether the convergence between our sites would have occurred without the disturbance.

This study offers some information about the effect of wind disturbance in the vegetation and a secondary succession analysis. If the global warming models are confirmed, the boreal forest dynamics could be altered by the beginning of the next century (Overpeck et al. 1990) due to these kind of disturbances. The accumulation of information about wind disturbances could be essential for the preservation of certain forests.

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Indicators and constraints for autogenic return to original forest vegetation in the Cévennes

Aronson, James, Gondard, Hélène, Grandjanny, Michel & Romane, François*

CEFE-CNRS, 1919 route de Mende, 34293 Montpellier Cedex 5, France;
**Fax +33467412138; E-mail romane@cefe.cnrs-mop.fr*

Abstract. Are there irreversible 'thresholds' which prevent present vegetation from spontaneously returning to the 'original' vegetation? This question is frequently discussed by researchers and managers of Mediterranean forests and woodlands of southern Europe, which have all been considerably modified by human activities since the last glaciation, ca. 10 000 yr ago, but which may return in some way now agricultural land is being abandoned, especially since the 1950s. According to trends observed, we hypothesized that an autogenic return to the original mixed hardwood-conifer forest dominated by the deciduous oak *Quercus pubescens*, and related species, would be fully possible in mid-altitude zones on more or less acidic soil substrates that have until recently been dominated by cultivated forests or coppice stands of *Castanea sativa*. In this case no 'threshold crossing' would be required for autogenic restoration to take place.

We tested the hypothesis with regard to two critical processes, i.e. (1) seed germination and early sapling establishment in *Q. pubescens* as compared to *Castanea sativa*, under a canopy cover of predominantly *Castanea sativa*, and (2) varying levels of resistance to invasion by an introduced and opportunist species, *Pinus pinaster* in land units of varying ages following agricultural abandonment. The results tend to support the hypothesis, even if local environmental factors largely influenced and modified the processes observed.

Keywords: Autogenic restoration; *Castanea sativa*; Germination; Invasion; Mediterranean climate; *Pinus pinaster*; *Quercus ilex*; *Quercus pubescens*; Vegetation dynamics.

Nomenclature: Tutin et al. (1964-1980).

Introduction

Many authors agree that at the end of the last glaciation (ca. 10000BP) landscapes dominated by chestnut (*Castanea sativa*) at mid-altitudes (ca. 300 - 1100 m) in the Cévennes mountains of southern France was a mixed deciduous oak forest (mainly *Quercus pubescens*, but also *Quercus petraea* and their hybrid ×*Quercus streimi*), with intermingled conifers including pines, junipers and possibly other taxa (Pons et al. 1974; de Beaulieu & Pons 1978; Pons 1981; Arnaud & Bouchet 1995). However, over the past millennia, and especially in the last few centuries, the deciduous oaks and other trees were progressively removed and replaced, especially by *Castanea sativa* tree farms and coppice stands planted on acidic to neutral soils. Similar processes occurred in the *matorral* or *garrigues* woodlands south of the Cévennes, and at lower elevations, mostly on limestone (Reille & Pons 1992; Bonin & Romane 1996; Debussche et al. 1996; Barbéro et al. 1998).

The economic importance of these *Castanea sativa* groves or orchards for nuts, and coppice stands for timber and wood, fluctuated over the centuries and reached a maximum in the middle of the 19th century (Arnaud & Bouchet 1995). Over the past few decades, however, the impact of agriculture has drastically decreased. This trend has been reinforced in the Cévennes because of the attacks of the chestnut blight (*Cryphonectria parasitica*), and more recently as a result of the set-aside land policy of the European Union (Bourdeau 1992). Similarly, *Quercus ilex* coppices in the garrigue zone, long exploited for fuelwood, charcoal and tannin, as well as acorns for livestock, are now increasingly abandoned.

Thus the question arises: 'Quo vadis? Or, what is to be the future of these ecosystems with *Quercus ilex* and *Castanea sativa*? Will they persist or will they progressively return to pre-existing vegetation? In the case of the *Quercus ilex* coppice stands in the garrigue woodlands, where the role of invasive species is minor, we have already shown that *Quercus pubescens* germinates and becomes established more readily than *Quercus ilex*. In this case there is no threshold to prevent a return of the original vegetation (Bran et al. 1990; Li & Romane 1997). In the case of the *Castanea sativa* dominated zones, experimental results obtained (Romane et al. 1992; Bacilieri et al. 1993, 1994) led us to hypothesize that spontaneous recovery by the prehistoric deciduous oak forest was possible. We analysed two critical vegetation dynamics processes to test this hypothesis: (1) comparative germination of the formerly dominant *Quercus pubescens* in *Castanea sativa*-dominated ecosystems on acidic and neutral soils, and (2) resistance to exogenous species that might compete with the oaks, and the chestnut, for light and other resources on land units in various stages of agricultural abandonment.

Germination and survival: *Quercus* vs. *Castanea*

Materials and Methods

We conducted a germination trial at two climatically contrasting sites in the Gard region of southern France:

1. Tourgueille (3° 40' 35" E, 44° 7' 30" N; rural district of St. André-de-Valborgne; 740 m a.s.l.), in the transitional zone between the Mediterranean and Atlantic climate zones. Estimated mean annual rainfall is 1600 mm, and mean annual temperature is about 10.0 °C (Canet unpubl.);

2. Falguérolles (3° 49' 58" E, 44° 1' 34" N, near Colognac, 580 m a.s.l.) with a more Mediterranean climate. Estimated mean annual rainfall is 1400 mm, and mean annual temperature is ca. 12.0° C (Canet unpubl.). The germination trial was conducted (Bouchet 1993) in cages with a 5 mm ×

5 mm metallic wire mesh partially buried 20 cm deep to deter birds, wild boars, livestock and small mammal granivores. We sowed 50 *Quercus pubescens* acorns and 50 *Castanea sativa* nuts in each of four 1-m^2 plots (i.e. one fruit/dm^2). We sowed at the end of October by burying the fruits just below the soil surface after removing all leaf litter to be able to observe seedling emergence. Initially, the experimental design was set up 2 × in Tourgueille (T) and in Falguérolles (F) , but wild boars overturned the cages in one of the Falguérolles sites.

Results and Discussion

In site Tourgueille I, seedling survival rate after one year of observation showed (Table 1) that *Castanea sativa* survived (48.0%) at a significantly ($p<0.001$) higher rate than *Quercus pubescens* (23.0%). In the Tourgueille II and Falguérolles sites, no significant differences were found between the seedling survival rate of the two species (36.0% and 31.5% in Tourgueille I, and 41.5% and 38.5% in Falguérolles).

The results clearly showed that *Quercus pubescens* is able to germinate in the *Castanea sativa* understorey, even if it is at much lower rates than in *Quercus ilex* coppice stands (Bran et al. 1990; Li & Romane 1997). This tends to support our original hypothesis of a possible autogenic return of *Quercus pubescens* in these *Castanea sativa* dominated ecosystems. Nevertheless, the higher, or nearly equal, germination rate of *Castanea sativa* suggests that *Castanea sativa* can spontaneously maintain populations in these landscapes for a long time to come. This supposition is supported by the observation that there are very few adult, seed-producing *Quercus pubescens* individuals remaining in the *Castanea sativa*-dominated life zones and ecosystems in the mid-altitude Cévennes. Notably, we did not find any evidence in these *Castanea sativa* ecosystems on acid soils of an allelopathic-like process inhibiting the germination of *Castanea sativa* as was demonstrated for *Quercus ilex* germination in *Quercus ilex* coppice stands on limestone (Bacilieri et al. 1993; Panaïotis 1996; Gonzalvez unpubl.).

Resistance to the invasive *Pinus pinaster*

Pinus pinaster was introduced in southern France and western France at the end of the last century for turpentine and timber production. In the Cévennes where it was introduced for gallery timber production, *Pinus pinaster* very quickly escaped cultivation and began invading the Cévennes, among other areas. What is its state today? Is it still invading the remaining *Castanea sativa* stands, or have dynamic processes of autogenic restoration begun to block or resist such invasions? At a third site in the Cévennes, Pallières, we initiated a preliminary study of this problem.

Table 1. Seedling survival rate (%) of *Castanea sativa* and *Quercus pubescens* in the Tourgueille and Falguérolles (Cévennes) sites.

Sites	Tourgueille I	Tourgueille II	Falguérolles
Castanea sativa			
Average	48.0	36.0	41.5
Standard Deviation	4.1	3.6	6.6
Quercus pubescens			
Average	23.0	31.5	38.5
Standard Deviation	3.3	5.0	7.6

Study site and experimental design

The Pallières site (3° 56' 34" E, 44° 4' 28" N; ca. 450 m. a.s.l. is located on deep, sandy granitic substrates with pH 4-5). Mean annual rainfall is 1 100 mm, and mean annual temperature is 12.5° C (Marek unpubl.), which points to a transitional position between Mediterranean and Atlantic climate zones.

The experimental design (Fig. 1) was a 40 m × 100 m rectangle where eight transect lines were established which traversed four successive zones of ca. 25 m each (for measurement we used exactly 25 m):

Zone A (0-25 m): a *Pinus pinaster* woodland planted ca. 50 yr ago;

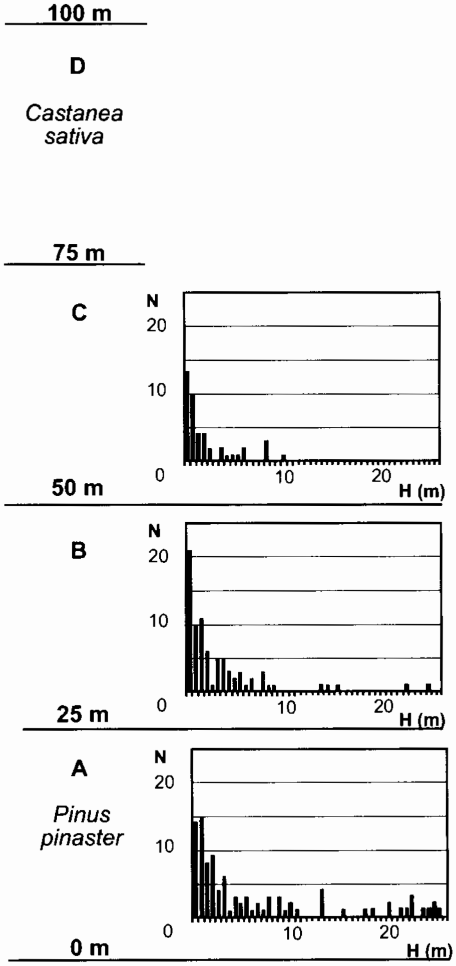

Fig. 1. Left: Sketch of the experimental design of Pallières (Gard, Southern France) to study the dynamics of *Pinus pinaster*. **A** is the *Pinus pinaster* area, **D** the *Castanea sativa* area, **B** and **C** the intermediate areas. Right: Frequency distribution (N) of the height of young *Pinus pinaster* in the areas A, B et C.

Zone B (25 - 50 m): appeared to be a 50-yr old fallow which was heavily invaded by *Pinus pinaster*, probably starting ca. 40 yr ago;
Zone C (50 - 75 m): also an old fallow, but here *P. pinaster* started to invade only 10 - 20 yr ago;
Zone D (76 - 100 m): abandoned ca. 40 yr ago; *Castanea sativa* grove, with very few pines present.

Along the 8 transect lines, 260 squares (2.5 m×2.5 m each) were randomly selected, with an average of 40 squares per transect. We recorded the tree height - known to be correlated with age, and the coordinates of each *Pinus pinaster* individual.

Results and Discussion

Data were analysed separately in each zone (A to D) by a frequency distribution curve of tree heights. In zone A, where 381 pines were recorded, we observed a high number of large individuals whose size ranged from 18.0 to 23.5 m in height, i.e. 40 - 50 yr old (bottom of Fig. 1). These are probably individuals of the first generation, and intentionally planted. In this zone A, a second group of individuals ranged from 12 to 16 m in height (25 - 35 yr old), probably belonging to the second generation. A third generation was also observed (4 - 9 m, 15 - 20 yr) as well as a fourth one (less than 4.0 m).

In zone B, the number of tall pine trees decreased as well as the number of individuals in younger generations (middle of Fig. 1). In contrast, the number of young saplings was again high; there were 317 individuals in all. In zone C, fertile individuals (i.e. >5 m) became rare and were all < 9.5 m tall. There were only 196 *P. pinaster* individuals in all. In zone D, where *Castanea sativa* trees dominated, there were only 25 *P. pinaster* individuals present and their maximum height was 0.5 m.

These results suggest that the invasion by *P. pinaster* was slow because there were only one or two generations in zone C. If this invasion would have been quicker we would have observed three or four pine generations in this zone, just as in zones A and B. This can be asserted since the jay (*Garrulus glandarius*) and other animals known to disperse pine (and oak) seeds are abundant in the area (Glutz von Blotzheim & Bauer 1993; Cramp & Perrins 1994).

The horizontal pattern of *P. pinaster* individuals in the 4000 m^2 study area supported the idea that the pine invasion proceeded slowly at the border of the first pine woodlot, i.e. only 30 - 40 m over a period of ca. 50 yr. Similar results have been reported for coniferous vegetation in other parts of the Mediterranean region. For example, Acherar et al. (1984) found that 91.8% of *Pinus halepensis* seeds fell to the ground less than 12 m from the mother trees and 97.0% less than 24 m. Trabaud & Campant (1991) also found that 94% of the seeds of *Pinus nigra* ssp. *salzmannii* fell less than 14 m from the mother trees. This rather short-range dissemination of *P. pinaster*, as well as the decreasing speed of this invasion, has been recently confirmed, also in the increasingly rare open areas (Pillet unpubl.; Shater unpubl.).

Concluding remarks about the sustainability of the chestnut ecosystems

The available pieces of the jigsaw describing the vegetation dynamics in this Cévennes region where human influence is drastically decreasing, allow us to say that this dynamics is rather slow considering the time scale of several decades and probably slower than in the nearby garrigue area where *Quercus ilex* is dominant.

It also appeared that the resilience (*sensu* Westman 1986) of these *Castanea sativa* ecosystems was sufficient to enable a return to original forest states (Allen 1989; Aronson et al. 1993). Nevertheless, elasticity of these ecosystems, i.e. the time needed for autogenic restoration to take place following a perturbation (Orians 1975; Westman 1978, 1986), is very low, especially due to the fact that the oaks have been removed almost totally throughout the area to make way for crops or groves during the last centuries. Thus, if full restoration is sought, extra measures to accelerate the process may be necessary. Alternatively, if in some areas at least it is desired to preserve *Castanea sativa*-dominated landscapes and ecosystems, interventions to restrain re-colonisation by *Pinus pinaster* and *Quercus pubescens* will clearly be required.

What about the role of *Pinus pinaster* in this dynamical process? It is difficult to forecast its dynamics in the Cévennes in the long run, as was attempted by Carcaillet et al. (1997) for the Corsica. Nevertheless, our results show that the speed of invasion of this species was probably slower than that of some decades ago when it first began to escape cultivation in the Cévennes. This process is probably due to the fact that the vegetation is denser now than when *P. pinaster* was first introduced.

However, an unknown factor remains: fire. Many authors consider that this factor is very important in *P. pinaster* dynamics (Carcaillet et al. 1997) and also for other pine species (Bergeron et al. 1997). Nevertheless, it appeared to us that the dynamics of *P. pinaster* could not lead to a 'paraclimax' in the Cévennes of the same type of those described by Barbéro et al. (1998), this because of the results obtained with the *Quercus pubescens* germination trial.

Additional pieces of the puzzle that will need to be put in place in order to predict, and advise land managers dealing with the future of these ecosystems, clearly include grazing, and the dynamics of seed dispersal by birds, rodents and other mammals. Ultimately, however, decisions will also have to be made on social, especially economic and environmental grounds, in order to develop a proper management of the increasingly abundant, and more or less consciously 'set-aside' lands throughout southern Europe.

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Limitations to species coexistence in secondary succession

Bartha, Sándor[1*], Pickett, Steward T.A.[2] & Cadenasso, Mary L.[2]

[1]*Institute of Ecology and Botany, Hungarian Academy of Science, Vácrátót, Hungary;*
[2]*Institute of Ecosystem Studies, Millbrook, NY, USA;*
[*]*Fax +3628360110; E-mail sanyi@botanika.hu*

Abstract. Constraints on species abundances are examined through time using permanent plot data from the Buell-Small Successional Study. Abundance is represented by the cover of species in 1-m^2 quadrats. Variance of total cover of species was compared to a patch based null model, which assumes no interactions between species. We found significant variance deficit in the total abundance of species in each year of the secondary succession, except the very early stage. The deficit, interpreted as the degree of constraint on abundance, fluctuates over time with no simple trend. We explain this pattern as a competition-based assembly rule in secondary succession. Our results suggest that assembly rules are more clearly expressed during the process of community assembly than in mature communities. If functional groups are considered separately, the variations of their abundances show significant deviation from randomness only during the period when the particular functional group is dominant across sampling units. Extending the 'Three phase' model of Gitay & Wilson (1995), we propose a 'Multiple phase' model for forest succession, that is, a composition of three-phase dynamics of distinct functional groups.

Keywords: Assembly rule; Community structure; Functional group; New Jersey: Permanent plot; Spatially constrained null model.

Introduction

Succession of vegetation is often represented as changes in the abundance of species based on average counts, where the sequence of species is explained by population level attributes (Noble & Slatyer 1980; Pickett et al. 1987; Walker & Chapin 1987; Tilman 1988; Pickett & McDonnell 1989). For practical reasons, most of these works focused on dominant species and attempted to explain the pattern of average abundances over time. Much less is known about the contribution of subordinated species and about the development of multi-species patterns in succession.

Recently, attempts have been made to develop methods for detecting plant community structure compared to null models of independent species distributions (e.g. Watkins & Wilson 1992; Bycroft et al. 1993; Bartha et al. 1995; Lepš 1995; Palmer & van der Maarel 1995; Wilson & Gitay 1995). The aim of these methods has been to find assembly rules (Diamond 1975; Drake 1990; Wilson 1994), i.e. regularities in the collective patterns of species occurrences and abundances which could be the result of interspecific interactions limiting species coexistence. Most studies examining community structure used presence/absence data (e.g. Palmer 1987; Wilson 1989; Wilson et al. 1992, 1995a, b, Klimeš 1995; Mucina & Bartha 1999) and found surprisingly few deviations from randomness. Wilson & Gitay (1995) proposed to examine the spatial patterns in species abundances as a potentially more sensitive indicator of assembly rules.

Here we examine assembly rules for abundance, represented by cover data, from a 33-yr-long permanent plot study of oldfield succession. We expect a general increase in constraints on species coexistence over time due to cumulative effects of mechanisms generating patterns. In parallel with increased deviation from randomness at the community level, more complex patterns of assembly rules are expected at the level of functional groups.

Study site

The Buell-Small Successional Study (BSS) is one of the longest continuous studies of old-field succession. The study site comprises 10 old fields around an old growth forest, the Hutcheson Memorial Forest (HMF), located 11 km from New Brunswick, NJ, USA (40° 30' N, 74° 24' W). The climate is subcontinental temperate with 1120 mm of precipitation distributed evenly throughout the year. Mean annual temperature is 11.7 °C, mean January temperature is 0 °C, mean July temperature is 24 °C. Soil is silt loam, shallow, poorly horizonated, endodynamomorphic soil. Each field contains a regular grid of 48 0.5 m × 2 m permanent plots. The distance between neighbouring quadrats is 10 m. Vegetation was sampled yearly in late July or early August from 1958 to 1979, and in alternate years since 1980. Field C-3, abandoned unplowed in the autumn of 1958 after a crop of soybeans (*Glycine max*) and sorghum (*Sorghum vulgare*), was chosen for the present study. For details about the post-agricultural vegetation trends see Pickett (1982).

Methods

For detecting constraints on the abundances of co-occuring species we used an index that was proposed by Wilson & Gitay (1995). Instead of biomass we used visually estimated cover values. $RV_c = V_{obs}/V_{exp}$, where V_{obs} is the observed variance of total cover per quadrat, and V_{exp} is the variance of cover per quadrat under the null model if there is no interaction among the species. V_{exp} is estimated as the average over 2500 randomizations. The variance deficit is calculated as the difference between $V_{obs} - V_{exp}$. To avoid the obscuring effects of environmental heterogeneity we used a patch-based null model (Watkins & Wilson 1992) with the algorithm of restricted swapping (Wilson & Gitay 1995). Our sampling units formed a rectangular grid. The cover value of a species was exchanged with one of the non-zero cover values of the same species chosen ran-

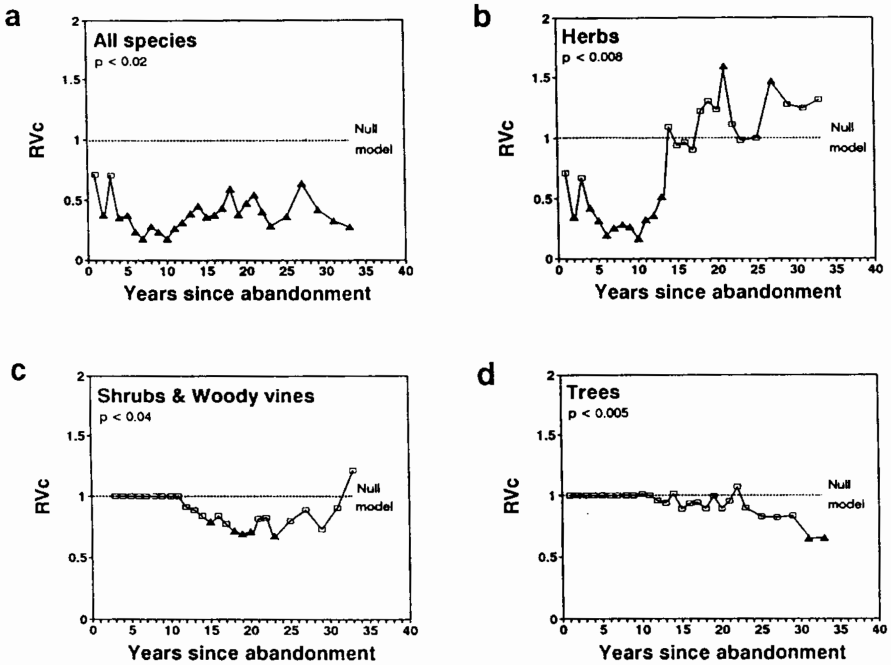

Fig.1. Relative variance of total cover (RV_c) in succession. **a.** Whole community; **b., c., d.** Functional groups analysed separately (▲) significant deviations from the null model (p values are one-tailed probability values) (☐) non-significant.

domly among six quadrats in its closest neighbourhood. 1000 swaps were used in each step of the analyses. The significance (i.e. probability of the observed result under the null model) was obtained from randomization tests as the proportion of the 2500 randomizations in which V_{exp} is more extreme than V_{obs}. RV_c was calculated for the whole community, for herbs, shrubs + woody vines, and trees (i.e. functional groups based on morphology and life form), separately. In the case of the functional groups the total cover of species belonging to each group was calculated. We classified species into functional groups according to Gleason & Cronquist (1991).

Results and Discussion

We found significant variance deficits in the total abundance of species during the 33-yr period of secondary succession, except in the 1st and the 3rd year (Fig. 1a). Our result suggests an assembly rule (i.e. the restricted co-occurrence of species) structuring the plant community in succession. The assembly rule simply means that the abundance of a particular species is limited by the abundance of other species. This rule implies that if one species is locally more abundant, the abundances of other species are restricted, i.e. $V_{obs} < V_{exp}$ (Wilson & Gitay 1995). Lower values of RV_c suggest stronger constraints. With similar methods, but based on the variation of species richness, a temporary loss of community structure (i.e. the relaxation of assembly rules) was reported after disturbance followed by a recovery of structure (Wilson et al. 1992, 1995a). Studies on secondary succession (Palmer 1987; Zobel at al. 1993) found variance deficits in species richness in the early stage (1 - 5 yr) of succession, and in the older stages either a significant increase of variance or randomness. Palmer (1987) and Zobel et al. (1993) applied a complete randomization of observed values among the quadrats (Site model, cf. Watkins & Wilson 1992). Therefore they detected an increasing variance and patchiness of species richness due to the increasing environmental heterogeneity over time. In the present study we used a spatially restricted randomization (a patch model, cf. Watkins & Wilson 1992) that removes the effects of habitat patchiness on the detected variance. This randomization helps to reveal the regularities and constraints on local coexistence within a habitat patch. The difference between non-spatial and spatial null models explains why we got more significant values and a consistent variance deficit over time despite the continuous changes in species composition. The most likely reason for this regularity is a competition-based assembly rule (Wilson & Gitay 1995) that is operating constantly in secondary succession.

If functional groups are considered separately, the consistent patterns disappear and there is more randomness in the variance of abundances (Fig. 1b-d). Each group shows significant RV_c values only during a restricted period, when that particular group is the most abundant in succession, and it dominates most of the sampling units (Fig. 2). During this period the variance of total cover of the functional group is constrained by species within that group, and the contribution of members of other functional groups is probably insignificant. Within the period of dominance of a functional group there is a decreasing trend of RV_c of the group over time, suggesting a cumulative effect of the mechanisms that constrain coexistence of species. This

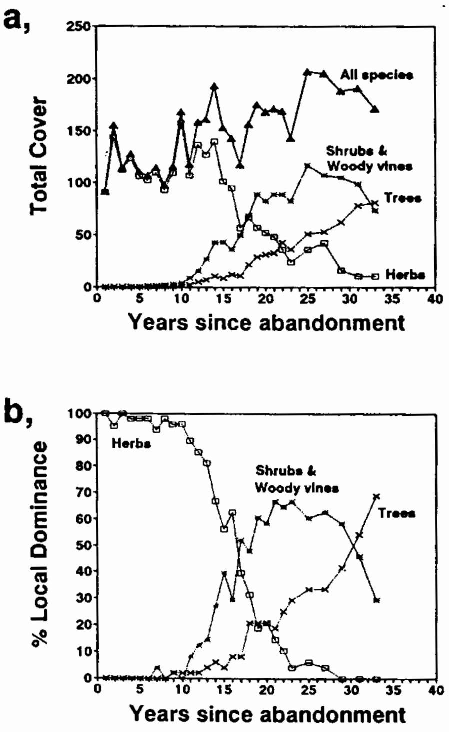

Fig. 2. Abundance of functional groups in succession. **a.** Mean (sub)total cover in 1-m^2 quadrats; **b.** Frequency % of quadrats where the particular functional group is dominant.

trend appears for herbs during the first 10 yr of succession and for shrubs and woody vines between the 10th and the 23th yr. When a functional group is losing dominance there is an increase of RV_c, indicating the relaxation of within-group constraints. Such relaxation happens after the 10th yr for herbs and after the 23th yr for shrubs and woody vines.

Although the most probable explanation for variance deficit in abundance is competition, the interpretation of patterns of RV_c requires caution. For example, the non-significant RV_c values of herbs after yr 13 of succession does not necessary mean that their abundances are unconstrained and no assembly rules are operating. Rather, herbs become subordinated and gradually overgrown by shrubs, woody vines and trees. Interpretation can be improved by analysing permanent plot data (Rejmánek & Lepš 1996) and by taking temporal contingencies into account. In our case, analysing temporal variation of the abundance of herbs reveals a clear decrease over time and suggests that some constraints are operating on their abundance. Significant variance excess of the total cover of herbs was detected in yr 21 and 27 of succession. The most probable explanation is that the abundance of herbs increased locally in small gaps which opened temporally in succession. In certain years (yr 14,16,17,22 and 28) there is no significant variance deficit in any of the functional groups but only in the whole community. This suggests mutual constraint between functional groups. Previous studies found surprisingly few assembly constraints in the spatial variation of guilds (defined by vertical stratification of the vegetation) in mature forests (Wilson 1989; Bycroft et al. 1993; Wilson et al. 1995b). Possible reasons for these results are that within-guild assembly rules are masked by between-guild constraints and such between-guild assembly rules are more expressed during the community assembly e.g. secondary succession than in steady-state forests.

There are numerous studies discussing methodological problems of detecting and interpreting assembly rules derived from presence/absence data (e.g. Bycroft et al. 1993; Bartha et al. 1995; Lepš 1995; Palmer & van der Maarel 1995). Uncertainties of interpretation are considerably decreased by examining abundance instead of presence/absence data, and the application of a patch model helps to remove the effects of environmental heterogeneity (Wilson & Gitay 1995). Our analyses were based on visually estimated cover values instead of biomass which was originally proposed by Wilson & Gitay (1995). Compared to biomass, cover value is a less precise estimate of abundance. Still, we found many significant deviations from the null model, and consistent patterns of deviations over time. Variance tests of community structure based on cover values can be applied if the covers of individual species are estimated independently and the estimated value of one species does not influence the estimates of other species. If the cover of subordinated species are systematically underestimated, randomization tests would detect variance deficit. There is a potential for this artefact in quadrats with overlapping tree canopies. In our case, such quadrats are present in ca. 20% of the sampling units beginning with the 20th yr of succession, still the first significant variance deficit in the functional group of trees appeared only in yr 31. Therefore, we believe that this potential sampling artefact did not influence our results.

Gitay & Wilson (1995) proposed a 'Three-phase' model of succession. Succession starts with distinctly unpredictable species composition in the first, 'Pioneer' phase because of the unpredictable dispersal limitation. Then a more predictable or constrained community structure develops in the second, 'Building' phase, mainly due to increased competition. In the third 'Mature' phase, heterogeneity increases due to spatially varying competitive exclusion and the greater differentiation of microhabitats. Our results can be interpreted in the frame of the 'Three-phase' model of Gitay & Wilson, if it is applied to each functional group separately. There are years with no significant deviation from randomness in the composition of herbs at the beginning of succession ('Pioneer' phase) (Fig. 1b). It is followed by a period of abundance constancy and increasing constraints on coexistence ('Building' phase). After the 11th yr of succession a new phase is starting with no detectable variance deficit but with a variance excess in a few cases, indicating increasing heterogeneity. However, it is still not a 'Mature' phase of the herbs, rather a 'Transitional' phase, which overlaps with the 'Building' phase of shrubs and woody vines, and the 'Pioneer' phase of trees. The 'Three phase' pattern is also recognizable for the functional group of shrubs and woody vines (Fig. 1c), while our 33 yr data set shows only the 'Pioneer' phase, and the beginning of the 'Building' phase of trees (Fig. 1d). Gitay & Wilson (1995) developed their 'Three phase' model for grassland succession, a succession with only the functional group of herbs. Based on the results of our analyses, we propose a 'Multiple phase' model for forest succession that is a composition of several three-phase dynamics of distinct functional groups representing the development of vertical strata.

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A spatial simulation model of vegetation change on British heathlands

Britton, Andrea J.[1*], Marrs, Robert H.[1], Carey, Peter D.[2] & Pakeman, Robin J.[3]

[1]Applied Ecology Research Group, School of Biological Sciences, University of Liverpool, P.O. Box 147, Liverpool, L69 3BX, UK; [2]Institute of Terrestrial Ecology Monks Wood, Abbots Ripton, Huntingdon, Cambridgeshire, PE17 2LS, UK; [3]Macaulay Land Use Research Institute, Craigiebuckler, Aberdeen, AB15 8QH, UK;
**Present address: Macaulay Land Use Research Institute;*
**Fax +44 1224 311556; E-mail a.britton@mluri.sari.ac.uk*

Abstract. It has been suggested that increased dominance by 'grassy' species is occuring on some British lowland heaths. However, the exact cause of this change is unclear. A number of possible causes have been put forward, including increasing nitrogen deposition and changes in management or climate. Here we present the design and development of a spatial simulation model of interactions between *Calluna vulgaris* and grasses on British heathlands. This simple model was constructed to allow investigation of the relative importance of environmental factors on vegetation composition and dynamics. The model takes a life history based approach, parameter values and transition probabilities being derived from field studies and the published literature. In this paper we describe the design and sensitivity analysis of the model and discuss some of the parameters highlighted as being of importance in determining the relative performance of grasses and *Calluna vulgaris*.

Keywords: *Calluna vulgaris*; Cellular model; Competition; *Deschampsia flexuosa*; Heathland-grassland transition; Regeneration.

Introduction

Lowland heaths dominated by *Calluna vulgaris* (hereafter referred to as *Calluna*) are found throughout the British Isles, where they occupy free draining soils low in nitrogen and phosphorus. Heathland is a scarce and declining habitat in Europe, loss of area having mainly occurred as a result of changing land-use, with heathlands on poor soils being taken into cultivation as agricultural techniques improved, afforested or used for urban expansion. Possibly the best known example of this decline is Dorset, in the south of England, where heaths have been reduced from 40 000 ha in 1750 to less than 6000 ha in 1978 (Webb & Haskins 1980).

Since 1983 a new threat to the integrity of heathland communities has become apparent. Eutrophication as a result of atmospheric nitrogen deposition was first observed in The Netherlands (Heil & Diemont 1983), where grasses including *Deschampsia flexuosa* (hereafter referred to as *Deschampsia*) and *Molinia caerulea* became dominant following damage to *Calluna* by the heather beetle (*Lochmaea suturalis*). Experimental work subsequently showed that high levels of aerial nitrogen deposition were almost certainly a contributory factor causing the change in these heathlands (Heil & Diemont 1983; Brunsting & Heil 1985; Aerts et al. 1990). Nitrogen deposition has been linked to a 30% increase in grass cover on Dutch heathlands (Heil & Aerts 1993).

During the early 1990s the first reports of an increase in grass cover on British heaths appeared. The Breckland heaths in East Anglia were one of the first sites where large increases in grass cover, particularly *Deschampsia* and *Festuca ovina*, were reported by heathland managers (Pitcairn et al. 1991; Dolman & Sutherland 1992; Marrs 1993). A number of potential reasons for this change have been suggested including climate, management and nitrogen pollution effects (Marrs 1993). By building a theoretical model of *Calluna*/grass dynamics we hope to understand the relative effects of climatic factors, nitrogen pollution and management regimes on British heathlands and to discover if these heaths are likely to experience similar changes to those seen in The Netherlands.

Model design

A spatially explicit cellular model was chosen as the most appropriate type for investigating the dynamics of invasion of grasses into *Calluna* heathland. *Deschampsia* was chosen as the model grass species since it is a common component of heathlands throughout the United Kingdom. The methods of spread of the two species have important differences. *Calluna* has a large seed bank that may persist for many years and enables it to exploit any gaps in the vegetation that may be created as a result of senescence of older plants, herbivory or management. *Deschampsia* has no persistent seed bank and germinates directly from seed shed in the early autumn. Thus *Deschampsia* is only able to exploit gaps which occur within the maximum dispersal distance for a seed. We modelled these processes of dispersal along with the *Calluna* cycle (as described by Gimingham 1972) which is a major component of heathland dynamics.

The model takes the form of a two dimensional grid of cells, each cell representing a 1 m × 1 m square of vegetation. This cell size was chosen to be approximately equivalent to the area occupied by a single mature *Calluna* bush. Cells may occupy one of four states: *Calluna*, grass, empty or *Calluna*-grass mix. The 'age' of each cell (i.e. the length of time it has occupied a particular state) is also recorded. Each iteration of the model represents one year.

Transitions between cell types are governed by probabilities. Each cell state has an associated 'life history', which describes the amount of bare ground within the cell at any age and also determines the life-span of the species if it is non-clonal. For example, in the case of a *Calluna* cell, the life history follows the *Calluna* cycle as described by Gimingham (1972). After 30 yr if the cell has not been colonised by a new *Calluna* plant it 'dies' and becomes an empty cell. Cells occupied by grasses do not have a determinate life span and are maintained in the 'closed sward' stage until colonised by *Calluna*.

At each time step of the model, the probability of invasion into each cell by *Calluna* or *Deschampsia* is calculated. The probabilities of invasion of the cell by *Deschampsia* or *Calluna* are each calculated slightly differently to take account of the variation in dispersal strategy between the two species. *Calluna* germinates predominantly from the seedbank and is modelled as having a constant germination probability in each cell. The probability of *Deschampsia* germinating is proportional to the number of surrounding *Deschampsia* cells, since it germinates directly from shed seed. The model uses only the four nearest neighbour cells, which share a boundary with the cell of interest, in its calculation of the proportion of *Deschampsia* neighbours. This method was used for simplicity, but may be a limitation of the model. Increasing the size of the neighbourhood interrogated around each cell or using a hexagonal grid might alter the dynamics of the model and would be an area for further investigation. For each species this probability of germination is then multiplied by the proportion of bare ground available within the cell to give a probability of successful establishment. Random numbers are used to decide which species colonise, based on the calculated establishment probabilities. The cell state at the next time step is then determined by the species that have colonised, as shown in Table 1. All cells in the grid are updated synchronously, at each iteration of the model.

Calibration

Parameters used in the model, such as the amount of bare ground available in cells of certain ages and vegetation types and the probability of species invading a cell, were derived from measured field values from experimental work undertaken as part of this project where possible (Britton 1998). Additional data was derived from the published literature or, where nothing had been published, parameters were estimated from field observations. Table 2 shows the main parameters used in the model and their sources.

Table 1. Possible cell type transitions within the model. C = *Calluna*, D = *Deschampsia*, E = empty, M = mixed, O = none. * Age changes to beginning of mature phase. † Age changes to 0 yr.

		Establishing species			
	×	**C**	**D**	**O**	**C+D**
Current species	**C**	C	M	C	M
	D	M*	D	D	M*
	M	M	M	M	M
	E	C†	D†	E	M†

Table 2. Internal parameters used in the model and their sources. Proportion of bare ground available within cells is given for each stage in the cell type life history.

Parameter		'Normal' value	Data source
Calluna germination probability		0.095	Britton (1998)
Maximum *Deschampsia* germination probability (four *Deschampsia* neighbours)		0.05	Britton (1998)
Proportion of bare ground within *Calluna* cells	Pioneer:	0.88	Gimingham (1972)
	Building:	0.07	
	Mature:	0.22	
	Mature2:	0.40	
	Degenerate:	0.59	
	Dead:	0.79	
Proportion of bare ground within *Deschampsia* cells	Seedling:	0.87	A.J. Britton pers. obs.
	Patchy:	0.50	
	Mature:	0.12	
	Mature2:	0.02	
Proportion of bare ground within mixed cells	Seedling:	0.87	A.J. Britton pers. obs.
	Patchy:	0.50	
	Mature:	0.00	

Sensitivity analysis

The effects of variation in *Calluna* germination probability, *Deschampsia* germination probability, initial grid species composition and initial ages of cells were tested by a sensitivity analysis. The analysis was conducted for each of the parameters in turn, by running the model with the calculated values for the parameter being tested, then varying the parameter between its extremes whilst all other parameters were held fixed. Simulations were run with a grid of 100 × 100 cells (equivalent to 1 ha) for 100 yr. Although the model is stochastic, the variation between simulations for any given set of initial parameters was extremely low. This may have been a result of the large total number of cells in the grid (10 000), as simulations using smaller grid sizes showed much greater variability of outcome.

All of the modelled parameters were shown to have some effect on the outcome of the simulations suggesting that there is no redundancy in the design. In addition none of the parameters were overly sensitive to small changes and it would appear that the model is relatively robust to erroneous parameterization. Results are shown here for variation in *Calluna* and *Deschampsia* germination probabilities. It can be seen (Fig. 1) that raising the value for *Calluna* germination above the normal value of 0.095 leads to a reduction in *Deschampsia* cover and rate of spread whilst a reduction in this value allows *Deschampsia* to increase its cover faster. When the *Deschampsia* germination probability is varied above and below its normal value of 0.025 (Fig. 2) a similar pattern is seen, with *Calluna* cover

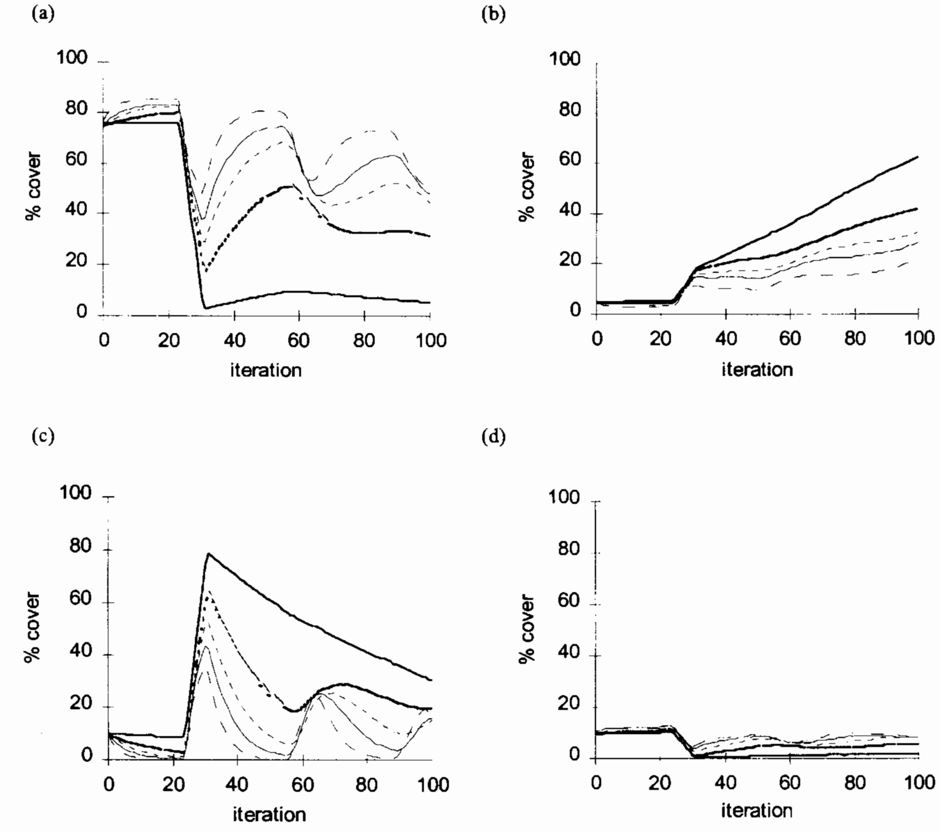

Fig. 1. The effect of varying *Calluna* germination probability (0.005 - 0.25) on model outcome (base model) for each of the four species groups.
(**a**) *Calluna*;
(**b**) *Deschampsia*;
(**c**) empty cells;
(**d**) mixed cells.

Key: 0.005 (———);
0.045 (- - -);
0.095 (- - -);
0.15 (———);
0.25 (— —).
Values are means of three runs.

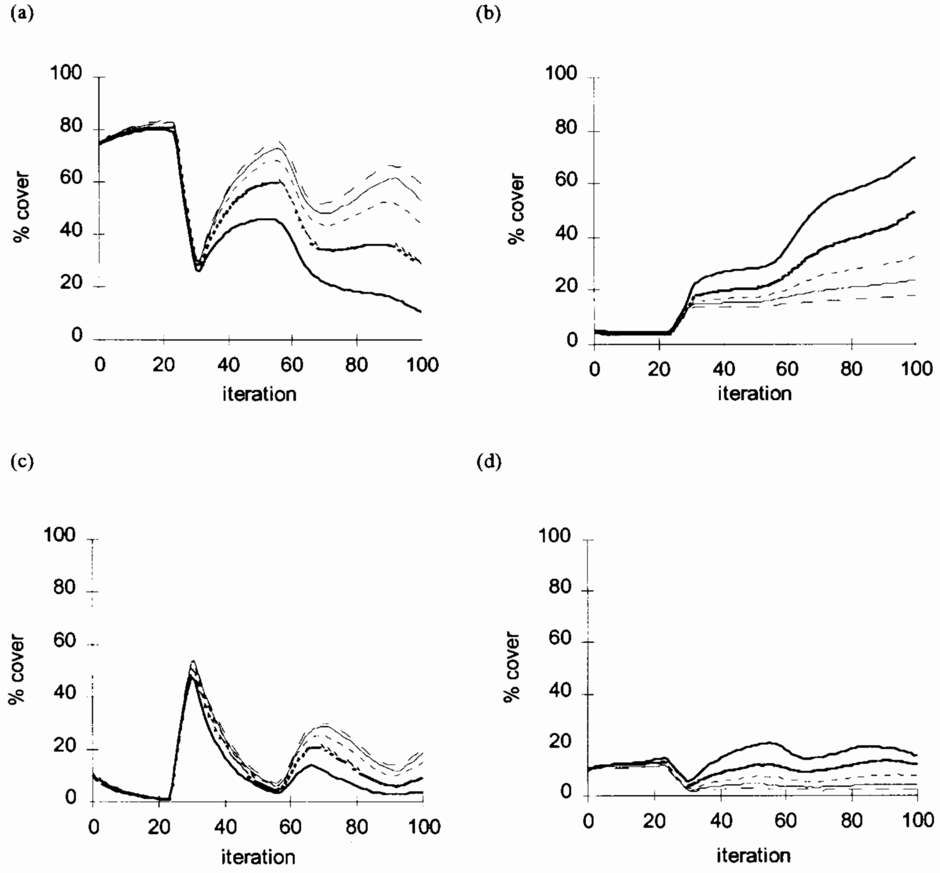

Fig. 2. The effect of varying *Deschampsia* germination probability (0.01- 0.2) on model outcome (base model) for each of the four species groups.
(**a**) *Calluna*;
(**b**) *Deschampsia*;
(**c**) empty cells;
(**d**)mixed cells.

Key: 0.01 (— —);
0.025 (———);
0.05 (- - -);
0.1 (- - -);
0.2 (———).
Values are means of three runs.

reduced when *Deschampsia* germination is high and increased when it is low. It is clear that it is the ratio of these two germination probabilities which is of importance in determining the outcome of the simulations.

Testing

For many ecological models getting adequate data for calibration and testing can prove problematic. If a model is calibrated with one set of data its performance must be tested using an independent set of data. There are no available data sets for heathland species composition which cover the time-scale or level of detail generated by this model. However, results from a study of historical aerial photographic material available for the Breckland region of Eastern England (Britton 1998), were used to give some idea of the typical variation in species composition through time that a single site may experience. When parameterized with data collected for a field site in this region the model results were within the range shown by the historical data. For example, between 1946 and 1995 *Calluna* cover at Cavenham heath in Breckland ranged between 35% and 11% with an overall downward trend, while grass cover varied between 20% and 46% with a general upward trend. When run for a 50-yr period, the results of the model showed a steady increase in grass cover from 20% to 46%, while *Calluna* varied between 30% and 7% but with an overall slight downward trend (Britton 1998). It must however be taken into account that the basic model described here does not include the impacts of the environmental factors or management activities that would affect the real data. The small number of time points available in the historical data set precludes a more detailed statistical comparison of modelled and real data.

Conclusions

Although the model uses a very simple rule based approach it generates dynamics that appear to fall within the range seen in the field. A comprehensive testing of the model remains problematic due to the lack of suitable field data for comparison. Sensitivity analysis of the model parameters highlighted the importance of the ratio between *Calluna* and *Deschampsia* germination probabilities for determining model outcome. A reduction in *Calluna* germination rate alone is sufficient to allow *Deschampsia* to expand without the need for an increase in its germination rate. Since *Calluna* seedlings are known to be sensitive to desiccation during the summer months (Gimingham 1972), this might suggest a potential for strong climatic effects on heathland dynamics. Further development of the model aims to explore this area.

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Plant succession on afforested farmland

Bråkenhielm, Sven

Department of Environmental Assessment, University of Agricultural Sciences, Box 7050, S-750 07 Uppsala, Sweden; Fax +4618673156; E-mail: Sven.Brakenhielm@ma.slu.se

Abstract. Farmland area in Sweden has decreased dramatically last century and woodland increased correspondingly. Most abandoned fields were planted with *Picea abies*, a measure much criticized by conservationists. In south Sweden the cover of understorey vegetation species on six arable fields and three pastures planted with spruce was observed on small permanent plots. Observations took place between 1966 and 1994. The period spanned 50 yr after plantation using a combined time-series and space-for-time-substitution approach. One permanent pasture, one managed mature forest stand and two protected old-growth forest stands served as references. The behaviour of 'ecological' groups (weeds, grassland, woodland species) was studied.

Arable field vegetation was dramatically reduced in cover and species number the first 25 yr. Weeds, starting with complete dominance, had practically disappeared after 15 yr. Grassland species dominated after 10 yr and then declined, but were still important after 50 yr. Woodland species started colonizing the arable field already the first year. They were codominants with grassland species after 15 yr and then declined. The total species number fell from maximum 88 to minimum seven.

On *pastures* succession was slower and species turnover less. The initially dominant grassland species declined and forest species increased during the first 20 yr, then all gradually decreased. Species number fell from maximum 114 to minimum 24. From widely different start field and pasture communities approached the managed and the natural forest communities regarding species content and dominance. It is concluded that some of the species richness may be restored later by appropriate thinning of stands.

Keywords: Old field; Old pasture; Permanent plot; Species richness; Spruce plantation.

Nomenclature: Österdahl (1985), Rosén (1988).

Introduction

During the 1960s and 1970s a lively debate between conservationists and silviculturalists was waged on the practice of turning abandoned farmland into woodland in Sweden (Malmer 1973; Romell 1964; Samuelsson 1968). These decades witnessed a sharp rise in the abandonment of arable fields and pasture and afforestation, mainly with *Picea abies* and mainly in southern Sweden. Planting of farmland in forest-dominated regions was supported by the state. One concern of the conservationists was that a great number of plant communities associated with the agricultural landscape were impoverished or eradicated and replaced by species-poor woodland communities (Ryberg 1968, 1975).

In Europe several studies on the understorey vegetation of abandoned farmland planted with conifers have been carried out (Bornebusch 1925; Hill & Evans 1976; Køie 1938; Malmström 1937; Nihlgård 1970; Ovington 1955; Warming 1919). The present paper is based on studies by Bråkenhielm (1977) and Persson (1989).

The aim is to show how and at which pace the understorey vegetation of field and pasture turns into forest vegetation as compared with the vegetation of managed mature and protected 'natural' old-growth forest sites in the region. The main stress is on species number and quantity in ecological groups of plants.

Sites and Methods

On the eastern slope of the south Swedish uplands, in the community of Vetlanda (57° 22'; 15° 24') six arable fields and three permanent pastures planted with *Picea abies* (Norway spruce) were selected on the basis of representativeness for the region and similarity with each other. The area of the sites ranged from 0.35 to 1.7 ha. The arable fields were abandoned between 1941 and 1965 and the pastures between 1936 and 1962. They were afforested either immediately following the last harvest, or within a few years. The densities of the spruce plants ranged initially between 1700 and 4900 per ha. (See Bråkenhielm 1977 for details.)

The cover values of all species in the field (vascular plants) and bottom (bryophytes, lichens) layers and of the planted spruce were visually estimated on 50 cm × 50 cm plots, 23 - 30 at each site, systematically distributed. Observations were carried out almost annually over 1966-1974 (Bråkenhielm 1977) and in 1987 (Persson 1989) and 1994. For each site and year the number of species and the mean cover of each species were calculated.

All sites were subjected to one or more of the normal silvicultural measures such as cleaning and thinning of the planted trees and colonized broadleaved trees, measures which affected the understorey vegetation.

For 'anthropogenic' references the species contents of one adjacent permanent pasture and one mature managed forest stand were inventoried. The forest stand had been pasture land about 50 yr previously and thus represented a later stage of development than the plantations. For 'natural' references two protected unmanaged old-growth sites were selected: Norra Kvill National park and Aneboda Nature reserve, situated 50 km NE and 60 km SW of the main area, respectively. They served as Integrated Monitoring sites (Anon. 1990). The species number and cover were derived from one plot with subplots at each of the two sites using roughly the same sampling procedure as at the plantations.

The species were assigned to 'ecological' groups based on their life form and preferences in the region: annuals and perennial weeds (e.g. *Erophila verna*, *Veronica arvensis*, *Elymus repens*), grassland species (e.g. *Galium verum*, *Plantago lanceolata*) and forest species (e.g. *Oxalis acetosella*, *Ptilium crista-castrensis*).

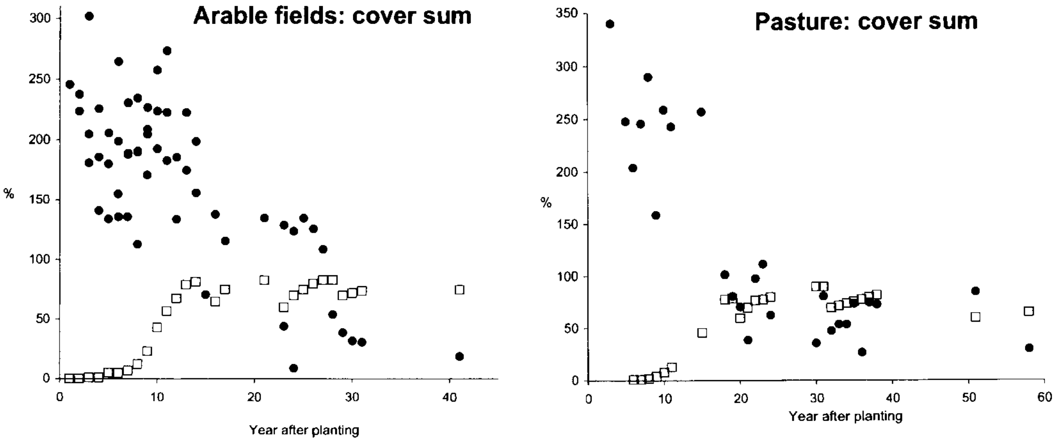

Fig. 1. Plant cover (●) in the understorey of spruce plantations on arable fields and pastures during succession after planting and cover of planted spruce (○). Cover sum is the mean of the sums of all species on all subplots per site per year. Each year between one and five values are given according to the number of sites observed that year.

Results

Overall dynamics

The overall succession during the first 50 yr after abandonment and conifer planting was, as could be expected, characterized by a dramatic decline of the understorey vegetation as regards both cover (Fig. 1) and species number (Fig. 2). There was a general convergence in species content and cover from the two widely different starting points, the open soil of the arable field and the dense grass sward of the pasture, towards the mature managed forest and the natural old-growth forest.

On the arable field a rapid secondary succession took place after abandonment, marked by an explosive development of biomass, invasion of new species and increased competition. The succession had hardly reached a somewhat more stable stage about 10 years after planting when the planted spruce began to influence the understorey. Both cover and species number were much reduced already 15 years after planting. Each time the spruce was thinned the understorey vegetation rapidly responded by increasing its cover, mainly the bottom layer, but the general trend was downward.

The pasture succession was considerably slower than that on the arable field. The thick grass sward only slowly reacted on the growing spruce stand, which also had more gaps in it, due to spots with drier soil. The number of species was initially higher than on the arable field and then declined more slowly. There was a marked decline in cover and species number 15 - 20 yr after planting but both parameters stayed above those of the arable fields even after 40 yr.

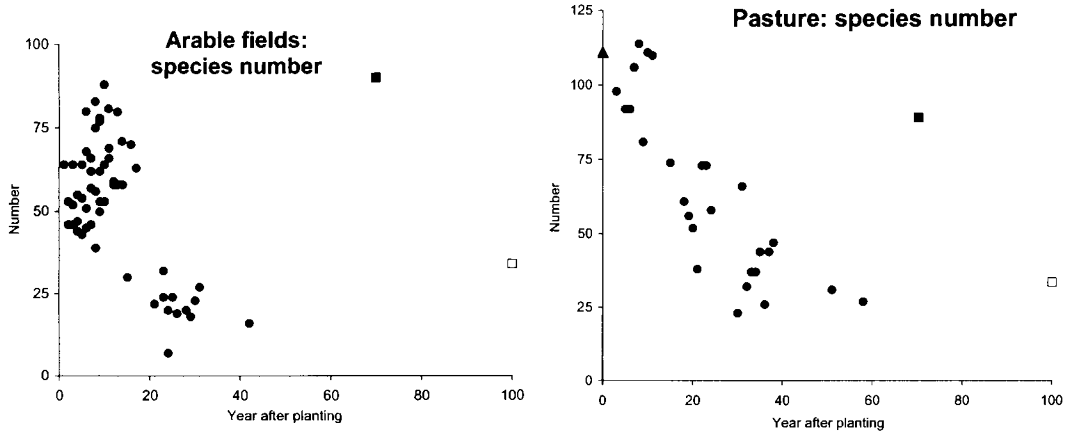

Fig. 2. Number of plant species in spruce plantations on arable fields and pastures (●) during succession after planting, on adjacent permanent pastures (▲) in mature managed forest (■) and in protected natural old-growth forest (□). Only species appearing on permanent subplots were included. Each year between one and five values are given according to the number of sites observed that year.

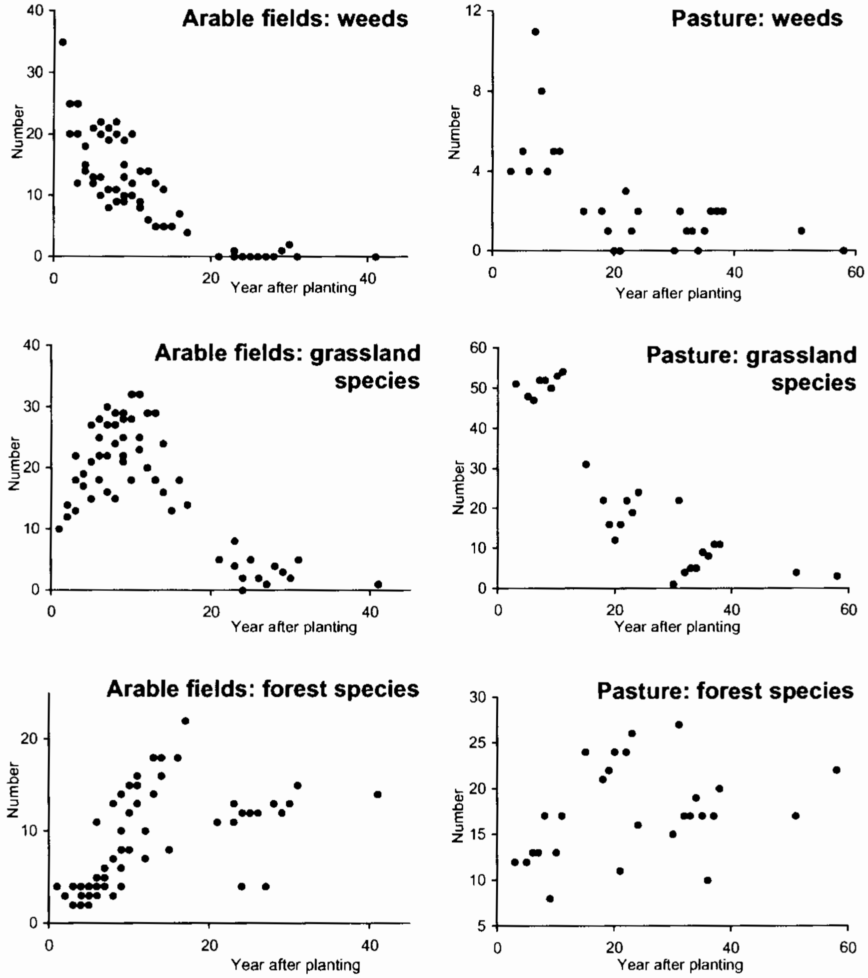

Fig. 3. Number of plant species in the understorey of spruce plantations on arable land and pasture through 41 and 58 yr succession respectively. Only species belonging to three different ecological groups appearing on the permanent subplots were included. Each year between one and five values are given according to the number of sites observed that year.

Species number

The number of species present increased on the arable fields the first 10 yr and then started declining (Fig. 2). On the pasture the species number was initially higher – about 100 compared with about 55 on arable land – and it declined steadily all the time. The total number of species present at any site throughout the years was 282 at the arable field sites and 225 at the pasture sites, a difference probably accounted for not only by the more frequent shifts of communities on the fields, but also by the fact that the arable sites were double as numerous as the pastures. The highest number of species any year at any site was 88 and 114 respectively, the pasture sites being species richer. The smallest number of species present any one year was seven on an arable field and 23 on a pasture. The turnover of species throughout succession was considerable, but will not be dealt with here. At the only observation on the adjacent permanent pasture there were 111 species, on the managed mature forest 90 and on the plots at the two protected old-growth sites only 36 and 32 respectively.

Behaviour of 'ecological' species groups

The ecological species groups described below behaved similarly with respect to both cover and species number. Therefore only graphs of species number are presented here (Fig. 3). Only the spruce plantations are considered, not the mature managed nor the natural forest.

1. *Arable field sites.* Annuals and perennial weeds (56 species) dominated the scene completely the first three years (Fig. 3 left). About 15 yr later their cover had been reduced to near zero and almost all species had disappeared. Concurrently many grassland species (68 species) colonized and reached a peak of cover and species richness about 10 yr after plantation. Then most of them disappeared and the few remaining species were reduced to insignificance as the spruce plantation closed. Forest species (48 species) started colonizing the field already the first year after abandonment, increased till about 15 yr later and then decreased only to dominate in the mature old-growth forest. A general feature during the period 20 - 50 yr after

planting was the small cover, where few species had more than one per cent. This occurred from around 20 yr after planting. The species number was very low from 25 yr onwards.

3. *Pasture sites*. The most striking difference from the arable field sites was the higher species richness – though declining – throughout succession, the few annuals and weeds (16 species) and the many grassland and forest species (82 and 49 respectively) from the very beginning (Fig. 3 right). Since there was a well established, species-rich sod of grass and herbs from the beginning the succession was much slower and the turnover of species much smaller than in the arable field succession. The most rapid decline of species number and cover took place ca. 20 yr after planting, but after it the change was rather small. The succession in general was characterized by decline in species richness and cover of grassland species.

3. *Mature managed and natural protected old-growth forest sites*. There was a marked difference between the mature managed and the natural forest communities. The mature forest adjacent to the plantations was species rich – it contained several species characteristic of both grassland and open forest as well as forest species. The natural forest was species-poor and contained no grassland species. However, the natural forest sites, besides having an entirely different history and being situated far from the cultural landscape, had also poorer and drier soil, which may account for some of the difference.

Discussion

The species richness of the main cultivated landscape elements, the arable fields and the pastures, is rapidly reduced under afforestation with *Picea abies*. Some of the species groups, e.g. weeds and grassland species, are more or less eradicated and should the succession continue without management measures then there would be a very species-poor flora left at least till natural gaps had developed. However, under repeated thinning and selective cutting, the stand is opened up and species from the soil bank and the adjacent open landscape are given an opportunity to germinate and recolonize.

The landscape in the region studied is characterized by small-scale variation in topography, soil and moisture as well as in land use. In such a landscape there are numerous edge, point and line habitats favouring a rich flora. For a broader study of the effects on a landscape basis of afforestation such habitats must be included. In this study they have not been considered.

It may be surprising that the natural forest houses so few species, compared with the cultural sites. However, some facts must be borne in mind: (1) man's activities for millennia in the cultivated landscape has created a number of habitats for synanthropic plants, (2) the natural sites are less fertile than the cultural ones, (3) if more habitats than one in the natural forest had been studied the number of species would have been greater and (4) the epiphytes, which are abundant in the old-growth forest and scarce in the plantation, were not considered in this study.

In conclusion it may be stated that afforestation with spruce on cultivated fields and pasture land is a disaster for the local vegetation and flora under a short term perspective. However, later there are opportunities for a different but comparatively rich forest flora to become established, provided that the stands are opened up by thinning.

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Successional and competitive mechanisms during early succession in a tidal salt-marsh

Castellanos, Eloy M.[1*], Nieva, F. Javier J.[1], Castillo, Jesús M.[2], Luque, Carlos J.[2] & Figueroa, M. Enrique[2]

[1]*Departamento de Ciencias Agroforestales, Facultad de Ciencias Experimentales, Universidad de Huelva, E-21071 Huelva, Spain;* [2]*Departamento de Biología Vegetal y Ecología, Facultad de Biología, Universidad de Sevilla, Apdo 1095, E-41080 Sevilla, Spain;*
[*]*Fax +34959530175; E-mail verdugo@uhu.es*

Abstract. This study discusses competitive interactions between *Spartina maritima*, *Arthrocnemum perenne* and *Arthrocnemum fruticosum*, considering the successional implications. Our results explain the origin of some of the most characteristic plant formations of the low and middle topographic levels of Mediterranean marshes.

Keywords: Accretion; *Arthrocnemum perenne*; *Arthrocnemum fruticosum*; Facilitation; Monospecific sward; Redox potential; *Spartina maritima*; Stability.

Introduction

The processes determining plant distribution in tidal marshes have been a topic of some controversy. The idea of successional change has underpinned most of the numerous treatments of coastal salt marsh vegetation, either explicitly or implicitly, since the early part of the 20th century (Chapman 1974); in contrast, the direct evidence for the existence of chronosequences, as opposed to spatial zonation, is actually rather limited (e.g. Adam 1990; Gray 1992; de Leeuw et al. 1993; Olff et al. 1997). A successional sequence involving replacement of *Spartina maritima* by *Arthrocnemum perenne* on the lower parts of the salt marshes in southwest Europe has been inferred by Beeftink 1977. Castellanos et al. 1994 suggested the existence of a variety of successional mechanisms (facilitation, inhibition, tolerance) in the interactions between *Spartina maritima* (*Gramineae*) and *Arthrocnemum perenne* (*Chenopodiaceae*) in the low topographic levels of the marshes. In this study we test our hypothesis, eight years later, about successional mechanisms for primary colonist species, explaining the origin of some of the more characteristic patterns in low and middle Mediterranean salt marshes. We analysed physiographic properties, sediment accretion rates, redox potential changes and modifications in population size and development of the plant communities in two sites of the Odiel salt marsh in 1990 and 1997, where *S. maritima*, with small tussocks, was the first colonist (Castellanos 1992), to test if facilitation by *S. maritima* is the principal process involving salt marsh succession in this area. The aim of this work was to contribute to a better understanding of zonation, succession and mosaic formation in changing environments.

Methods

The results presented are based on the comparison of different recordings made during 1990 (Castellanos et al. 1994) and 1997, using identical methodologies in two coastal lagoons. The work was carried out in the Odiel marshes (Huelva, SW Spain), in two closed lagoons with very different drainage properties: one of them (Lagoon 1) with a low accretion rate and with impeded drainage by sand spits such that standing water persists for a long time after high tides, and the other (Lagoon 2) well-drained and a high accretion rate. A more detailed description of the study area can be found in Castellanos et al. (1994).

Values of the redox potential (E_7) on top of the *S. maritima* tussocks (0 - 10 cm) previously selected in 1990 were recorded *in situ* using a Crison pH/mV meter and redox electrode system. The top level of tussocks, relative to Spanish hydrographic zero (mean sea level at Huelva is +1.85 m relative to the Spanish hydrographic zero level), was recorded with a Zeiss Wolzhausen theodolite; the reference point was determined in relation to measurements of tidal extremes using the method of Ranwell et al. (1964). Flooding period at the top of the tussocks was calculated using the datum chart of the Port of Huelva and our own data on topographic levels.

The area occupied by each species in the tussocks was calculated. The aboveground biomass of the species was recorded in transects across three of the previously selected tussocks at each lagoon in 1990. All transects were situated in a belt across the maximum diameter of a tussock, with contiguous quadrats 15 cm (radially) × 25 cm. Dry mass was determined after drying at 75 °C for 48 h.

The vertical distribution of belowground biomass of species was determined by taking five replicate cores (10.5 cm in diameter × 25 cm deep) at each area dominated by each one of the species present in the tussocks. Cores were divided into 5-cm layers, before roots and rhizomes were carefully separated. Dry mass was determined as previously mentioned.

Results and Discussion

After eight years, environmental parameter changes were less clear in Lagoon 1 than in Lagoon 2 (Table 1), although the same differences between the two sites as described in Castellanos et al. 1994 were observed. In Lagoon 1, permanent flooding of sediments maintained low accretion rates and low redox potential, preventing the invasion of *A. perenne*, which needs better-oxygenated sediments if it is to compete successfully. In this site tussocks of *S. maritima* increased their area greatly and sometimes coalesced. This is the beginning of the stable monospecific swards of *S. maritima*, frequent in Mediterranean low and protected marshes (Castellanos et al. 1998). Primary colonization

Table 1. Comparison of some abiotic and biotic factors in two lagoons of Odiel saltmarshes during 1990 and 1997. Lagoon 1, $n = 20$; Lagoon 2, $n = 10$. SHZ = Spanish Hydrographic Zero. *Without coalesced tussocks, $n = 8$.

	Lagoon 1			Lagoon 2		
	1990	1997	Increase (%)	1990	1997	Increase (%)
Increase (%)						
Redox potential on the top (mV)	-275±7	-299±12	-	-184±07	+166±03	-
Top level of tussocks over SHZ (m)	2.53±0.02	2.61±0.02	3	2.42±0.02	2.57±0.03	6
Flooding period at the top (% hours/year)	21	18	-	26	8	-
Maximum surface of tussocks (m^2)	15±2	36±6*	140	41±4	64±6	56
Arthrocnemum perenne surface (m^2)	-	-	-	10±3	25±4	150
Spartina maritima surface (m^2)	15±2	36±6	140	31±3	39±3	25
Ratio *Arthrocnemum/Spartina*	-	-	-	0.32	0.64	-

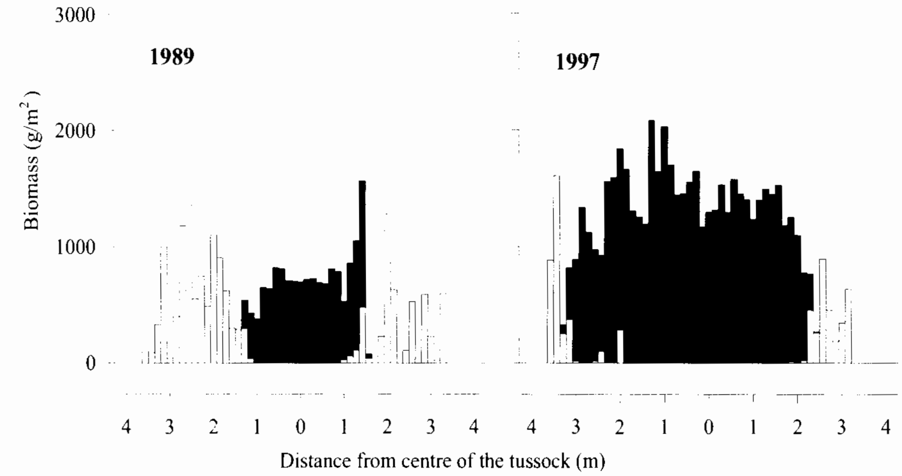

Fig. 1. Diametric transects across a representative tussock of *Spartina maritima* invaded by *Arthrocnemum perenne* at Lagoon 2, showing aboveground dry mass of *Spartina* (white bars) and *A. perenne* (black bars) in contiguous 15 cm × 25 cm quadrats recorded in 1990 and 1997.

events that lead to clonal tussocks, which themselves may coalesce into larger, irregular clumps, have been documented for other *Spartina anglica* marshes on the coast of Britain (Hubbard 1965; Thompson et al. 1991).

In Lagoon 2, with high accretion rates and positive redox potential values on sward tops and a marked decrease in the period of flooding, the area covered by *A. perenne* increased more than that by *Spartina*, and the *A. perennis/Spartina* ratio doubled (Table 1). Accretion, helped by the presence of *S. maritima* stems, resulted in fewer hours of flooding and better soil oxygenation. Such conditions favour the radial expansion of *A. perenne*. This, once established, grows over the stems of *Spartina*, which remains confined to the periphery of the clone, where the redox potential is still very negative (unpubl.). The dense canopy of *A. perenne*, with high values of aboveground biomass (Fig. 1), together with a similar preponderance in the belowground structures (Castellanos et al. 1994), makes it difficult for the stems of *S. maritima* to move into zones already occupied by *A. perennis*, whose presence is limited to a very few isolated ramets. Such is the origin of a Mediterranean middle marsh of *Arthrocnemum*. However, this process looks like it had not been finished yet.

Thus, in lagoon 2, during the last three years a new *Chenopodiaceae*, *Arthrocnemum fruticosum* invaded some tussocks (Fig. 2), growing over tussocks tops (from 2.70 to

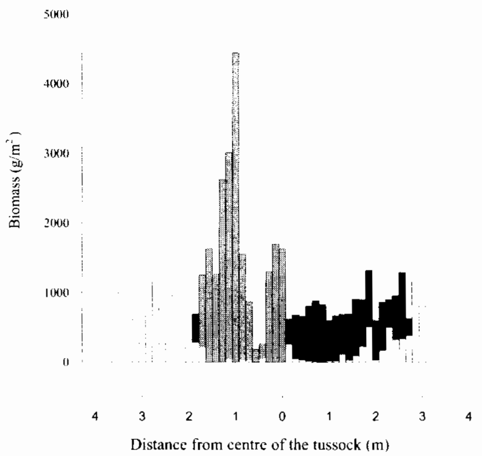

Fig. 2. Diametric transect across a representative tussock of *Spartina maritima* invaded by *Arthrocnemum perenne* and *Arthrocnemum fruticosum* at Lagoon 2, showing aboveground dry mass of *Spartina* (white bars), *A. perenne* (black bars) and *A. fruticosum* (grey bars) in contiguous 15 cm × 25 cm quadrats recorded in 1997.

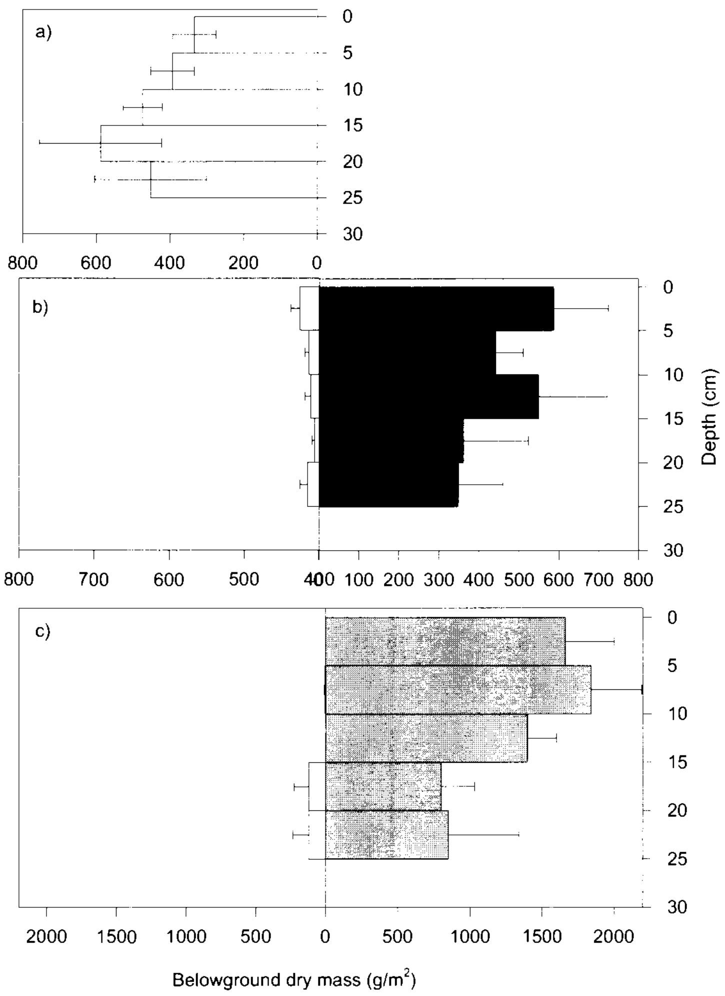

Fig. 3. Vertical distribution of belowground dry mass in tussocks of *Spartina maritima* invaded by *Arthrocnemum perenne* and *Arthrocnemum fruticosum* at Lagoon 2 recorded in 1997. **a.** below-ground dry mass in the area dominated by *Spartina*; **b.** below-ground dry mass in the area dominated by *A. perenne*; **c.** below-ground dry mass in the area dominated by *A. fruticosum*. *Spartina* (white bars), *A. perenne* (black bars) and *A. fruticosum* (grey bars). Means (± SE) for five replicates tussocks are shown.

2.73 m over SHZ) with higher redox values in sediments (from +156 to +193 mV), higher than those in zones colonized by *A. perennis*. Although *S. maritima* extends its belowground system under the whole area occupied by the tussocks invaded by *A. fruticosum*, its abundance decreased progressively (Fig. 3): at the edges it was completely dominant, but in the highest, central part, its presence was very scarce, and it was displaced to deeper zones, while *A. fruticosum* occupied the surface levels. In the area of the tussocks dominated by *A. perenne*, although *S. maritima* extended its belowground biomass more uniformly through the soil profile, the belowground mass was clearly dominated by the belowground structures of *A. perenne*. Thus, when one of these species is dominant in a particular area of a tussock, it is so in terms of both above- and belowground structures.

Finally, positive interactions (facilitation) is the main process involving successional mechanisms in this area, when the drainage is not impeded by sand spits. So, in well drained and high accretion rate areas, the main change taking place between 1990 and 1997 was the existence of competition involving three species, against the two in 1990, with *A. fruticosum* being the last species to arrive. Castellanos et al. (1994), still dealing with only two species, show a variety of successional mechanisms (Connell & Slatyer 1977) including facilitation, inhibition, and tolerance, in the relationship between *A. perenne* and *S. maritima*. Although the appearance of *A. fruticosum* means a higher level of complication, future monitoring of this process will be of interest, because changes in the situation could explain the plant formations of Mediterranean middle marsh, with a large cover of *A. perenne* and isolated individuals of *A. fruticosum*.

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Directing succession: experimental sowing and transplantation of vegetation into an abandoned field

Kailová, J.

Faculty of Biological Sciences, University of South Bohemia, Branišovská 31, CZ-370 05 České Budějovice, Czech Republic; Fax +4203845985; E-mail Janik@tix.bf.jcu.cz

Abstract. A newly abandoned field located in the south of the Czech Republic was used to determine how plant community development can be directed by varying the level of enrichment of the soil with diaspores of plants typical of species-rich meadows, while regular mowing is applied. Two types of diaspore enrichment were used at the experimental 2 m × 2 m plots (each type with three levels, giving eight combinations) arranged in five completely randomized blocks: seed mixtures of plants characteristic of species-rich meadows (high diversity mixture of 15 spp., low diversity mixtures of 4 spp. and unsown control) and blocks of vegetation transplanted from a species-rich meadow to the plots (blocks transplanted in spring, autumn and control). In addition, soil from the source meadow was broadcasted on all plots with meadow blocks to test, if soil organisms present at the meadow could positively affect development of the plant community. Vegetation cover in plots and meadow blocks has been estimated annually since the start of the experiment in 1996.

Data analysis revealed that there is a significant effect of sown species on species representation and this effect is larger in plots sown with a high diversity mixture. There are significant changes in species composition inside transplanted meadow blocks. Broadcasting soil did not show any significant effect on species composition.

Keywords: Constrained ordination, Grassland; Species richness; *Trisetum flavescens*; Vegetation removal.

Nomenclature: Rothmaler (1978).

Introduction

Intensifying human impact on (semi)natural communities, is associated with the overall decline of their species' diversity, to the extent that preservation and restoration of biodiversity has become one of the key issues of nature conservation. It is supposed that many ecosystem features such as stability, productivity, respiration, decomposition, nutrient and water retention are, in many cases, diversity-dependent. Impacts of species diversity on population dynamics and ecosystem functioning have long been debated, with many theoretical explorations and field studies (Tilman et al. 1994, 1996, 1997; Naeem et al. 1994; Hooper & Vitousek 1997; Scherer-Lorenzen 1998; Symstad et al. 1998).

I provide results from direct experimental manipulation of diversity using meadow plant communities which differed in the number of species. These communities were artificially established onto a recently abandoned field. Two kinds of diaspore enrichment were used: seed mixtures of meadow species and blocks of vegetation transferred from a species-rich meadow ('stepping stones').

The aims of the experiment are both theoretical and applied: (1) to study the effects of community complexity as well as of the manipulation of community development by increasing plant species diversity and by regular mowing; and (2) to examine if, and how, a stepping stone approach may be used to enhance the colonization of bare soil in an abandoned field by the addition of plant diaspores and soil (micro)organisms typical of the desired successional stages.

Material and Methods

Study site

The experimental field was located near the village Benešov nad Lipou, in the southwest corner of the Bohemian-Moravian Upland, Czech Republic, at an altitude of 665 m a.s.l. The locality has a moderately humid climate typical of the highlands (mean annual temperature 6.4 °C, mean annual precipitation 677 mm). The field was withdrawn from agricultural use after its last crop harvest in autumn 1995; the experiment was established in spring 1996.

Design of the experiment

Two types of diaspore enrichment were combined (each with three levels, giving nine combinations) in five completely randomized blocks in 2 m × 2 m plots with 2 m walkways. Treatments were (1) seed mixtures of plants characteristic of species-rich meadows (high diversity mixture of 15 species, low diversity mixture of four species, and unsown control), and (2) blocks of vegetation ('stepping stones') transferred from a species-rich meadow to the plots (stepping stones transferred in spring, autumn, and control). All the plots were regularly mown.

Percentage species cover was estimated at mid summer in three successive years (1996-1998). Three data sets were collected: (1) 1-m^2 samples of centre of each 2 m×2 m plot; (2) samples of vegetation of transplanted stepping stones; and (3) 25 cm × 25 cm samples of vegetation adjacent to each stepping stone.

Seed mixtures

Some main factors were taken into account before the selection of species suitable for seeding: (1) relatively wide ecological range with an optimum in *Arrhenatherion* and *Cynosurion* grassland communities; (2) presence in a local flora pool of native grasslands in the vicinity of the study site; (3) balanced ratio of functional plant groups; and (4) availability of a sufficient amount of seeds.

Another problem has also emerged concerning the supply of sufficient seed mixtures as well as the preservation of genetic diversity respecting a certain region. Seeds used in this experiment were received from several Czech companies (Planta Naturalis in Markvartice u Sobotky, and others), because it was the only possible way of obtaining such a number of meadow species.

Based on specific plant characteristics, the functional groups were assembled as grasses, legumes, and other forbs. 15 species (five per functional group) – the first five grasses – were sown as a high diversity (HD) treatment:

Cynosurus cristatus	*Festuca rubra*	*Holcus lanatus*
Phleum pratense	*Trisetum flavescens*	*Centaurea jacea*
Galium verum	*Lathyrus pratensis*	*Lotus corniculatus*
Lychnis flos-cuculi	*Medicago lupulina*	*Plantago lanceolata*
Prunella vulgaris	*Trifolium dubium*	*Trifolium pratense*

Four species assemblages (two grasses, one legume, and one forb) were sown as low diversity (LD) treatment. The unsown plots were established as a control natural colonisation (NC) treatment. Different species combinations in LD treatment were used in each block. In both HD and LD seed mixtures a constant seed density per plot was used, with each species sown in proportion (grasses: 2500 seeds/m^2, legumes: 500 seeds/m^2, and for the other forbs 500 seeds/m^2 yielding altogether ca. 4.35 g/m^2).

Before sowing the field in spring 1996, soil samples were collected to determine the field seed bank. The amount of available nitrogen was determined in the second year. Detailed results are summarized by Hejcman (1997). The most frequent species found in the seed bank are:
Fallopia convolvulus, *Myosotis arvensis*, *Plantago major*, *Poa annua*, *Spergula arvensis*, *Veronica arvensis* and *Veronica persica*.

Stepping stones

The first half of stepping stones was transplanted in April 1996 and the second half in October 1996. This design allowed to test for the transplantation season which was less harmful to the meadow plants. A relatively species-rich meadow was chosen as a source for the stepping stones. The most dominant species were:
Poa pratensis, *P. trivialis*, *Alopecurus pratensis*, *Alchemilla monticola*, *Dactylis glomerata*, *Phleum pratense*, *Taraxacum* spec., *Ranunculus auricomus*, *R. acris* and *Veronica serpyllifolia*.
The size of each stepping stone was 25 m × 25 cm and ca. 20 cm in depth; four stepping stones were transplanted per one 2 m × 2 m plot.

In addition, in April 1996, the top soil from the source meadow was distributed on all 2 m × 2 m plots assigned to the spring and autumn stepping stones. Soil was taken after the removal of a thin sod layer (2 - 3 cm), homogenized (visible plant material was sorted out) and dispersed as 10 l per plot. To determine which plant diaspores were present, 10 l of homogenized soil were collected and the seed bank was determined using standard methods (McDonald 1993).

Data analysis

The data on changes in species composition were evaluated using the program CANOCO (ter Braak & Šmilauer 1998). The following nominal explanatory variables were used (with classes in brackets): sowing (HD, LD, NC) and stepping stones (spring, autumn, no stepping stones transplanted). These factors are coded as a series of dummy variables (Jongman et al. 1987). Factor time is coded as a sole quantitative variable. Because the changes of particular treatments in time were confirmed to be linear and the majority of explanatory variables were nominal ones, the Redundancy Analysis (RDA) was used for evaluating the results of the experiment. All data sets are in the form of repeated measurements, and the analyses have to reflect this fact (including the permutation scheme in the Monte Carlo permutation test). In all the analyses, the sown species were made passive. This means that one is interested in the response of natural colonizers.

Similarly, as in the univariate repeated measures, the interaction term of treatment with time corresponds to differential development. If the interaction is zero, then all differences from the beginning are conserved over time; this means that the successional trajectories are parallel. So the difference in development means a non-parallel successional trajectory. In practice, this usually means that plots under differing treatments become more dissimilar with time.

Two types of analyses were used: standardized and non-standardized. Standardization in this paper means standardization by sample norm. In this way one is able to distinguish differences in the absolute representation of species (in our case, species cover) and relative representation (proportion of species cover within a community). This distinction is important because the total cover of natural colonizers differs between treatments. Consequently, a significant result from non-standardized analysis shows that there are some differences between treatments; the species respond to the treatment, but it is not clear whether the species differ in their response (the proportion of species need not be changed). If the standardized analysis shows some significant differences, one can conclude that species respond, and that not all species respond in the same way. The results of CANOCO analyses were displayed as ordination diagrams using the CanoDraw 3.1 program.

Results

Emergence of seedlings from the source-meadow seed bank was observed in 21 species, of which only eight were perennials. The similarity according to Sörensen's Index, between the actual meadow vegetation and the meadow seed bank, was 43%.

Most of the sown species have become established, except *Lychnis flos-cuculi*, *Medicago lupulina* and *Galium verum*. The highest species number of natural colonizers was observed in the first year. Total percentage cover of natural colonizers was negatively correlated with the diversity treatment and this relation became more intensive in the second and third years: two-way ANOVA, year ($p \ll 0.0001$); treatment ($p \ll 0.0001$); treatment × year ($p \ll 0.0001$). The HD, LD, and NC plots were compared regardless of the stepping stone treatment, because only a few stepping stone species have spread through the whole plots so far. The effect of the stepping stone treatment is included in the CANOCO analyses.

Redundancy analysis

The following variables were used to characterize the results of particular analyses (with abbreviations in brackets): the sum of all constrained eigenvalues – i.e. the ratio

Table 1. Results of the RDA analyses. Explanatory variables are environmental variables in the CANOCO terminology; factors, whose effect was excluded from the analysis are listed as covariables. If standardization by samples was applied, the results of a particular analysis are given in brackets. Names of variables: T = time; D = diversity treatment (HD, LD, NC); S = stepping stone treatment; R = season of stepping stone removal (spring/autumn); B = block; A = samples originating from areas adjacent to the central squares. The interactions of couples of treatments are indicated with an asterisk.

Questions and answers of particular analyses	Explanat. variables	Covariables	S all constr.	P
(1) Is the species composition related to explaining variables? YES	T, D, S, T*D, T*S	B	0.35 (0.34)	0.002 (0.006)
(2) Is there a common successional trend in species composition? YES	T	B, D, S	0.26 (0.25)	0.01 (0.01)
(3) Is there any effect of sown plants on species composition? YES	D, D*T	B, S,T	0.07 (0.07)	0.002 (0.002)
(4) Is there any large-scale effect of stepping-stone treatment on species composition? YES	S, S*T	B, D, T	0.02	0.04
(5) Is there any small-scale effect of stepping-stone treatment on species composition? YES #	A, T*A	B, D, T, R	0.03	0.002
(6) Did the season of the stepping stone transplantation and/or the kind of the treatment (sowing) have any effect on the composition of the stepping stone vegetation? Is there any effect of time? YES	R, D, T	B	0.20	0.01
(7) Is there a common successional trend in species composition inside stepping stones? YES	T	B, D, R	0.08 (0.08)	0.008 (0.008)
(8) Did the stepping stones differ with respect to the season of transplantation? YES	R, R*T	B, D, T	0.05	0.002
(9) Did the stepping stones differ according to the diversity treatment of the plot? WEAK SUPPORT	D, D*T	B, R, T	0.02	0.08

Comparison of samples recorded from the central $1 m^2$ of each 2m × 2m plot and from the areas adjacent to the stepping stones.

of variability explained by all the explanatory variables used in the test (S all constr.); corresponding probability value obtained by Monte Carlo permutation test (P) – i.e. the type one error probability in testing the hypothesis that the effect of all explanatory variables is zero. Results are summarized in Table 1. The sown species, although passive in the analyses, were also displayed in the ordination diagrams.

First, all environmental variables were used as explanatory ones to obtain the total part of explainable community variability and then separate tests were used to single out the effects of the particular treatments from each other. The first overall analysis revealed that the constrained canonical axes explained about 35% of the data variability (S all constr. = 0.35). The first axis was determined mainly by the factor time, whereas the differentiation along the other axes was mainly due to the type of sowing (HD, LD, NC). Stepping stone treatment had the weakest explanatory power. The greatest explanatory power (26% of total data variability, i.e. about 70% of constrained variability calculated in analysis 1) could be ascribed to the time (analysis 2). Species with a high score on axis 1, i.e. those with increasing density, were few: *Poa trivialis* (it spread from both the stepping stones and the area surrounding the site into the field), *Trisetum flavescens* (sown species which became dominant wherever it was sown) and *Taraxacum* spec. Low scores on the first axis were found for a number of annual weed species:

Veronica arvensis, *V. persica*, *Fallopia convolvulus*, *Viola arvensis*, *Plantago major*, *Polygonum persicaria*, *P. hydropiper*, *Galeopsis tetrahit* and *Poa annua*.

The cover of *Trifolium repens* has slightly decreased. Despite the fact that few seedlings were recorded from the seed bank (Hejcman 1997), this species reached almost 40% cover in the field in the first year. Similar results were experienced by McDonald (1993). The density of *Agropyron repens* (the second most frequent natural colonizer after *Trifolium repens*) did not show any common trend in time, and hence it was not depicted in the ordination space.

The other question is whether there was any effect of sown species on the proportion of natural colonizers: a third analysis yielded that only 7% of total variability, i.e. about 20% of constrained variability, could be ascribed to the effect of sown species. The ordination diagram has shown that sown species were partly able to suppress the most problematic and persistent weeds *Agropyron repens* and *Trifolium repens*.

The hypothesis that the application of stepping stones and meadow soil will enhance the succession was tested by analyses 4 and 5. This environmental variable explained only 2% of total variability. The most successful colonizers originating from the stepping stones were *Poa trivialis*, *Achillea millefolium*, *Cerastium holosteoides*, *Stellaria graminea*, and *Agrostis tenuis*. Only a very slight positive effect of the stepping stone treatment on sown species was observed: *Festuca rubra* and *Prunella vulgaris* performed better in the vicinity of stepping stones.

Data on vegetation changes of stepping stones were tested separately (analyses 6-9). Similarly, as in the case of data from the central 1-m^2 samples, all environmental variables were used as explanatory ones to obtain the total part of explainable community variability and then separate tests were calculated to single out the effects of the particular treatments from each other. In analysis 6 with all environmental variables, the first ordination axis was determined mainly by time, whereas the differentiation along the second axis was mainly due to the season when the stepping stones were transplanted (environmental variables explained together only 20% of total community variability). Results are displayed in the ordination diagram (Fig. 1). The comparison of sums of all constrained eigenvalues from the particular tests revealed that the most powerful explanatory variable was time (ca. 10% of the total variability); season of transplantation explained ca. 5%; and statistically significant differences among stepping stones transplanted into different diversity treatments were not found.

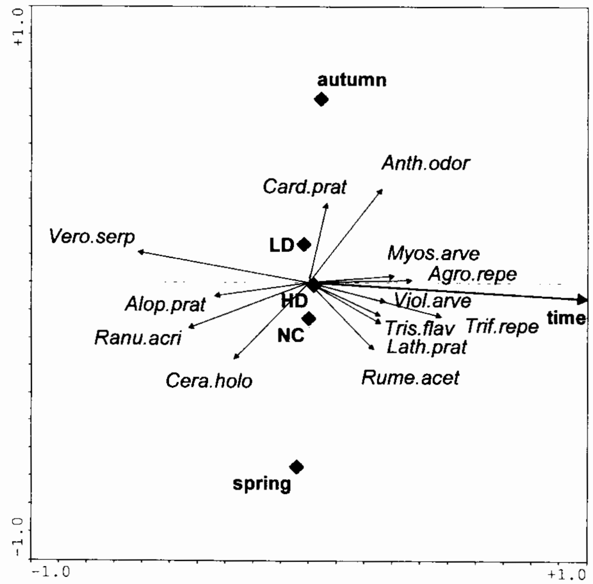

Fig. 1. Ordination diagram showing the changes of plant community inside stepping stones (analysis 6). The density of *Veronica serpyllifolia* decreased probably due to the more intensive competition for light. *Anthoxanthum odoratum* performed best after the autumn transplantation. *Trisetum flavescens* and *Lathyrus pratensis* are the only sown species which were able to expand inside stepping stones. The diagram explains 20% of the variance in the fitted species data. For clarity, only species with the highest correlation with the ordination axes are displayed. HD = high diversity treatment; LD = low diversity treatment; NC = natural colonization treatment; autumn/spring = season of stepping-stone transplantation.

Discussion

It can be stated that sowing of meadow plants was successful: most species became established and have created a community quite similar to the desired hay meadow. The levels of dry matter yield ($t \cdot ha^{-1} \cdot yr^{-1}$) were 10.08 for HD, 9.16 for LD and 7.92 for NC (Šmilauer & Lepš pers. comm.). The values were as high as those obtained from intensively fertilized high-productive species-poor meadows (Oomes 1990, 1992). Oomes observed a significant decrease in dry matter production, especially during the first three to five years (depending upon the soil type) after fertilization had been stopped and regular mowing began. Similar changes are also expected in our experiment.

Results show that there are significant differences among the three diversity treatments. Sown species were able to compete successfully with natural colonizers and their effect was more intense in the high diversity treatment. The higher competitive ability of a species-richer community can be ascribed primarily to the following reasons:

First, the more diverse ecosystems are more likely to contain some species which thrive well in particular environmental conditions (Tilman & Downing 1994; Naeem et al. 1994; Symstad et al. 1998). The presence of such dominant species may have great effect on ecosystem functioning and in some cases may be more important than the species number per se (Symstad et al. 1998). Our data imply that the difference between the HD and LD treatments is partly caused by the absence of such well-thriving species in some of the five alternative species assemblages used in LD treatments.

Second, plant productivity and resource utilization are usually greater at higher diversity (Tilman et al. 1996; Naeem et al. 1994; Symstad 1998; Scherer-Lorenzen 1998), so that more intensive competition for resources, notably nutrients or light may occur. Under such conditions, plants with pure ruderal strategy (annual field weeds in our case) may be strongly outcompeted by C-S-R strategists (late-successional meadow species). For the same reason, the weaker ability of sown species to compete with *Agropyron repens* and *Trifolium repens* – plants having C-S-R to C-R strategy (Grime 1988) – was observed. Such species (ruderal-perennials sensu Grime 1979) are most abundant in circumstances in which the impact of disturbance is less intensive. Both *A. repens* and *T. repens* are clonally spreading perennials.

Agropyron repens has an extensive rhizome system which allowed the plant to cover a large area. *A. repens* was only rarely recorded from the seed bank but it regenerated from numerous rhizome fragments (Hejcman 1997). Experiences of many researchers (for example, Schmidt & Brübach 1993; Grime 1979) confirm that it is species which did not change either its spatial pattern or mean annual cover for a long time: it is the most persistent natural colonizer in the site. *Trifolium repens* is intolerant to shade (Grime 1988), and hence it could be partly suppressed in the tall vegetation of HD as well as LD-treated plots.

The other natural colonizers show a predominantly strong decrease, which is independent of the kind of treatment. These results imply that the plants are weak competitors specialised on the colonization of bare soil.

With regard to the performance of sown species, the absolute dominance of sown *Trisetum flavescens* (ca. 54% in HD as well as LD treatment) can hardly be explained in a straightforward way; there are more alternative explanations here. *T. flavescens* has an early seed set and almost intermediate germination has been documented in sites subject to summer drought. This may be an advantage in hayfields. (Grime 1988). *T. flavescens* appears to show only modest specialization towards any ecological factor or turf structure, and Grime concluded that the species is a 'congenital subordinate', i.e. never more than a minor component of grassland communities, which is in contrast to our observations. One can argue that *T. flavescens* is a quite frequent component of mesic upland meadows in the Czech Republic but, unfortunately, it is often caused by resowing those sites with mixtures containing cultivars of *T. flavescens*. For the same reason it is still not clear whether the clone used in our experiment originated from an unaffected source.

Lychnis flos-cuculi, *Medicago lupulina*, and *Galium verum* did not survive in any experimental design probably due to their poor germination. The low densities of *Centaurea jacea* (one percent in LD only) are probably also due to weak germination. I have evidence from another similar experiment close to our field, where *C. jacea* was sown and performed very well (Lepš & Šrůtek pers. comm.). The other sown species are present in amounts close to values expected for comparable meadow communities.

From the botanical point of view, the transplantation of stepping stones can be considered as 'medium successful'. Although almost all species survived the transplantation and performed well, the stepping stones had only a slight impact on the surrounding vegetation. They contributed significantly to the spreading of *Poa trivialis*. This is a grass with a high potential for the colonization of such recently disturbed habitats that are dominated by larger perennials and it has often been observed in disturbed meadows (Grime 1979, 1988; McDonald 1993). Other stepping-stone species have spread only occasionally while the pool of species invading stepping stones was considerably larger. Since insignificant differences between the spring and autumn stepping stones were observed, it could therefore be concluded that both ways of transplantation are possible.

Dispersing soil on the stepping stone plots did not show any significant effect on species composition. A positive result can hardly be expected with regard to the known composition of a source-meadow seed bank.

Comparison of the stepping stone transplantation versus simple sowing revealed in our case a clear answer: the stepping stone approach can be recommended only as a 'last chance' practice if all alternatives to preserve some extremely rare habitat have failed and there is the possibility to remove the vegetation to a place close by.

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Patterns of succession of xerophylous vegetation on the Balkans

Redžić, Sulejman

Department of Biology, Faculty of Science, University of Sarajevo, 71 000 Sarajevo, Bosnia & Hercegovina; Fax +38771668071; E-mail sredzic @usa.net

Abstract. Investigations of successional relationships along both horizontal and vertical profiles have been carried out in the central and western Balkans over the last 20 years, in all belts and climatogenic climax communities, from the Eu-mediterranean zone towards the Mediterranean mountain belt (from sea level to 900 m a.s.l.). For the data collection a modified version of the Zürich-Montpellier school was used. Certain progressive-regressive patterns were detected on the basis of the presence of plant species – indicators of regressive or progressive trends in the development of plant communities, and on the basis of habitat determinants. Particular attention was paid to so called transitional communities in which the most intense competitive relations are present. Climatogenic vegetation of the study area is represented by the *Quercion ilicis* in the Mediterranean belt; *Paliurion aculeati, Carpinion orientalis* and *Quercion trojanae* in the Sub-mediterranean belt, *Quercion frainetto*, *Seslerio-Ostryon and Quercion petraeae-cerris* in the mountain belt, and *Quercion petraeae, Fagion moesiacae* and *Fagion illyricae* in the Mediterranean mountain belt. Besides the presence of certain patterns in the directions and development of vegetation, there are pronounced features and patterns in relation to type of climatogenic vegetation. In each of the communities of the above-mentioned alliances of climatogenic vegetation numerous successional stages were found including shrublands, meadows, rocky grasslands, screes and cliff vegetation.

Keywords: Dinaric Alps; Mediterranean; Secondary succession, Sub-mediterranean; Syndynamics; Xerophilous vegetation.

Nomenclature of syntaxa: Lakušić et al. (1978); Jovanović et al. (1986).

Introduction

Anthropogenic influences on the Balkan peninsula were very intensive and heterogeneous in the past. This produced significant changes in the spatial and temporal organization of natural or climatogenic phytocoenoses and vegetation cover in general. The results of many studies (e.g. Horvat et al. 1978; Horvatić 1934, 1973; Lovrić 1993; Redžić et al. 1991/1994) carried out in this region have confirmed that vegetation cover of the Balkans is very heterogeneous, both in floristic and phytocoenological composition. Many thermophilous forests, low forests, shrublands, meadows, rocky grasslands, screes, rock fissures, are present here. There are specific syndynamic relationships among these plant communities.

Various patterns of succession are established in each climatogenic or oroclimatogenic community, going from the most complex communities and their development stages to the most degraded and floristically poorest communities, such as rock fissures and screes.

So-called secondary successions play an important role in the establishment of general patterns of vegetation development. In studies of vegetation diversity and development of vegetation the greatest attention was paid to these successions, since they contain essential information for the estimation of ways and patterns of other types of succession, such as regeneration succession, cyclic dynamics, patch dynamics, gap dynamics, fluctuation, as well as certain ways of development of primary and secondary successions (van der Maarel 1978, 1988; Redžić 1984; Lakušić et al. 1984). Although in secondary successions plant communities directly participate in determination of syndynamic and development patterns, patches, populations and individuals, the state of the ecosystems in question also plays an important role.

Particularly significant changes in both structure and dynamics of plant cover occurred in arid and warm regions of the central and western Balkans, notably the Mediterranean and Sub-mediterranean regions. The documentation of the main directions in the development of vegetation, as well as recognition of syndynamic relationships among certain plant communities in this region were the main objectives of this study.

Material and Methods

A slightly modified method based on the Zürich-Montpellier school (Braun-Blanquet 1964) was used as the basic method of data collection. In certain cases permanent plots (Kent & Coker 1992) were used. Definition of certain progressive-regressive stages was carried out on the basis of the presence of certain plant species, indicators of regression or progression, trends in the development of plant communities, as well as on the basis of habitat determinants: geological foundation, physical, chemical and biological features of soil, ecoclimatic conditions (hydrothermal regime, intensity and direction of wind, snow cover, aspect and slope of terrain, etc.) (Redžić 1988a; Redžić & Barudanovic 1981).

General characteristics of the investigated area

The study area is located between 40° and 46° N and 12° and 22° E.

Geology. The central and western Balkans are heterogeneous as regards geological and petrographic characteristics. Mesozoic limestone sediments dominate in the whole region. In the Mediterranean and Sub-mediterranean belts Paleogenic sediments cover large areas, and in the hilly-mountain belt towards Pannonian Jurassic and Triassic sediments are dominant. Palaeozoic sediments occur here and there, as well as basic and ultrabasic eruptives.

The larger part of the Balkans was not under the influence of the last glaciation, except for the peaks of the highest mountains. However, there are indirect glacial influences. This follows from *i.a.* degradation of rocks, formation of colluvium in the valleys and sediments in karst depressions.

Orography. The Balkan mountains range from northwest to southeast. The region is intersected by numerous river valleys with a direction north - south. The vertical profile from the Adriatic sea towards the peaks in the littoral mountains is ca. 2400 m. Many karst fields and depressions occur on the plateaus surrounded by a dynamic relief. As a result there are clearly differentiated belts: Eu-mediterranean, Sub-mediterranean, hilly belt, mountain belt, subalpine, alpine and subnival to nivale belts.

Ecoclimate. As regards the climate, the region is very heterogeneous and dynamic. Along the profile of ca. 2400 m towards the Adriatic, there is regular succession of ecoclimatic types from the Eu-mediterranean towards the subnival and nival belts. This is region with the highest temperature and precipitation extremes and dynamics in Europe. Mean annual temperatures are (Lakušić 1975):

Eu-mediterranean belt	20 - 16 °C
Sub-mediterranean belt	15 - 12 °C
Hilly region	11 - 8 °C
Mountainous belt	7 - 4 °C
Alpine belt	3 - 0 °C
Subnival belt	0 - −4 °C

Absolute maximal temperatures in the Eu-mediterranean belt are around 50 °C, while the absolute minimal temperature in mountain belt are down to −42 °C. Over the year certain places (e.g. Gorski Kotar and Orjen) receive more than 3000 mm of precipitation, mostly in the early spring and late autumn. During the vegetation period precipitation is significantly lower and arid conditions prevail in summer.

The wind is most frequently from the southwest and this wind has also a strong influence on the formation of vegetation cover.

Soil conditions. There is a mosaic of soil types. However, there are certain global patterns in the distribution and genesis of basic types of soils on the horizontal and vertical profile. The main pedogenetic factors in this region are humidity, temperature, wind and snow cover. From the most arid towards the most humid habitats the system of pedogenesis begins with the formation of lithosols, regosols and sirozems, which in more humid conditions and on gentle slopes show gradual transitions to calcomelanosols, rendzinas, and in even more humid situations in calcocambisols, and terra rossa in the Eu-mediterranean belt.

Luvisols are developed on gentle slopes and in the absence of strong winds. On silicate rocks, humus silicate soils or rankers, as well as distric cambisols and distric luvisols are developed.

Phytogeography. Concerning the large number of plant species the region of the Balkans is similar to the richest subtropical regions of the world. There are numerous endemic and relict plant species (Trinajstić & Šugar 1972; Lakušić et al. 1978; Jovanović et al. 1986).

The vegetation can be divided into three regions:
- Mediterranean, including the Adriatic province;
- Eurosiberian, with the Ilirian, Moesian and the province of relic pine forests;
- Alpine- high nordic, with the province of the high Dinaric Alps (Lakušić 1969).

The belt of xerotherm oak and moesian beech forests represents the optimal habitat for human populations. Under anthropogenic influence significant transformation in vegetation cover happened in this region.

Results and Discussion

Forest and shrub vegetation

Xerotherm vegetation on the vertical profile of this part of the Balkans reaches its optimum in the Mediterranean, Sub-mediterranean and one part of the hilly belt. It can be found in the mountain belt only on southern aspects and steeper slopes. Variation in ecoclimatic, orographic, geological and pedological conditions caused the development of variation in climatogenic vegetation on vertical profiles of certain regions on Balkan peninsula, from the Eu-mediterranean, towards the Sub-mediterranean hilly and the Mediterranean montane belt.

Basic types of climatogenic communities in the regions and altitudinal belts, as well as their syndynamical relationship are presented in Fig. 1.

In the littoral southeastern Dinaric Alps climatogenic xerotherm vegetation in the Mediterranean belt is represented by evergreen forests of the *Quercetum ilicis*, in the Sub-mediterranean belt from around 200 m by low forests of the *Aceri-Carpinetum orientalis*, with many evergreen elements, and the *Dioscoreo-Carpinetum orientalis* with dominant broadleaved deciduous elements. At some locations, forests of Macedonian oak (*Quercetum trojanae*) intergrade with the *Quercetum ilicis*.

The forests of the *Seslerio autumnalis-Ostryetum carpini-*

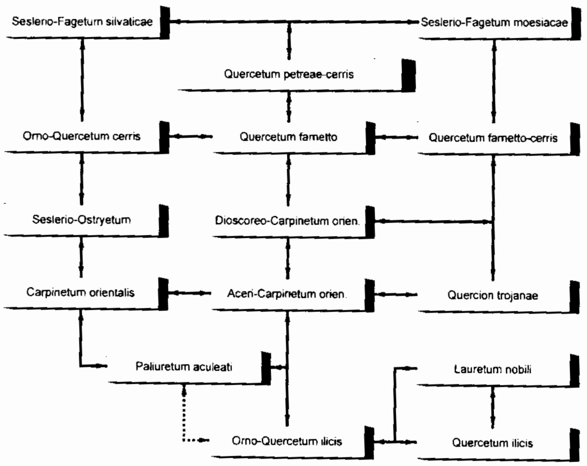

Fig. 1. Syndynamic relationships between the main forest- and low forest vegetation types in the Mediterranean and Submediterranean zones of the central and western Balkans.

foliae are developed in the hilly region and they often continue into the mountain belt. Forests of the *Quercetum frainetto-cerris Quercetum cerris mediterrano-montanum* are found on gentle slopes and on deep soils, the latter forests reaching into the mountain belt.

Communities of the *Quercetum frainetto-cerris* in the continental region are syndynamically related to the forests of *Quercetum petraeae-cerris*. Relict low forests of the *Seslerio autumnalis-Ostryetum carpinifoliae* on steep slopes, shallow soils and southern aspects are syndynamically related to thermophilous beech forests of the *Seslerio autumnalis-Fagetum moesiacae* (Fig. 1).

The forests of the *Orno-Quercetum ilicis*, with a significant participation of broadleaved deciduous elements, occur in the northwestern littoral Dinaric Alps in the Mediterranean belt. They merge with *Carpinetum orientalis* forests in the Sub-mediterranean belt, which, on warm sites and shallow and eroded soils, are syngenetically connected with the *Paliuretum aculeati*. These communities merge with the thermophilous *Seslerio autumnalis-Ostryetum carpinifoliae*, and on gentle slopes and on brown limestone soils with the *Orno-Quercetum cerris*, which in the mountain belt merge with the thermophilous beech forests of the *Seslerio-Fagetum sylvaticae* (Fig. 1).

Intensive anthropogenic influences in the past caused significant changes in the structure and dynamics of the climatogenic communities, which is reflected today in the presence of numerous types of so-called secondary vegetation – meadows, rocky grasslands, pastures, screes, and rock fissures. These secondary communities vary according to the type of climatogenic vegetation they are related to (Fig. 1). Some patterns of development of vegetation and secondary succession of xerotherm vegetation in the Eu-mediterranean and Sub-mediterranean belts are presented in Fig. 2.

Grasslands and rocky grasslands

Pioneer communities of the *Rhizocarpion* and *Ctenidion mollusci* occur in most regions and vary with the ecoclimate belt and geographical and ecological position. The main patterns of development for the thermophilous vegetation, as well as syndynamical relationships, are presented in Fig. 2.

A dominant role in the Mediterranean belt, on eroded terra rossa soils, is played by rocky grasslands of the *Cympopogo-Brachypodion ramosi*, which, on more shallow calcomelanosols and regosols, are syndynamically connected with *Peltarion alliaceae* scree vegetation, and, on hard limestone substrata and very arid soils, with rock fissure communities from the *Moltkaeion petraeae, Ctenidion mollusci* and *Rhizocarpion*. In the vicinity of the Sub-mediterranean belt, the *Cympopogo-Brachypodion ramosi* merges with Sub-mediterranean rocky grasslands of the *Koelerion pyramidatae* and *Peucedanion neumayeri.* These are syngenetically related to the *Alyssetum moelendorfianii* and *Thymetum aureopunctati,* on the more shallow rendzinas, as well as with the *Scabiosetum graminifoliae* and *Koelerion pyramidatae* on deeper rendzinas and calcomoelanosols. On eroded soils, the associations of the *Peucedanion neumayeri* syndynamically merge with the Sub-mediterranean rocky grasslands of the *Satureion montanae* with a very high floristic diversity, which in colder habitats are ecologically related to communities of the *Satureion spicatae*. Sub-mediterranean rocky grasslands are related to arid pastures of the *Fumano-Scabiosenion leucophyllae*, which are syngenetically connected to the *Xerobromion erecti*, in cooler and wind-exposed habitats.

Thermophilous meadows of the *Chrysopogoni-Danthonion alpinae* are related to *Festucion illyricae Astragalo-Potentillion* and *Festucion vallesiacae* communities on more arid habitats and to meso-thermal meadows of the *Filipendulo-Danthonion* and *Cirsio-Bromion erecti* (*Mesobromion erecti*) in more humid habitats. Under the absence of anthropogenic influences these meadows may develop into *Querctum frainetto-cerris*, *Quercetum petreae-cerri* and *Ostryo-Quercetum pubescentis* forests, and on deeper

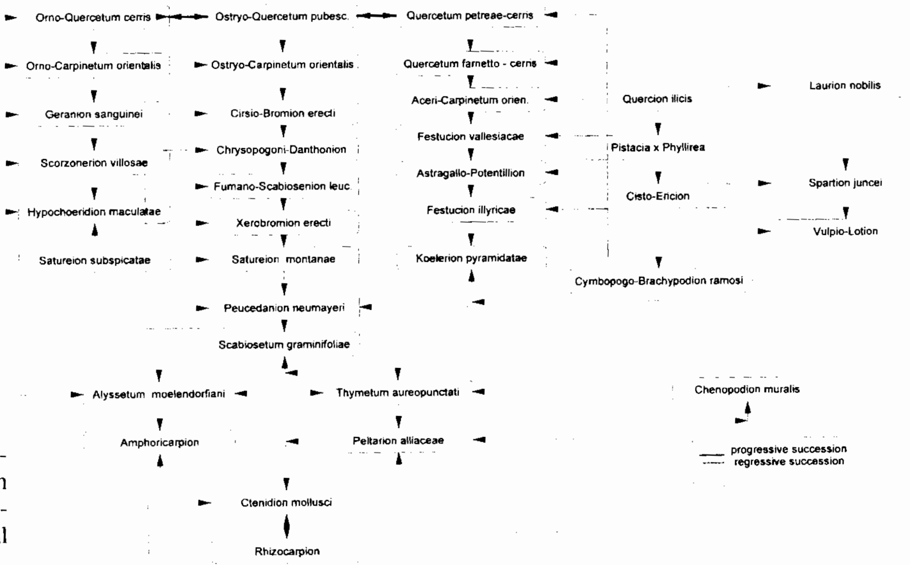

Fig. 2. Patterns of secondary succession of xerophyllous vegetation in the Eu-mediterranean and Sub-mediterranean zones of the central and western Balkans.

calcocambisols, the *Lathyro-Quercetum petraeae*.

In the northwestern Dinaric Alps, communities of rocky grasslands on deeper soils and gentle slopes, in the zone of *Quercus cerris* and *Fraxinus ornus* forests, are connected to Sub-mediterranean meadows of the *Hypochoeridion maculatae* and *Scorzonerion villosae*, and to *Geranion sanguinei* borderline communities. They may further develop through stages of the *Orno-Carpinetum orientalis* into the climatogenic *Orno-Quercetum cerris* (Fig. 2).

The depth of the soil profile is positively correlated with degree of vegetation cover. Vegetation of the alliances *Rhizocarpion, Ctenidion mollusci, Peltarion* and *Amphoricarpion* is developed on soils with a (A)-C profile, of the *Alyssetum, Thymetum, Satureion, Fumano-Scabiosenion* and *Xerobromion* are linked to an A-C profile and *Hypochoeridion, Scorzonerion, Chrysopogoni-Danthonion* and *Cirsio-Bromion erecti* to an A-(B)-C profile.

As to the factor snow, vegetation of rocky meadows, *Fumano-Scabiosenion leucophyllae* is usually developed on the places where snow lasts very shortly. In the vicinity, in places with deeper snow, the *Bromo-Danthonietum kitaibelli* is found.

Riter-Studnička (1956), Gaži Baskova & Šegulja (1978) and Ilijanić & Hecimović (1981) have shown very different directions of succession depending on the bedrock. Usually, after pioneer stages of the *Rhizocarpion* on silicates and shallow rankers, *Hyperico-Scleranthion* communities develop, and on limestone and shallow calcomelanosols and rendzinas rocky grasslands of the *Peucedanion neumayerii*, and *Koelerion pyramidatae, Chrysopogoni-Danthonion* and continental rocky meadows of the *Fumano-Scabiosenion leucophyllae* (Redžić 1984; Lakušic et al. 1984). Relations between climatogenic vegetation and ecoclimatic conditions have also been demonstrated elsewhere (Piotrowska 1988; Poli Marchese et al. 1988).

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Plant age stages during succession in woodland clearings in Central Russia

Ulanova, Nina G.

Department of Geobotany, Biological Faculty, Moscow State University, Moscow, 119899 Russia;
Fax +70959390939; E-mail Nina@Nulanova.home.bio.msu.ru

Abstract. The population dynamics of the main woodland clearing species were studied in southern taiga forest (Tver' region, Russia). Clear-cutting areas of different age were selected in different forest types. For each species 100 - 300 clones were excavated and studied. So-called, 'age state' descriptions were defined for the following clonal species: *Chamaenerion angustifolium*, *Calamagrostis epigeios*, *C. arundinacea*, *Rubus idaeus* and *Juncus effusus*.

Age structure diagrams were produced for each species against age after cutting (or successional stage). The herb population structure in 1 - 2 yr clearings is of an invasive type with mainly virginile ramets. Sexually reproducing ramets predominate in 3-4 yr clearings. The senescence of *Chamaenerion angustifolium* and *Calamagrostis epigeios* populations starts after 4 - 5 yr as a result of competition with birch and spruce saplings. Senescence of *Rubus idaeus*, *Calamagrostis arundinacea* populations starts later (after 6 - 7 yr) and follows tree canopy closure (aspen and birch). Within 10 yr *Rubus idaeus* and herb ramets are mostly senile; the population density decreases drastically. Sparse colonies with 1 - 2 shoots of formerly dominating species remain under the young forest canopy. Partial rejuvenation of populations is possible after stand clear-cuttings or at disturbed microsites.

Keywords: *Calamagrostis epigeios*; *Calamagrostis arundinacea*; Clear-cutting; *Chamaenerion angustifolium*; *Juncus effusus*; Forest succession; Population structure; *Rubus idaeus*.

Nomenclature: Czerepanov (1995).

Introduction

Recognition of age states has greater significance than calendar age in analysing the structure and dynamics of populations. Individual plants of different age states may play different roles in a plant community (Rabotnov 1978, 1985). The renewal and ontogenetic development of plants results in a complex utilization of habitat resources both in space and in time. That may contribute significantly to the coexistence of many species in diversified plant communities (Watt 1947; Rabotnov 1978; Uranov 1975; Grubb 1977). Thus the role of a plant in the community is determined more by its age state than by the number of years lived (Gatsuk et al. 1980). Furthermore, the definition of calendar age of many herbs and woody plants is practically impossible, for example for *Calamagrostis arundinacea*, whereas a classification by age states is quite feasible (Ulanova 1995a,b).

I used the Russian classification of age states according to Rabotnov (1978, 1985), Uranov (1975), and their co-workers (Gatsuk et al. 1980; Zhukova 1985) (Table 1). The ontogeny of plants may be divided into periods or stages based on the rise and extinction of the reproductive function and on certain juvenile and adult characteristics: on this basis pre-reproductive (juvenile), reproductive (adult) and post-reproductive (senile) periods can be distinguished.

The aim of our investigation was to describe the ontogeny and its age states of abundant species during succession after clearings in spruce forests. They were *Calamagrostis epigeios*, *Calamagrostis arundinacea*, *Chamaenerion angustifolium*, *Juncus effusus and Rubus idaeus*.

Material and Methods

The investigations were carried out mainly in the taiga (southern taiga zone) of the Central Forest Reserve in the centre of the Russian plain in the southwestern part of the Valday Uplands at the watershed of the Volga and Western Dvina rivers (Karpov 1973). Climatically this is a humid forest area with *Picea abies* as the dominant tree. The spruce forests found here vary in composition, depending on the geomorphology.

The study plants were carefully collected in such a way that the whole individual was preserved. After careful morphological description the individuals were classified into age states.

About 300 clones of *Chamaenerion angustifolium* and *Rubus idaeus*, 1000 tufts of *Calamagrostis epigeios*, 200 tussocks of *Juncus effusus* and *Calamagrostis arundinacea* were carefully excavated and described.

The chronosequence approach ('space-for-time substitution' was used for the description of the succession (Pickett 1989) by taking 6 - 8 clearings in similar environments but of different periods after cutting. The resulting vegetation sequence is assumed to be the successional sequences. If succession is a population process, an understanding of succession requires an understanding of the life histories of species.

Table 1. Ontogenetic periods and age states of plants (Gatsuk et al. 1980 with some changes).

Ontogenetic period	Symbol	Age state
Latent	se	Seed
Pre-reproductive	pl	Seedling
	j	Juvenile
	im	Immature
	v_1	Young virginile
	v_2	Mature virginile
	v_3	Old virginile
Reproductive	g_1	Young reproductive
	g_2	Mature reproductive
	g_3	Old reproductive
Post-reproductive	ss	Subsenile
	s	Senile

Results and Discussion

All the study species are perennial polycarpics. In clearings they exhibit some features typical of competitive ruderals (C-R strategists; Grime 1979). They adapt to habitats mechanically disturbed by such disruptive event as clear-cutting. Two of them, *Chamaenerion angustifolium* and *Calamagrostis epigeios* are in the group of the most expansive perennial herbs in recent times in the temperate zone of Europe (Prach & Wade 1992). They have the ability for intensive vegetative spreading by long horizontal rhizomes (*Calamagrostis epigeios*), roots (*Rubus idaeus*), stolons (*Chamaenerion angustifolium*) or intensive lateral growth of tussocks (*Calamagrostis arundinacea*, *Juncus effusus*). At the same time they combine high seed productivity and dispersibility of generative diaspores in their regenerative strategy. Most of them are anemochorous and have light seeds with pappus. Such species can be very successful in expansion over large areas (Prach & Pyšek 1994).

Calamagrostis epigeios

Seedlings can be found only on hardly disturbed microsites (Ulanova 1995a; Lehmann 1997), but then up to 30 seedlings/m^2. *C. epigeios* colonizes disturbed sites also by vegetative reproduction from surviving parts of rhizomes, during the first year since a clearing was formed. Then vegetative spread may be more that 1 m/yr and nearly 10 new young plants may appear from one rhizome part.

The population structure in 1-2 yr old clearings is of the invasive type, with a predominance of virginile tufts (Fig. 1). The great speed of colonization allows *C. epigeios* to dominate even in 2-3 yr old communities. The number of tufts per m^2 is near 180 in 2-yr old clearings while the maximum production is reached in 3-4 yr populations. The older populations of *C. epigeios* have regressive features with subsenile and senile plants. The further development of *C. epigeios* is determined by competition with *Rubus idaeus*, *Betula pendula* and *Picea abies*. The number of tufts per m^2 decreases to 50 in 7-yr old clearings. Population degradation begins after 10 yr and is finished at 15 yr after a close canopy of birch or spruce has developed. At open places the population can survive for many years, but the number of tufts will be not large.

Chamaenerion angustifolium

Chamaenerion angustifolium colonizes clearings by seeds (Broderick 1990; van Andel 1975; Zabelkin & Ulanova 1995). In the first year the population expands; in the third year most plants flower (Fig. 2). Seedlings can be found only during the first 3 yr. Roots grow fast and can be 5 m long; colonies may occupy 15 - 20 m^2. *C. angustifolium* is a dominant species 4 - 10 yr after clearing when there are only reproductive plants. Subsequent abundance of the species is largely determined by vegetative propagation. After 10 yr one can see some virginile colonies appearing after disintegration of senile colonies. There are two groups of secondary colonies: young and old. *C. angustifolium* can survive for a longer time only not entirely closed tree canopy and in gaps.

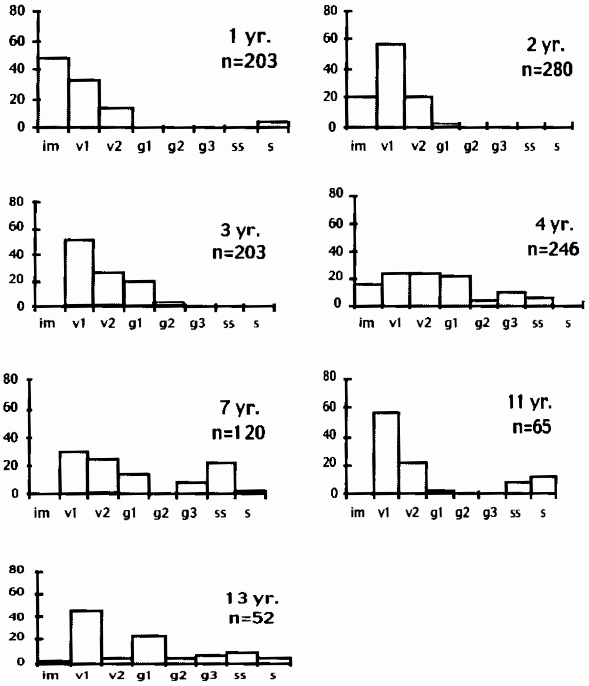

Fig 1. Age-spectra of *Calamagrostis epigeios* in clearcuts of different age; x-axis: age stages (Table 1); y-axis: frequency (%).

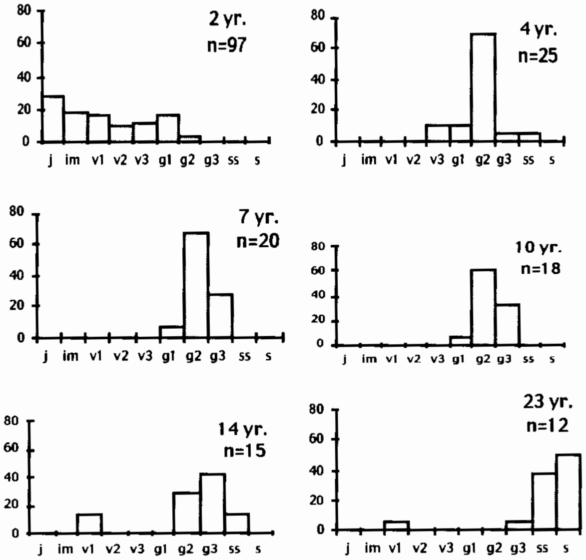

Fig. 2. Age-spectra of *Chamaenerion angustifolium* in clearcuts of different age; x-axis: age stages (Table 1); y-axis: frequency (%).

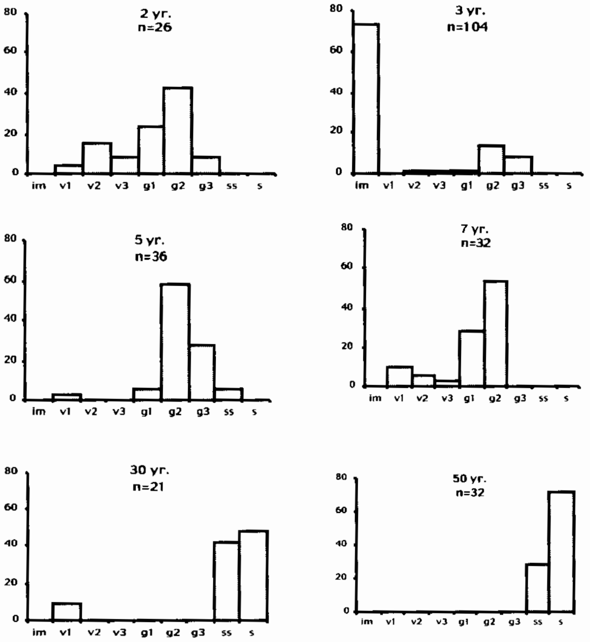

Fig 3. Age-spectra of *Calamagrostis arundinacea* in clearcuts of different age; x-axis: age stages (Table 1); y-axis: frequency (%).

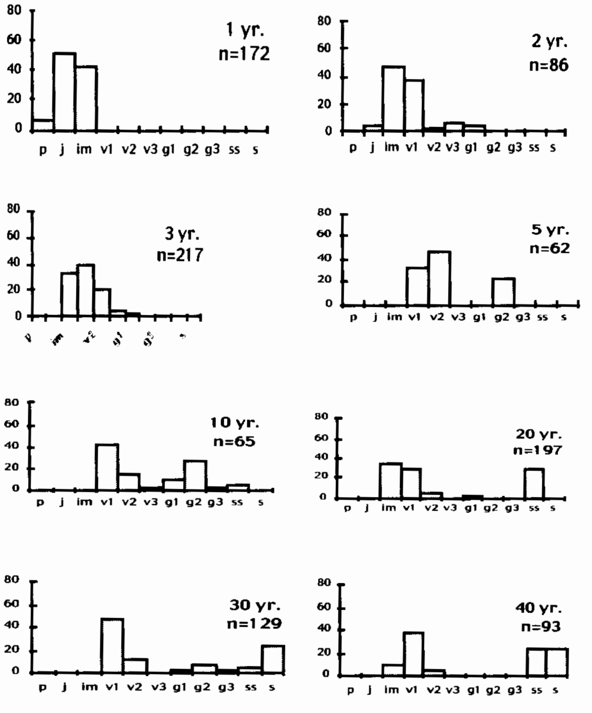

Fig 4. Age-spectra of *Rubus idaeus* in clearcuts of different age; x-axis: age stages (Table 1); y-axis: frequency (%).

Calamagrostis arundinacea

Calamagrostis arundinacea is a rather large tussock grass that is abundant in forests and clearings (Ulanova 1995b). A tussock can reach up to 1 m in diameter. The high competitive ability is supported by the production of compact litter which decays very slowly. Because of this few herbs can coexist around a tussock up to a distance of 1 - 2 m.

After clear-cutting *Calamagrostis arundinacea* tussocks survive partly and begin to grow actively at open places. New seedlings appear rather rarely, as there is no soil seed bank. This explains why the age state diagram in 2-yr clearings shows a predominance of generative tussocks (Fig. 3). A great number of seeds actively disperse and germinate during next spring. *C. arundinacea* exhibits R-strategy characteristics (Grime 1979). This is reflected by a high percentage of biomass allocated to generative reproduction (Fiala & Zelena 1995). So in the third year clearings young immature plants dominate and mature plants are less abundant. This new generation forms an even-age spectrum again at the 5-yr clearing. *C. arundinacea* is a dominant species from the 5th until the 10th yr.

Senescence of *C. arundinacea* populations starts after 8 - 10 yr; it follows the closure of the tree canopy. Within 10 yr after the clearing most if not all tussocks are mostly senile and subsenile; the population density decreases drastically. After 30 yr one can find remaining sparse tussocks with 1 - 2 shoots of former dominating species under the canopy of young forest.

Rubus idaeus

Rubus idaeus is a root sucker shrub. It colonizes clearings by recruitment from seeds (Ulanova & Davletshina 1996). Seedlings can be found only during the first 3 yr (Whitney 1986). The population is of a typical invasive type during this period (Fig. 4). In 3-4-yr clearings most plants are virginile. Flowering shrubs dominate at 4-5-yr clearings. *Rubus idaeus* is a dominant species with constant abundance from 5 till 10 yr since clear-cutting. Senescence process starts after 10 yr as a result of competition with birch and spruce. The population has regressive features when a tree canopy closes up. There are two peaks in the age-state chart: first with young virginile and second with subsenile and senile shrubs. In young forests *Rubus idaeus* is rather rare but it could survive in gaps or near tree trunks.

Juncus effusus

Juncus effusus is a large perennial tussock plant. It grows on wet hardly disturbed soils. Many seedlings appear from seed bank at first summer since clear-cutting (Minaeva & Ulanova 1991). They grow rapidly and the same year most of them reach virginile age state. The population has typically invasive structure. Then it changes to the predominance of generative plants. You can see really some senescence processes at the forth year clearing. Juncus can be dominant species from 2 till 6 year since clear-cutting. Tussocks of generative states are rather big (half of meter in diameter, 1 m in height) with compact litter which decays very slowly. New seedlings can not appear in that conditions. And there are only big flowering tussocks in the oldest clearings. Usually more competitive species as young trees or shrubs change the dominant role. From 12 yr onwards the population has regressive features. Plants can survive only in old roads or local depressions.

Conclusions

Population dynamics of all discussed species has many common features. Age-state distribution of populations change from the invasive type to normal and than to senile. During the first three years features of ruderal (R) species strategy prevail in the life strategy. After 5 yr we can observe a change from a R- strategy to a competitive (C) strategy. Later, after ca. 10 yr the strategy type moves to stress-tolerant (S). This means that all species studied change their strategy during secondary succession and their position in the 'Grime triangle' during secondary succession.

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An earthquake's impact on the structure and dynamics of a New Zealand *Nothofagus* forest

Allen, Robert B.*, Bellingham, Peter J. & Wiser, Susan K.

**Landcare Research, P.O. Box 69, Lincoln, New Zealand; Fax +6433252418; E-mail allenr@landcare.cri.nz*

Abstract. Previous analyses of the pattern and causes of earthquake-induced damage to forests in mountainous regions have usually focused on the complete removal, or inundation by, catastrophic landslides. In contrast, this study quantifies damage by the 1994 Arthur's Pass earthquake (M_w 6.7) to a mountain beech forest [*Nothofagus solandri* var. *cliffortioides* (Hook. f.) Poole] in New Zealand's Southern Alps at individual tree, stand and landscape scales. Data from randomly located permanent plots (400 m^2) established in 1970 throughout Basin Creek (28 plots in 920 ha), 10 km southeast of the epicentre, and Broken River (34 plots in 2060 ha), 30 km southeast of the epicentre, were used to determine the distribution, intensity, and causes of earthquake damage. Assessments of earthquake-induced damage in 1995 showed, on average, there was 24.0±5.9% tree mortality and 22.5±4.0% tree injury on Basin Creek plots, but only 0.6±0.2% tree mortality and 3.3±1.1% tree injury on Broken River plots. As a consequence, average stem biomass declined from 149±13.8 Mg/ha in 1993 to 114±15.3 Mg/ha in 1995 on Basin Creek plots. Low intensity stem biomass mortality was common in Basin Creek with 25% of plots losing 1 to < 20% of their live stem biomass. Of note was our observation that 2.0 ± 0.9% of trees emigrated up to 100 m off the plots during the earthquake but still remained alive in 1995. Earthquakes with a magnitude of >6.0 are common events in New Zealand forests with return times likely well within the longevity of dominant tree species. Thus it is not surprising that these forests may have a structure reflecting past disturbance by earthquakes over extensive areas.

Keywords: Disturbance; Forest; Landslide; Mortality; Permanent plot.

Introduction

Although the distribution, intensity, and frequency of earthquakes are readily determined for forested areas using seismological data, their impacts on forest structure and dynamics is poorly quantified. On a global scale, earthquake epicentres are concentrated along the tectonically active major plate boundaries, and the boundary of the Pacific Plate forms a zone of intense earthquake activity (Fig. 1; Strahler 1981). Several studies determining how earthquakes impact on forests have been conducted in this zone (e.g. Robbins 1957; Simonett 1967; Veblen & Ashton 1978; Garwood et al. 1979; Jacoby et al. 1988; Nakashizuka et al. 1993). Forests described in these studies occur on steep mountainous slopes and most of these studies have determined the area where forest has been completely removed, or inundated, by earthquake-induced catastrophic landslides (e.g. Simonett 1967; Veblen & Ashton 1978; Garwood et al. 1979). This denudation is striking and can be a considerable proportion of relatively large areas. For example, in the Madang area, Papua New Guinea, interpretation of aerial photography showed that 25% of a 240 km^2 area was denuded by a force 8.2 earthquake (Johns 1986). However, such studies likely underestimate earthquake damage because they only include the impacts of large landslides. This contribution summarizes a study by Allen et al. (1999) that quantified the pattern and causes of immediate earthquake-induced damage at the individual tree, stand and landscape scale.

Methods

We quantified the immediate impact of an earthquake (M_w 6.7 in 1994) on a *Nothofagus solandri* var. *cliffortioides* (mountain beech) forest in the Southern Alps, New Zealand. Because mountain beech is the only canopy tree species present we were able to examine patterns and causes of damage without differences among species confounding the results. Data from randomly located permanent plots (400 m^2) established in 1970 throughout Basin Creek (28 plots in 920 ha), 10 km southeast of the epicentre, and Broken River (34 plots in 2060 ha), 30 km southeast of the epicentre, were used to determine the distribution, intensity, and causes of earthquake damage (see Allen et al. 1999). Such a network of plots allowed us to demonstrate the utility of having many small dispersed plots to capture disturbance impacts. Trees were tagged and diameters measured on all plots in 1974, 1976, 1978, 1980, 1983, 1985, 1987, 1995 and 1996 (Allen 1993). Basin Creek plots were also measured in 1993 (six months before the earthquake) and Broken River plots in 1994 (six months after the earthquake).

Results and Discussion

68% of Basin Creek plots were affected by earthquake-induced landslides compared with only 6% of Broken River plots. Assessments of earthquake-induced damage in 1995 showed, on average, there was 24.0±5.9% tree mortality and 22.5 ± 4.0% tree injury on Basin Creek plots, but only 0.6 ± 0.2% tree mortality and 3.3 ± 1.1% tree injury on Broken River plots. As a consequence, stem biomass declined from 149 ± 13.8 Mg/ha in 1993 to 114± 15.3 Mg/ha in 1995 on Basin Creek plots. On average, earthquake-induced landslides caused 74% of stem biomass mortality in Basin Creek. Although landslide-caused mortality was greatest on steep slopes there was no relationship between mortality and 1993 stand structure or previous forest dynamics. Low intensity stem biomass mortality was common in Basin Creek with 25% of plots losing 1 to < 20% of their live stem biomass. Damage intensity here depended on the scale of observation; 100% mortality occurred on 7% of 400 m^2 plots, 15% of 10 m × 10 m

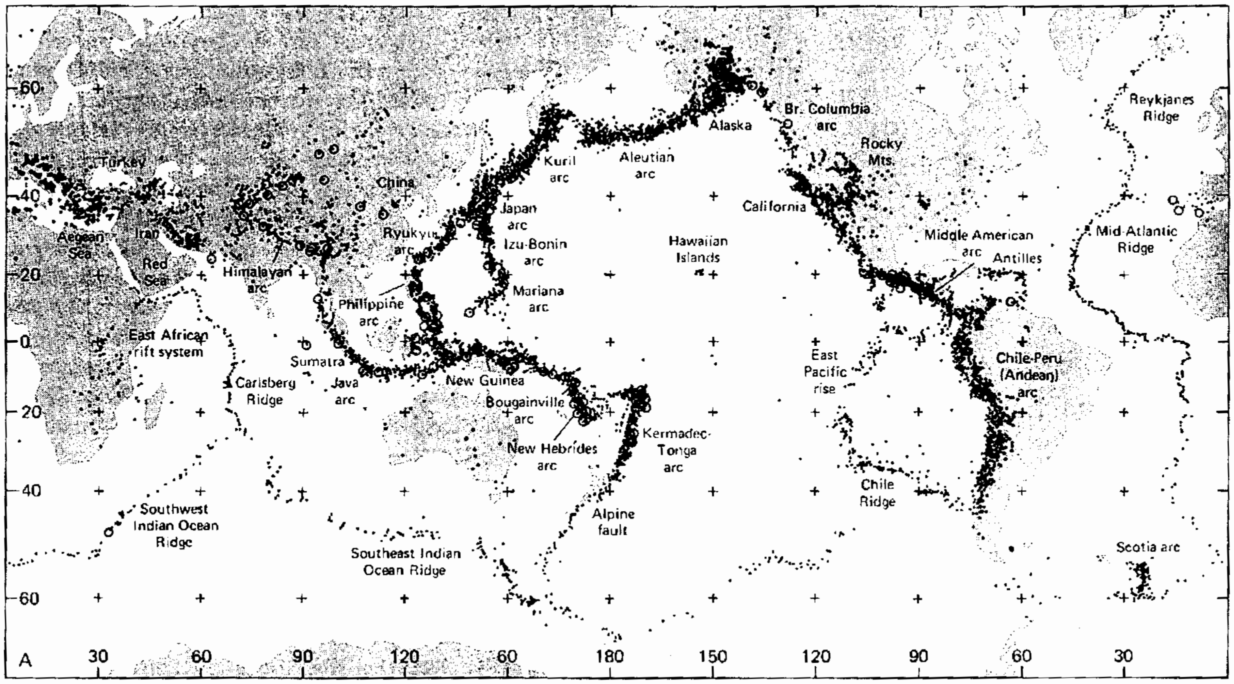

Fig. 1. Global distribution of earthquake epicentres for the period 1961-1967. Epicentres of earthquakes with a magnitude of <8.0 (•) and ≥ 8.0 (○) are mapped (modified from Strahler 1981 and reprinted with permission of Harper and Row Limited).

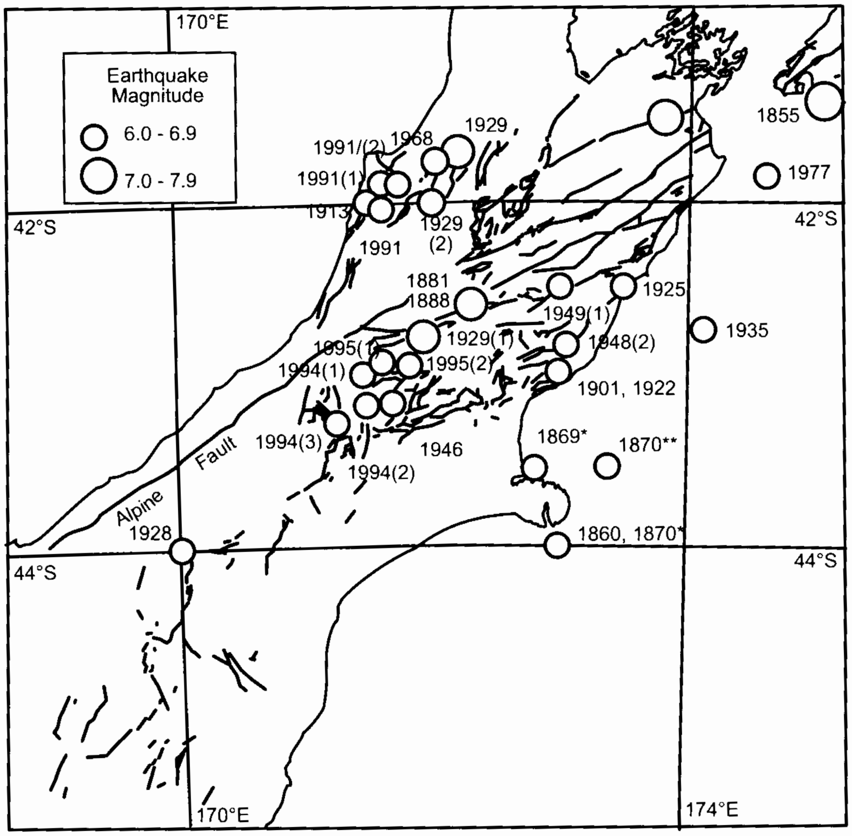

Fig. 2. Distribution of northern South Island earthquake epicentres for the period 1840-1998. Epicentres of earthquakes with a magnitude of 6.0 - 6.9 and 7.0 - 7.9 are mapped (modified from an unpubl. report provided by J. Pettinga, University of Canterbury). Multiple earthquakes in any year are indicated by the number in parentheses.

subplots, and 21% of 5 m × 5 m subplots.

The higher frequency of complete stem biomass mortality at smaller scales suggests partial loss at the 400-m^2 scale is mostly the result of complete loss at smaller scales. In Basin Creek, tree injury was largely the result of damage by other trees. There was no difference in the diameter, or previous diameter growth, of undamaged versus injured trees occurring on the same plot. Of note was our observation that 2.0±0.9% of trees emigrated up to 100 m off the plots during the earthquake but still remained alive in 1995.

Our results show that although an earthquake can cause catastrophic damage, much of an earthquake's immediate impact is through widespread, low intensity damage to forests (Allen et al. 1999). 54% of Basin Creek plots had partial stem biomass mortality, and 46% of these had less than 20% stem biomass mortality. Nearly as many trees were injured in the earthquake as died, and these could well contribute to significant ongoing tree mortality and the long-term dynamics of these beech forests. Earthquakes with a magnitude of >6.0 are not an unusual event in South Island forests with return times likely well within the longevity of dominant tree species (Fig. 2). Thus it is not surprising that existing South Island forests may have a structure reflecting past disturbance by earthquakes over extensive areas (Wardle 1980; Wells et al. 1998). Earthquakes do not impact on forests in isolation from other disturbance events, and in our study area we have quantified a sequence of disturbance events over a 26 year period that have influenced forest structure, including: snow, wind, pathogens, and earthquakes (Harcombe et al. 1998; Allen et al. 1999). This combination of events has resulted in a catchment level mean plot stem biomass decline of 19% in Broken River and 35% in Basin Creek (Allen et al. 1999). It is unlikely that a similar sequence of events will occur in our study area over another 26-yr time period, and as a consequence we suggest that any forested area is subjected to a sequence of disturbance events that may not be repeated in time or space.

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Spatial distribution and regeneration of *Laurus azorica* in a laurel forest on Tenerife

Arévalo, José Ramón & Fernández-Palacios, José María

Departamento de Ecología, Universidad de La Laguna, Tenerife, Islas Canarias, Spain;
Fax +34922318311; E-mail jarevalo@ull.es

Abstract. We conducted a study to assess the spatial distribution of trees (> 4 cm DBH) and the effect of these distributions in the regeneration of *Laurus azorica*. Univariate spatial analysis (performed with Ripley's K_1) revealed that all species showed significant aggregation at short distances, but two groups could be differentiated: shade-intolerant species showed a significant trend towards aggregation at all distances (especially *Erica scoparia*) and shade-tolerant species only showed significant aggregation at short distances (*L. azorica* and *Prunus lusitanica*). Spatial analysis of trees using Ripley's bivariate $K_{1,2}$ showed no significant differences in the spatial distribution of analysed species pairs.

Univariate spatial analysis for *L. azorica* seedlings revealed that in all the plots the distribution tended to be clumped up to 3 m and the remaining distances analysed also showed clumped distributions (10 m was the maximum distance analysed), except for two plots. For saplings, five plots revealed clumped distributions up to 3 m, and only two up to 10 m.

We suggest that the high rate of asexual regeneration by basal sprouts and the environmental conditions are the most important factors in the spatial organization of trees, seedlings and saplings of *L. azorica*.

Keywords: Ripley's *K*; Sapling; Seedling; Shade tolerance; Spatial pattern.

Nomenclature: Hansen & Sunding (1985).

Introduction

Spatial patterns of trees help reveal the nature of forest dynamics. They reveal aspects of canopy replacement (Horn 1975; Busing 1996), regeneration (Condit et al. 1992; Norton 1991), changes of forest dynamics under disturbance (Alekseev & Zherebtsov 1995; Vacek & Lepš 1996) and spatial relationships between tree species (Duncan 1991; He et al. 1997). Also, the spatial distribution of trees could be an important factor in the process of management of natural areas (Moeur 1993).

This paper describes the spatial relationships among the trees of the laurel forest and the spatial distribution of the most abundant sapling and seedling species of the laurel forest, *Laurus azorica* (Arévalo 1998).

Material and Methods

Study site

The study was conducted in the Anaga Natural Park in the northeast corner of Tenerife, Canary Islands (28°19' N, 16°34' W). The park encompasses a 7 to 8 million year old basaltic massif (Ancochea et al. 1990) covering ca. 130 km^2 and representing 7% of Tenerife's area. We selected two stations in the park as representing the best conserved laurel-forest remnants of Anaga: 'El Moquinal' on the windward slope and 'Monte de Aguirre' on the leeward slope. We chose ca. 300 ha of the best conserved forest at each station.

The canopy height of Anaga's laurel forest varies between 10 and 20 m depending on slope. Dominant species include *Laurus azorica*, *Erica scoparia*, *E. arborea*, *Ilex canariensis*, *Prunus lusitanica*, *Myrica faya* and *Viburnum tinus* (*V. tinus* is a short understorey tree which occasionally reaches the canopy, so it was not considered a canopy tree in this study). Further information about the study site is given in Arévalo (1998).

Data collection

In June and July of 1996, we randomly selected four 625-m^2 square plots in each of the two sites with different altitude and aspect (plots 1 to 4 were situated in Moquinal and plots 5 to 8 in Aguirre). We defined 'trees' as stems of at least 4 cm DBH, 'saplings' as stems taller than 50 cm and less than 4 cm DBH with a sexual origin, and 'basal sprouts' as sapling-size stems of asexual origin (connections with parent stems, with some exceptions, were apparent). Previous studies recommended these classes in accordance with the physiognomy and phenology of this forest (Fernández-Palacios & Arévalo 1998). We mapped all trees, saplings and basal sprouts of the plots (with an accuracy of 0.05 m). A detailed summary of tree density, basal area and sapling and seedling density of the plots can be found in Arévalo (1998).

Spatial analysis

We studied the spatial distributions of canopy tree species categories with more than 10 stems per plot using the univariate $K_1(t)$ function, which is the expected number of other individuals within a distance t of any individual, and the bivariate $K_{1,2}(t)$ function, which is the expected number of other individuals of other species within a distance t (Ripley 1977). These analyses are effective in detecting spatial relations between points on a map (Bailey & Gatrell 1995) and are recommended when information of multiple neighbour (closest regenerative stems to every tree) distances are available (Busing 1996). The null hypothesis is the complete randomness of the spatial distribution of tree stems of one species for $K_1(t)$ and complete randomness of spatial distribution of tree stems for each pair of species for $K_{1,2}(t)$. Because a minimum number of stems is required for carrying out these analyses, the number of plots in which we ran the analyses differs for the different species.

The spatial distribution of seedlings and saplings of *Laurus azorica* were analysed with the univariate $K_1(t)$ function. For a graphical representation we used the transformation of the $K_1(t)$ to the $W_1(t)$ proposed by Szwagrzyk (1992). This graphical display allowed us to visualize in only one curve which of the values of the index at different distances differ from a random spatial distribution (for $p < 0.05$). When the spatial distribution of the stem at the given distance does not differ from a random distribution, the value of the curve at that distance is 0. When aggregation is detected, the values of the curve are positive (the value will increase depending on the differences among the expected value and observed value). Negative values of the curve indicate repulsion at the given distance.

Results

The univariate spatial analysis revealed significant clumping for species at different distances (Table 1). All species showed significant aggregation at short distances, but two groups could be differentiated: shade-intolerant and indifferent species showed significant aggregation at all distances in the majority of the plots calculated (especially *Erica scoparia*) and shade-tolerant species only showed significant aggregation at distances < 2 m (*Laurus azorica* and *Prunus lusitanica*). All the trees included in the analyses use asexual reproduction (primarily by basal sprouts), and consequently all the species are aggregated at short distances. Clumped distributions of trees have been observed in other studies (Okuda et al. 1997; Kohyama et al. 1994).

As to the spatial relationships between different tree species as revealed by the Ripley's bivariate $K_{1.2}$, no significant differences were shown in the spatial distribution of analysed species pairs and random distributions for all of the analysed distances.

Figs. 1 and 2 represent the values of the transformation *Wt* of Ripley's univariate $K_1(t)$. Figs. 1a and 2a show that the analysis of seedlings in all the plots revealed aggregation up to 3 m in all the plots, and except for two plots, the rest of them showed significant aggregation up to 10 m (the maximum distance analysed). For saplings (Figs. 1b and 2b), the aggregation distribution is not as consistent as seen in seedlings. Only five plots showed significant aggregation up to 3 m, and only two plots up to 10 m.

Table 1. Results of Ripley's univariate $K_1(t)$ function analysis for species with a density per plot > 10. No significant repulsion has been detected in any of the plots. Data in the table indicate number of plots that showed significant ($p < 0.01$) aggregation at the given distance.

Distance (m)	No. plots*	1	2	3	4	5	6	7	8	9	10
Species											
Erica scoparia	3	3	3	3	3	3	3	3	3	3	2
Ilex canariensis	8	8	8	7	5	3	3	2	2	2	2
Laurus azorica	8	8	4	2	1	0	0	0	0	0	0
Myrica faya	5	5	5	5	4	1	1	1	1	0	0
Prunus lusitanica	4	4	3	0	0	0	0	0	0	0	0

*Number of plots where the analysis was developed. For the other plots the data were not sufficient to satisfactorily run the analysis.

Discussion

Shade-intolerant species could be characterized by their dependence on light (*Myrica faya*) and the preference of the species (*Erica arborea* and *E. scoparia*) for a transitional habitat between laurel forest and pine forest or mountains peaks lashed by winds. The dependence on these habitats result in a clumped spatial distribution. The univariate spatial analysis placed *Ilex canariensis* in the group of shade-intolerant species. The effect of seed predators, herbivores, or pathogens is not documented, but since these factors should lead to spatial repulsion (Augspurger 1983; Clark & Clark 1984), our results suggest that they play a minor, if any, role. We assumed that the proximity of different or the same species would not affect the saplings' ability to reach the canopy as much as other factors (space, light, physiology of species). Asexual regeneration, mainly by basal sprouts in these forest, plays an important role in the spatial distribution of the trees

The univariate analysis of spatial distribution of seedlings of *Laurus azorica* showed a strong trend of aggregation. This trend was less evident for the sapling class, and was almost non existent for the trees, which maintained aggregation only at short distances due to the asexual regeneration. The change from significant clumped to significant regular spatial distribution with increasing age of the stems has been reported in different studies

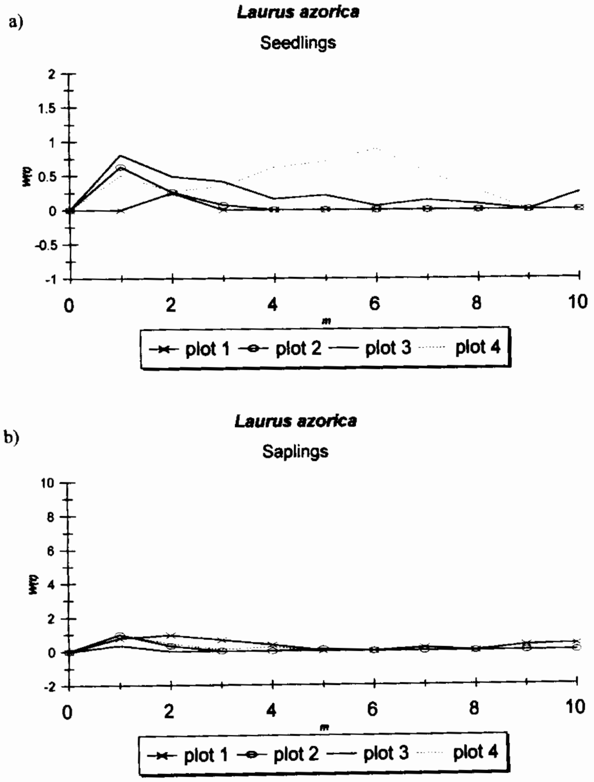

Fig. 1. Values of the index *Wt* for seedlings (**a**) and saplings (**b**) in the four plots (1, 2, 3 and 4) of El Moquinal. The index was calculated every m up to 10 m.

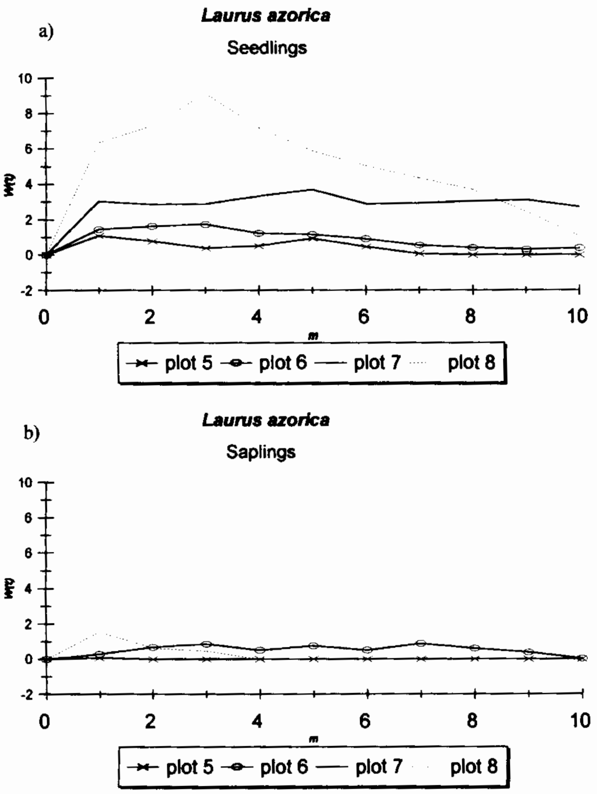

Fig. 2. Values of the index *Wt* for seedlings (**a**) and saplings (**b**) in the four plots (5, 6, 7 and 8) of El Monte de Aguirre. The index was calculated every m up to 10 m.

(Whipple 1980; Good & Whipple 1982). Significant regular distribution of the stems has been related with later successional stages of the forests (Oliver & Larson 1990), but in this forest, the high rate of asexual regeneration could be responsible for the lack of repulsion or random distribution.

With these results, we suggest that the environment could be a more important factor than species interactions on the spatial distribution of the trees, saplings and seedlings of *Laurus azorica*. The effect of the environment on the spatial distributions has been shown in other studies (Manabe & Yamamoto 1997). A low number of species could confirm this hypothesis for the laurel forest.

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Stand structure of *Pinus* forests affected by pine wilt disease

Fujihara, Michiro[1*], Hada, Yoshio[2] & Toyohara, Gentaro[3]

[1]*Natural History Museum and Institute, Chiba; 955-2 Aoba-cho, Chuou-ku, Chiba 260-8682. Japan;*
[2]*Faculty of Informatics, Okayama University of Science, 1-1 Ridai-cho, Okayama 700-0005, Japan;* [3]*Faculty of Science, Hiroshima University, 3-1 Kagamiyama, Higashi-Hiroshima 739-8526, Japan*
[*]*Fax +81432662481; E-mail fujihara@chiba-muse.or.jp*

Abstract. Species composition and stand structure of secondary forests affected by pine wilt disease were studied in western Japan. On the basis of species composition, the vegetation was divided into four types; 1. *Cladonia rangiferina*; 2. *Wikstroemia sikokiana;* 3. *Quercus glauca* and 4. *Gleichenia japonica* type. Height of trees increased from the *C. rangiferina* type to the *Q. glauca* type, whereas conversely the number of trunks decreased. Relative basal area of *Rhododendron reticulatum* and *Juniperus rigida* in the *C. rangiferina* and *W. sikokiana* types was larger than that in the *Q. glauca* type. Relative basal area of *Quercus serrata, Clethra barbinervis* and *Eurya japonica* in the *C. rangiferina* and *W. sikokiana* types was smaller than that in the *Q. glauca* type. The numbers of species and components of evergreen broad-leaved natural forests were reduced because pine forests in the study area had been cut frequently and the land had degraded. Although pine wilt disease has shifted the dominance of pine forests from *Pinus densiflora* to deciduous oaks such as *Quercus serrata*, seed dispersal of evergreen oaks seems to be important for succession to evergreen broad-leaved forest.

Keywords: Degradation; Distribution pattern; Evergreen broad-leaved forest; Mortality rate; Phytosociology; *Pinus densiflora*; *Quercus serrata*; Species-poor forest; Succession; Topography.

Nomenclature: Ohwi & Kitagawa (1983) for seed plants, Ohwi & Nakaike (1978) for ferns and Yoshimura (1974) for lichens.

Introduction

One of the most representative vegetation types in western Japan is *Pinus densiflora* forest, since most natural evergreen broad-leaved forests have been converted to secondary pine forests after disturbances such as clear-cutting, land clearing and fire. In addition, many forest areas have been degraded because of frequent and severe artificial factors, especially in the eastern part of the San-yo district. The numbers of species and individuals of evergreen broad-leaved trees, which are the main component of lucidophyllous forests, are small in this area. After the 1960s, however, pine forests were abandoned and succession has been progressing. Pine wilt disease has also affected the vegetation of pine forests and landscapes. Stand-level dieback has been reported from many kind of forests (Mueller-Dombois 1991) and pine wilt disease is considered to result in stand-level dieback (Fujihara 1996, 1997; Toyohara & Fujihara 1998). Some of the disturbed pine forests have changed to evergreen broad-leaved forests after the disease, especially in the case of species-rich pine forests (Fujihara 1995, 1997). Abrams & Scott (1989) documented a hypothetical example of disturbance-mediated accelerated succession. Fujihara (1996) clarified that the growth of suppressed *Quercus serrata* was accelerated after pine wilt disease and the dominant species changed through pine to deciduous oak from the growth of individual trees of dominants. Disturbance influences the stand structure through modification of the physical environment (White & Pickett 1985). However, the response of each tree species to disturbance by pine wilt disease and structural changes in the forests are still not clear, especially in species-poor forests.

The aim of this study was to examine the structure of pine forest affected by pine wilt disease and to clarify the process of vegetation recovery after the disease in the degraded area.

Study site and Methods

The study site (3.79 ha) is located at 205 to 237 m a.s.l. in the San-yo district at 34° 28' N and 133° 48' E. Geologically, rhyolite covers the site. Mean annual temperature and annual precipitation are 15.2 °C and 1202 mm, respectively, at Kurashiki, the nearest meteorological station (Anon. 1982). In the study area much bare ground is present, and land degradation has occurred because of previous forest fires and frequent cutting over a long period. Pine wilt disease occurred around 1970 (Fujihara 1996).

The field surveys were carried out from 1989 to 1990. Cover-abundance and sociability (Braun-Blanquet 1964) were recorded in 63 quadrats established randomly in the study area. Classification of communities was made on the basis of species composition using phytosociological methods (Braun-Blanquet 1964; Muller-Dombois & Ellenberg 1974). A vegetation map was made based on the occurrence or absence of the differential species by the field survey.

In order to clarify the structure of stands, eight plots (40 to 100 m^2) were established on two belt transects on an east-facing slope (Fujihara 1996). Cover-abundance and sociability (Braun-Blanquet 1964) of all vascular plants in each layer were recorded in each plot. Species name, tree height (H) and trunk diameter at breast height (DBH) were recorded for living trees taller than 1 m in each plot. Species name and number of dead trees were also recorded. To estimate the severity of disturbance by pine wilt disease, mortality rates of pine trees were calculated using the following equation:

Mortality (pine) = (number of fallen dead pine trees/total number of dead and living pine trees) × 100

To estimate change in structure after pine wilt disease, mortality of light-demanding trees (*Juniperus rigida, Rho-*

Table 1. Species composition of forest vegetation in the degraded area. 25 species occurring with low frequencies are omitted.

Vegetation type[1]	*Cladonia rangiferina* type		*Wikstroemia sikokiana* type		*Quercus glauca* type		*Gleichenia japonica* type	
Number of stand	5		18		30		7	
Mean number of species	21		16		17		9	
1. *Pinus densiflora* group								
Pinus densiflora	V[2]	2-4[3]	V	1-5	IV	1-5	IV	1-2
2. *Rhododendron reticulatum* group								
Rhododendron reticulatum	V	1-3	V	2-3	V	+-3	V	+-2
Quercus serrata	V	+-1	V	+-2	V	+-4	IV	+-4
Lyonia ovalifolia var. *elliptica*	IV	2	V	+-3	V	+-3	III	1-3
3. *Cladonia rangiferina* group								
Cladia aggregata	V	+-1	.		.		.	
Cladonia rangiferina	V	+	.	.	.			
4. Wikstroemia sikokiana group								
Miscanthus sinensis	V	+-2	IV	+-1	.		.	
Rhododendron kaempferi	V	1-2	V	+-1	I	+	.	
Wikstroemia sikokiana	IV	+-1	III	+-1	.		.	
Vaccinium bracteatum	IV	1	II	+-1	.		.	
5. *Quercus glauca* group								
Dendropanax trifidus	.		I	+	III	+	.	
Myrica rubra	.		I	+	II	+-2	.	
Pinus densi-thunbergii	.		.		II	+-2	II	+-1
Ligustrum japonicum	.		.		II	+	.	
6. *Gleichenia japonica* group								
Gleichenia japonica	.		I	+	I	+-2	V	4-5
7. *Eurya japonica* group								
Eurya japonica	V	1-2	V	1-3	V	2-5	V	4-5
8. *Pieris japonica* group								
Ilex pedunculosa	V	1-2	V	1-3	V	1-2	IV	1-2
Clethra barbinervis	V	+-1	III	+-2	V	+-5	IV	+-2
Ilex crenata	V	+-2	V	+-1	V	+-1	II	+
9. Others								
Smilax china	V	+-1	V	+-1	V	+-1	V	+-2
Juniperus rigida	V	3	V	2-3	V	1-3	V	1-2
Rhus trichocarpa	V	+	V	+	V	+-1	II	+
Vaccinium oldhamii	V	1-2	V	1-3	III	+-1	.	
Dicranopteris linearis	III	+-1	V	+-5	IV	+-5	I	3
Symplocos prunifolia	II	+	I	+	IV	+-3	.	
Ternstroemia gymnanthera	.		I	+-1	II	+-1	.	

[1] All vegetation types belong to *Querco glaucae-Pinetum densiflorae*;
[2] Frequency (Braun-Blanquet 1964); [3] Range of cover-abundance (Braun-Blanquet 1964).

dodendron reticulatum, *Vaccinium oldhamii* and *Lyonia ovalifolia* var. *elliptica*) were calculated from the following equation:

Mortality (light-demanding trees) = (number of standing dead light-demanding trees/total number of dead and living light-demanding trees) × 100

Results

Vegetation types

Vegetation types were classified into four types on the basis of species composition (Table 1). The *Cladonia rangiferina* type is characterized by the occurrence of lichens, such as *Cladonia rangiferina* and *Cladia aggregata*. The *Wikstroemia sikokiana* type is characterized by the occurrence of full-light demanding plants, such as *Wikstroemia sikokiana*, *Rhododendron kaempferi*, *Miscanthus sinensis* and *Vaccinium bracteatum*. The *Quercus glauca* type is characterized by the occurrence of evergreen broad-leaved trees, such as *Dendropanax trifidus*, *Myrica rubra* and *Ligustrum japonicum*. The *Gleichenia japonica* type was characterized by the dominance of *G. japonica*. Evergreen *Quercus*

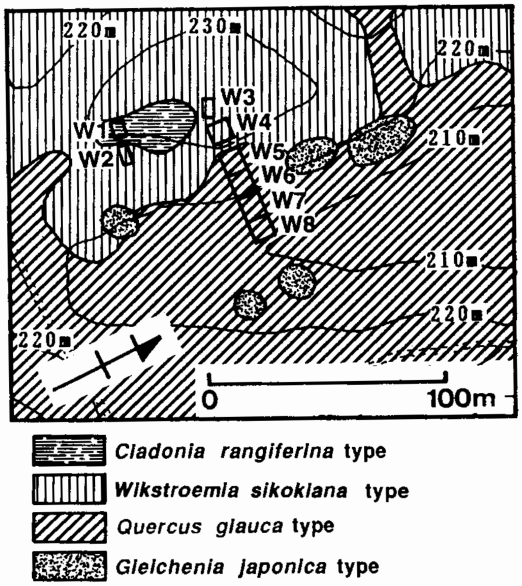

Fig. 1. Vegetation map for 1989 based on the field survey.

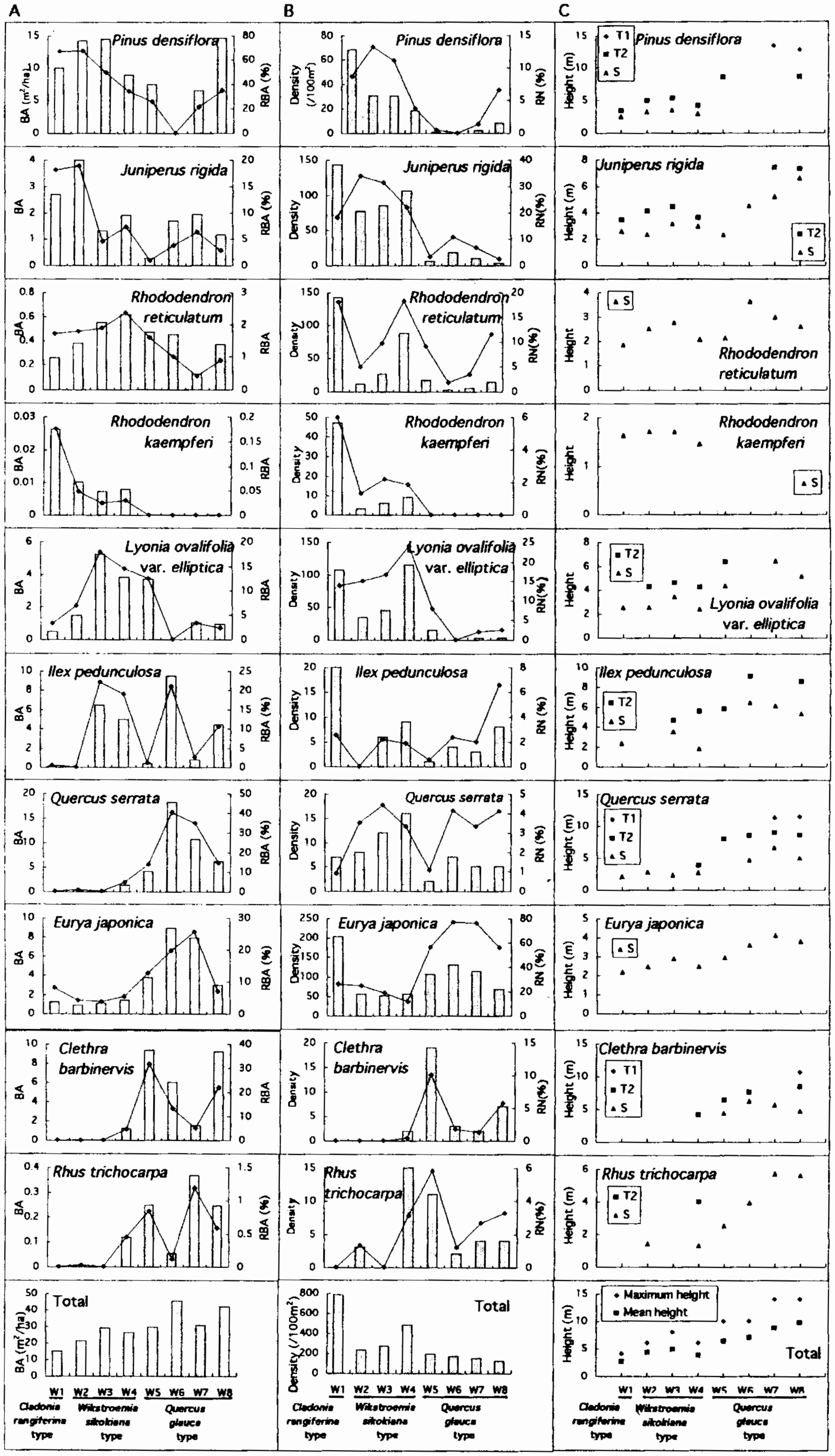

Fig. 2. Basal area (BA), density and height of trees in each vegetation type. **A.** Basal area (column) and relative basal area (line). **B.** Density (column) and relative number (line). **C.** Mean height of main tree species in each layer and maximum and mean height of all trees. T1: tree layer. T2: subtree layer. S: shrub layer.

and *Castanopsis* were not found in the quadrats.

The number of plant species in each vegetation type was small (9 to 21) in the present study area, indicating that severe disturbances such as fire, clear-cutting, land clearance had occurred frequently.

Fig. 1 shows the distribution of each vegetation type. The *Cladonia rangiferina* type was located on ridges. The *Wikstroemia sikokiana* type was located on ridges and the upper parts of slopes, whereas the *Quercus glauca* type was located on the middle and lower parts of slopes. Plot W1 belonged to the *Cladonia rangiferina* type, plots W2, W3 and W4 to the *Wikstroemia sikokiana* type, and plots W5, W6, W7 and W8 to the *Quercus glauca* type (Fujihara 1996).

Mortality rate of Pinus trees

Mortality rate increased from the *Cladonia rangiferina* type (mean+s.d.: 0.0 %) through the *Wikstroemia sikokiana* type (12.8 + 10.2 %) to the *Quercus glauca* type (58.8 + 36.8%). The basal area of dead pine trees was larger for the *Quercus glauca* type (12.0 + 10.0 m^2/ha). Pine wilt disease was severe in the late successional stages.

Basal area of trees in each vegetation type

Fig. 2A shows the basal area (BA) and relative value of basal area (RBA) of trees. Total basal area increased from the *Cladonia rangiferina* type to the *Quercus glauca* type. The relative basal area of *Pinus densiflora*, *Juniperus rigida*, *Rhododendron reticulatum*, and *R. kaempferi* was larger in the *Cladonia rangiferina* and *Wikstroemia sikokiana* types than in the *Quercus glauca* type. *Pinus densiflora* still dominated in the *Cladonia rangiferina* and *Wikstroemia sikokiana* types after pine wilt disease. The basal area and relative basal area of *Quercus serrata*, *Eurya japonica*, *Clethra barbinervis* and *Rhus trichocarpa* were large in the *Quercus glauca* type. After pine wilt disease the growth of *Quercus serrata* increased markedly (Fujihara 1996) and *Quercus serrata*, *Clethra barbinervis*, and *Pinus densiflora* became the co-dominant tree species in the *Quercus glauca* type.

Density of trees in each vegetation type

Total tree density decreased from the *Cladonia rangiferina* type (786/100 m^2) through the *Wikstroemia sikokiana* type (227 to 479/100 m^2) to the *Quercus glauca* type (122 to 189/100m^2) (Fig. 2B). These densities were higher than those of species-rich pine forests. The densities and relative value of densities of light-demanding trees, such as *Pinus densiflora*, *Juniperus rigida*, *Rhododendron reticulatum*, *R. kaempferi* and *Lyonia ovalifolia* var. *elliptica* were higher in the *Cladonia rangiferina* and *Wikstroemia sikokiana* types than in the *Quercus glauca* type. Relative density values (RN: relative number of trees) for *Eurya japonica* and *Clethra barbinervis* were higher in the *Quercus glauca* type than in the *Cladonia rangiferina* and *Wikstroemia sikokiana* types. There were no evergreen oaks, which are the dominant species of natural evergreen broad-leaved forests in western Japan.

Height of trees in each vegetation type

Mean height of trees in each layer is shown in Fig. 2C. Tree height increased from the *Cladonia rangiferina* type to the *Quercus glauca* type. Differences in size were not related to age. Mean height of pine trees exceeded 8 m in the *Quercus glauca* type, compared to less than 6 m in the *Cladonia rangiferina* and *Wikstroemia sikokiana* types. *Quercus serrata* constituted a shrub layer in the *Cladonia rangiferina* and *Wikstroemia sikokiana* types, while *Q. serrata* constituted an upper canopy layer in the *Quercus glauca* type.

Mortality of light-demanding trees

The mortality of light-demanding trees (*Juniperus rigida*, *Rhododendron reticulatum*, *Vaccinium oldhamii* and *Lyonia ovalifolia* var. *elliptica*) was higher in the *Quercus glauca* type (mean+s.d.: 60+5 %) than in the *Wikstroemia sikokiana* type (20+2 %) and the *Cladonia rangiferina* type (15 + 10 %).

Discussion

The density of trees decreased from the *Cladonia rangiferina* type through the *Wikstroemia sikokiana* type to the *Quercus glauca* type, whereas conversely, the size of the trees increased. Soil conditions in the *Cladonia rangiferina* and *Wikstroemia sikokiana* types appear to be dry, because they are located on ridges and the upper parts of slopes. On the other hand the soil conditions seem to be mesic in the *Quercus glauca* type, because it is located on the lower parts of slopes.

Disturbance influences the structure of stands through modification of the physical conditions (White & Pickett 1985), and disturbance releases resources to surviving plants (Chanham & Marks 1985). In low-diversity biomes, where only a few canopy species dominate the vegetation cover, these dominants often play a key role in the dynamics of such ecosystems (Muller-Dombois 1991). The canopy layer of pine forests was composed of pine trees before the appearance of pine wilt disease, and the disappearance of canopy pines affected the ecosystem drastically. The growth of previously suppressed small oak (*Q. serrata*) trees was accelerated after dieback of the pine trees (Fujihara 1996). In addition to *Q. serrata*, *Eurya japonica* and *Clethra barbinervis* became co-dominant trees after the disease in the *Q. glauca* type.

After the rapid growth of *Q. serrata* and other species, light conditions seem to have changed. Mortality of light-demanding trees was higher in the *Quercus glauca* type than in the *Cladonia rangiferina* and *Wikstroemia sikokiana* types. Light-demanding tree species were considered to have died during this decade, because most of the dead trees were standing. Light conditions became dark and soil conditions became moist after the rapid growth of *Q. serrata* and other species in stands that were severely affected by the disease. The main component species changed from light-demanding plants to relatively shade-tolerant ones in terms of basal area and number of trees, thus creating physical conditions for shade-tolerant evergreen broad-leaved trees.

In the species-rich forests, the dominant species change from pine to evergreen broad-leaved types directly after pine wilt disease (Fujihara 1995, 1997). At the present study site, the numbers of species and individuals of components of natural evergreen broad-leaved forests were less than those in species-rich pine forests. To stimulate the succession from deciduous oak to evergreen oak forests in degraded areas, it is important to establish evergreen broad-leaved trees, such as *Quercus glauca* and *Castanopsis cuspidata*.

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Soil seed banks in primeval deciduous forest in Bialowieża, Poland

Jankowska-Blaszczuk, Malgorzata

Department of Botany, Pedagogical University of Kielce,
15 Konopnicka Street, 25-406 Kielce, Poland
Fax + 41 3686642; E-mail mjanko@pu.kielce.pl

Abstract. Three hypotheses are tested concerning size and diversity of the seed bank composition in primeval deciduous *Tilio-Carpinetum* forest in Bialowieża, NE Poland: 1. In undisturbed patches the seed bank is small and species-poor and dominated by the herbs on the forest floor; 2. There is no difference in seed bank between primeval forest and regeneration forest at least 90 yr old; 3. In the seed bank from patches of secondary tree stands more species from the aboveground vegetation are absent.

During 4-yr observations the primary tree stand had 3167 seeds/m^2 belonging to 40 species, the secondary tree stand 3827/m^2 with 42 species. There were no significant differences between the primary tree stand and the 90-yr old regeneration stand. As to hypothesis 3, species absent or scarce in the herb layer were more abundant in the secondary tree stand.

Keywords: Disturbance; Herb layer; Primary tree stand; Secondary tree stand; *Tilio-Carpinetum*.

Nomenclature: Tutin et al. (1964-1980).

Introduction

One of the soundest generalizations concerning soil seed banks of primeval, temperate deciduous forest community is that they are small and species-poor and diverge from the standing vegetation at the site (Pickett & McDonnell 1989; Thompson 1992). The main components of such banks are early successional, light demanding species, which life strategy is connected with periodically appearing disturbance.

The aim of the present study is to test three hypotheses concerning the size and diversity of seed bank species composition in a natural deciduous forest community, as well as in a comparison of such bank with the bank deriving from the patches within the secondary tree stand that spontaneously appeared 90 yr ago after clear-cutting.

1. In undisturbed patches of the natural *Carpinus* forest the seed bank is small, species-poor and dominated by the herbs present on the forest floor.
2. There is no difference between the size and species diversity of the seed bank in the primary *Carpinus* forest and patches where the regeneration process after clear-cutting began about 90 yr ago.
3. The seed bank taken from the patches within the secondary tree stand is characterized by a higher percentage of species absent in aboveground vegetation

Study sites

The studies were conducted in a part of the primeval forest in the Bialowieża National Park assigned to the *Tilio-Carpinetum* (Faliński et al. 1988). There are three parallel forest belts with a secondary tree stand originating from a clear-felling (ca. 90 yr ago), each 1076 m (1 verst) × 108 m; they alternate with, and are enclosed by, primary forest. The primary forest is dominated by *Carpinus*, *Tilia* and *Quercus* with abundant *Acer* and *Picea*, while the patches within the secondary tree stand is dominated by *Betula* and *Populus* with some *Picea*, all of which invaded spontaneously. In both forest types there is virtually no shrub layer, and the moss layer is sparse and species-poor. The herb layer is species-rich and quite similar in composition in the two forest-types.

Methods

The seed bank was estimated by the seedling emergence method. Plots for the study of the herb layer structure and the seed bank were established within the permanent site of the Bialowieża Geobotanical Station of Warsaw University (Faliński et al. 1988). The dominance structure of vascular plants in the herb layer was determined by analysis of species frequency in 50 plots 2 m × 2 m each. The soil samples were taken early spring 1993 from these 50 plots which were situated in primary forest (25 plots) and in forest with a secondary tree stand. Altogether 50 samples (31 cm × 31 cm × 5 cm) were dug from the centre of each 2 m × 2 m quadrat. The litter layer was removed from samples, while stolons and rhizomes and larger roots were pulled out, and was then replaced. Soil samples were kept in an unheated glasshouse, observations were made at 10-day intervals during the growing season from April 1993 to 30 October 1996. On each occasion the numbers of identifiable seedlings were recorded by species, and the seedlings then removed. After each recording the soil surface of each soil monolith was stirred to a depth of 2 - 3 cm avoiding only seedlings left to grow on. When the sample yielded no new seedlings at two successive recording sessions, and no seedlings were left to grow on, the soil was stirred to its full depth. Identification was based on the forest herbarium of seedlings and the atlas of Čsapody (1968).

Results

The hypothesis that the seed bank of a natural deciduous forest community would be poor in species and of low density has not been confirmed. In 25 soil samples taken under the primary tree stand 7610 seedlings (3167/m^2) and 40 species were recorded during the four-year observation, whereas in the samples from the secondary tree stand were 9195 (3827/m^2) seedlings of 42 species occurred. In both stands there were 46 species in total, and 36 were common (Fig. 1). Of all seedlings 319 grasses and 4 dicots were not identified by species.

The mean number of seedlings per sample amounted to

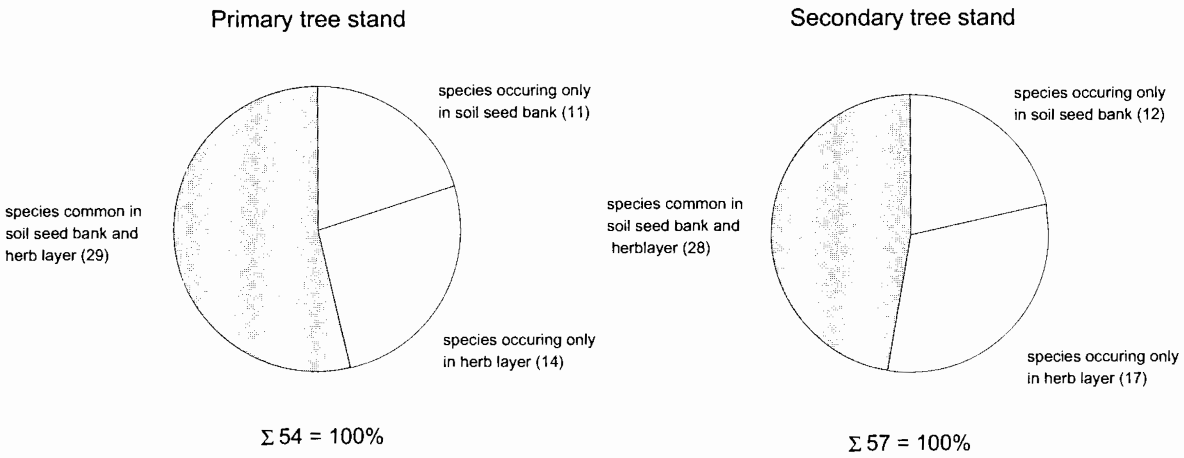

Fig. 1. Percentage of number of species occurring in the soil seed bank and herb layer of a deciduous forest with primary and secondary tree stands.

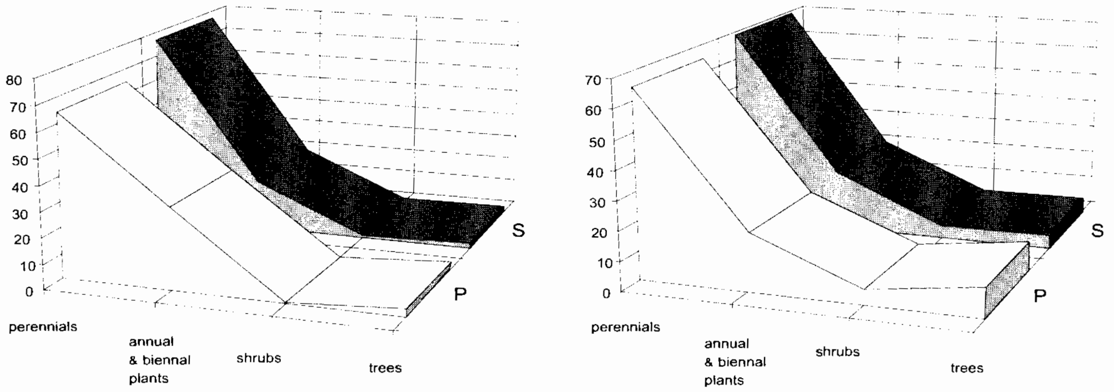

Fig. 2. Percentage of different biological groups of species in the soil seed banks of a deciduous forest with primary (P) and secondary (S) tree stands.

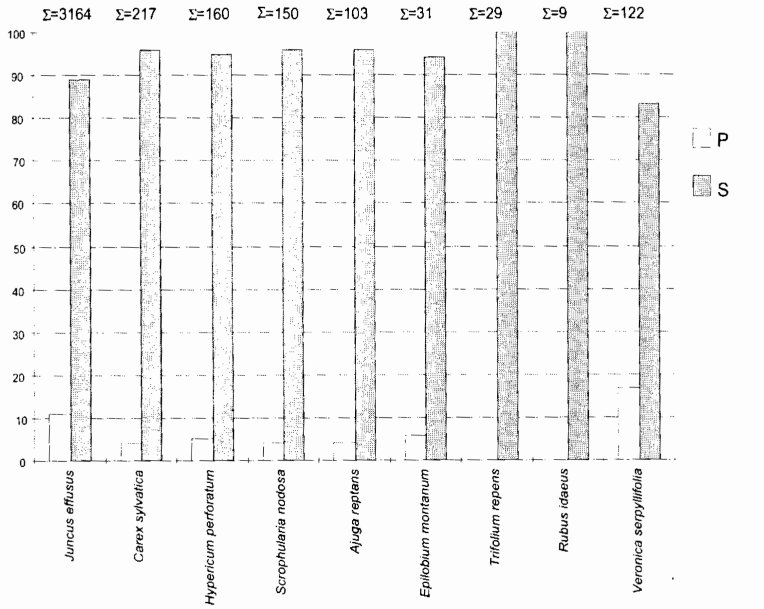

Fig. 3. Number of seedlings emerging from soil seed banks of deciduous forest with primary (P) and secondary (S) tree stands – referring to species which were absent or sparse in the herb layer.

304.4±220.2 for the samples taken under the primary stand and 367 ± 187.8 for those taken under the secondary one. The mean number of species was 15±3.4 in the seed bank of the primary tree stand and 17.2 ± 3.5 in that of the secondary one.

The diversity of the seed banks in each forest stand turned to be very similar, the Shannon Index amounted to 2.21 for the primary tree stand and 2.25 for the secondary one. In both forest types the seed banks were dominated by herbs (Table 1, Fig. 2).

It was found that in both cases the species structure of the herb layer was similar to that of the seed bank in 68% for the primary and 67% for the secondary tree stand. In both types of the species that appeared exclusively in the seed bank or vegetation cover was very similar.

The hypothesis that species absent from the herb layer or present there only sporadically are much more abundant in the seed bank from forest with secondary tree stand was confirmed (Fig. 3). This group includes: *Juncus effusus*, *Carex sylvatica*, *Hypericum perforatum*, *Trifolium repens*, *Epilobium montanum*, *Ajuga reptans*, *Veronica serpyllifolia*, *Scrophularia nodosa*. The seedlings of these species constituted more than one third of all seedlings that emerged in the samples from the secondary tree stand and only 5% in those from the primary one.

Table. 1. Numbers of seedlings emerged from soil the seed bank (bank) originated from forest with primary and secondary tree stand. Frequency of species in current herb layer (herb l.). Number of sample $n = 25 + 25$ ($P + S$). Size of sample 31 cm × 31 cm × 5 cm.

	Primary tree stand				Secondary tree stand			
	Σ	Mean no. /sample ± SE	Frequency bank	Frequency herb l.	Σ	Mean no. /sample ± SE	Frequency bank	Frequency herb l.
Perennials								
Urtica dioica	2571	102.84 ± 167.43	96	76	1445	57.80 ± 74.65	96	72
Chrysosplenium alternifolium	1183	47.32 ± 44.70	96	72	1549	61.96 ± 79.26	88	68
Juncus effusus	340	13.60 ± 26.09	84	0	2824	112.96 ± 117.51	96	0
Geranium robertianum	237	9.48 ± 11.84	84	68	230	9.20 ± 10.16	88	40
Oxalis acetosella	173	6.92 ± 6.24	96	92	111	4.44 ± 4.26	96	88
Ranunculus lanuginosus	42	1.68 ± 3.86	28	64	8	0.32 ± 0.80	16	60
Ranunculus repens	34	1.36 ± 3.50	28	8	54	2.16 ± 7.73	20	12
Geum urbanum	31	1.24 ± 3.05	32	36	11	0.44 ± 1.64	12	28
Anemone nemorosa	23	0.92 ± 1.66	40	80	9	0.36 ± 0.75	24	72
Stachys silvatica	22	0.88 ± 2.88	20	32	16	0.64 ± 1.32	28	28
Glechoma hirsuta	16	0.64 ± 1.08	32	76	35	1.40 ± 2.42	52	88
Stellaria nemorum	16	0.64 ± 0.86	44	88	14	0.56 ± 1.64	24	84
Rumex sanguineus	14	0.56 ± 0.87	36	16	27	1.08 ± 3.58	32	12
Carex sylvatica	9	0.36 ± 0.57	32	4	208	8.32 ± 11.80	80	4
Hypericum perforatum	8	0.32 ± 1.07	12	0	152	6.08 ± 11.06	60	0
Lamiastrum galeobdolon	7	0.28 ± 0.84	16	96	2	0.08 ± 0.28	8	68
Taraxacum officinale	6	0.24 ± 0.83	12	0	6	0.24 ± 0.66	16	0
Trifolium repens	6	0.24 ± 0.52	20	0	144	5.76 ± 6.6	92	0
Circaea lutetiana	5	0.20 ± 0.50	16	16	62	2.48 ± 8.75	16	8
Mentha arvensis	5	0.20 ± 1.00	4	0	0	0.00 ± 0.00	0	0
Scrophularia nodosa	4	0.16 ± 0.37	16	4	99	3.96 ± 14.36	36	8
Aegopodium podagraria	3	0.12 ± 0.44	8	40	0	0.00 ± 0.00	0	32
Cardamine amara	2	0.08 ± 0.28	8	12	4	0.16 ± 0.62	8	0
Cirsium arvense	2	0.08 ± 0.28	4	0	3	0.12 ± 0.33	12	0
Epilobium montanum	2	0.08 ± 0.28	8	0	29	1.16 ± 3.09	20	0
Mycelis muralis	2	0.08 ± 0.40	4	8	1	0.04 ± 0.20	4	4
Ajuga reptans	0	0.00 ± 0.00	0	0	29	1.16 ± 1.68	48	8
Asarum europaeum	0	0.00 ± 0.00	0	0	1	0.04 ± 0.20	4	4
Lathyrus vernus	0	0.00 ± 0.00	0	4	2	0.08 ± 0.28	8	0
Veronica serpyllifolia	0	0.00 ± 0.00	0	0	9	0.36 ± 0.96	16	0
Viola reichenbachiana	0	0.00 ± 0.00	0	8	2	0.08 ± 0.28	8	8
Annual and biennial plants								
Impatiens noli-tangere	1083	43.32 ± 52.19	76	72	779	31.16 ± 26.32	88	76
Cardamine flexuosa	660	26.4 ± 40.61	76	48	837	33.48 ± 38.77	88	58
Lapsana communis	288	11.52 ± 50.17	44	36	29	1.16 ± 3.94	16	12
Moehringia trinervia	262	10.48 ± 20.86	76	64	59	2.36 ± 3.33	60	80
Galeopsis tetrahit	32	1.28 ± 2.03	44	16	28	1.12 ± 3.19	40	12
Stellaria media	20	0.80 ± 2.27	24	8	4	0.16 ± 0.47	12	16
Polygonum hydropiper	3	0.12 ± 0.44	8	0	6	0.24 ± 0.66	16	0
Gnaphalium uliginosum	1	0.04 ± 0.20	4	0	2	0.08 ± 0.28	8	0
Capsella bursa-pastoris	0	0.00 ± 0.00	0	0	1	0.04 ± 0.20	4	0
Shrubs								
Rubus idaeus	21	0.84 ± 1.89	32	16	101	4.04 ± 3.81	76	28
Cornus sanguinea	3	0.12 ± 0.44	8	0	4	0.16 ± 0.37	16	0
Trees								
Betula pendula	192	7.68 ± 5.01	96	4	197	8.00 ± 5.72	100	12
Carpinus betulus	14	0.56 ± 0.65	52	76	0	0.00 ± 0.00	0	58
Picea abies	4	0.16 ± 0.37	16	12	1	0.04 ± 0.20	4	8
Tilia cordata	2	0.08 ± 0.28	8	32	0	0.00 ± 0.00	0	24
Gramineae	260	10.40 ± 15.6	60	-	59	2.36 ± 2.68	68	-
Unknown	2	0.08 ± 0.40	4	-	2	0.08 ± 0.28	8	-

Conclusion

In natural and not disturbed patches of *Carpinus* forest the seed bank is relatively species-rich and dense. However, if we compare the results given in this study with those for early successional communities, it seems obvious that such communities are characterized by more abundant seed banks (Symonides 1986; Leck & Parker 1989; Falinška 1999).

The results of the study show that in the patches with primary and secondary 90-yr-old tree stands seed banks do not differ in their density and species composition. There is only visible difference in the contribution of species absent from the herb layer. In the seed bank of the patch, where the trees were cut about 90 yr ago, there are many more species missing from the herb layer; those missing are characterized by high light-demand. It seems highly probable that these species would appear abundantly in the gaps as soon as the trees were cut, whereafter they began to withdraw from the forest floor as a result of the closing of the tree canopy and shading. In the ecological literature many data show that these are ubiquitous long-lived seeds that occur in the seed banks of entirely different plant communities (Thompson et al. 1997).

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Landscape changes caused by forest fire and vegetation regeneration processes

Lee, C.-S.[1]*, Moon, J.-S. & Kim, J.-E.

[1]*Faculty of Environment and Life Sciences, Seoul Women's University, Seoul 139-774, Korea;*
**Fax +8229705822; E-mail leecs@swift2.swu.ac.kr*

Abstract. The effects of fire on landscape changes were investigated in eastern Korea. Three types of fire in the order of decreasing intensity were recognized: crown fire, severe surface fire, and light surface fire, and their occurrences were depicted on a fire map. Fire types were different according to vegetation type: most pine forests were disturbed by crown fire, while oak and mixed forests were disturbed by light surface fire. As a result of an analysis using GIS, the area disturbed by crown fire was the largest, followed by light surface fire. The regeneration strategy in burned areas was to make sprouts from burned oak stumps. The species composition of burned pine forest changed similarly to that of oak forest, but changes in the burned oak forest were small. A higher density and growth rate of oak sprouts, as compared to the unburned areas, facilitated vegetation succession from *P. densiflora* forest to oak forest and consequently led to change of landscape pattern.

Keywords: Landscape change; Fire type; GIS; *Pinus densiflora*; Regeneration strategy.

Introduction

Changes in landscape pattern are significantly correlated with the type of artificial or natural disturbances and the intensity, probability and frequency of that disturbance (Franklin & Forman 1987; Turner & Bratton 1987). Human activity is one of the important causal factors of disturbance (Holzner et al. 1983; Zonneveld 1989; McDonnell & Pickett 1990). Fire has been considered as the most important natural and human-induced disturbance, inducing ecosystem and landscape heterogeneity because of its intensity and high frequency (Romme 1982; Pickett & White 1985; Turner & Bratton 1987; Turner et al. 1994; Trabaud & Galti 1996).

Ignition sources of forest fires in Korea are generally artificial, such as misuse of fire for agricultural and forest management, burning of rubbish, and accidental fire from discarded cigarette butts (Forest Research Institute 1996). Propagation of forest fires is largely influenced by weather and forest conditions (Whelan 1995). The resistance of trees to fire varies among species. For example, broadleaved trees composing climax forests are not burnt easily. However, most post-fire invaders of secondary forest tend to burn easily (Nakagoshi 1984; Nakagoshi et al. 1987).

The regeneration sources of plant species in burned stands are sprouts from burned stumps, belowground organs, buried seeds, and newly invading seedlings (Nakagoshi 1987). Regeneration strategies by those sources are influenced by fire intensity, burning season, and fire interval (Malanson 1987). Therefore, it is necessary to understand the effect of fire as one of the disturbance factors causing changes in landscape pattern and landscape structure to establish the ecological framework for restoration of fire-disturbed vegetation (Hong & Lee 1997).

The purpose of this study is: (1) to map fire types through defining the landscape patch as identified by field survey according to fire intensity ; (2) to evaluate the successional trends of vegetation after fire of different intensity; and (3) to predict changes in landscape pattern by analysing such results in relation to land-use pattern of the region.

Study area

The largest forest fire in modern history of Korea occurred in 1996 in Kosung-Gun, eastern Korea. Kosung-Gun is located on the east of the Taeback Mountains, which divides Kangwon Province into the Youngdong region and Youngseo regions.

The total area of Kosung-Gun is 62 138 ha, the vegetated area is 46 920 ha (75.5%), and the area burned by the 1996 fire is ca. 5000 ha (8.0%). Before the fire the vegetation in this area was mainly composed of *Pinus densiflora* forest and pine-oak mixed forest (ca. 65% of the total vegetation cover) (Table 1). This pine forest, situated in a rural region, had been dominated by traditional landscape management practices, such as logging for timber and harvesting undergrowth for fuel, compost, and feed for livestock, slash and burn agriculture. Additionally, edible mushrooms (*Tricholoma matsutake*) are a remarkable economic asset and this product also contributed to the conservation of the pine forest.

Methods

This study focused on changes of landscape structure and pattern by disturbance of fire. Fire was classified into three types. When whole parts of tree including crown and stem as well as undergrowth on the forest floor were burnt, it was classified as crown fire. When all parts below the crown were burnt, it was classified as severe surface fire. When only the lowest part of the tree was burnt and the cambium under the bark was not burnt, so that most tree leaves remained alive, it was classified as light surface fire.

Fire types were mapped on a topographic map at scale 1:25 000. The smallest patch size on the map was 625 m^2 (25m × 25m). Smaller patches were ignored. LANDCADD (GIS supported by AutoCAD) was used for mapping vegetation and fire types. We established permanent 100-m^2 quadrats at each site with different fire types. Location of all woody plants within each permanent quadrat was plotted. Successional trends were interpreted by analysing changes of importance value and diameter (mature tree: diameter at breast height, seedling and sapling: diameter at the base. Location of all woody plants within each perma-

Table 1. Size (ha) and percentage of landscape elements in the fire-disturbed area of Kosung, Korea.

Landscape element	Size (ha)	Percentage
Pine forest	3134	45.6
Mixed forest	1304	19.0
Oak forest	407	5.9
Plantation	24	0.3
Agricultural land	1543	22.5
Inhabitated area	350	5.1
Aquatic area	108	1.6

Table 2. Size (ha) and ratio (%) of fire types according to the landscape elements in burnt forest, Kosung, Korea.

Landscape element	Light surface fire	Severe surface fire	Crown fire
Pine forest	722 (14.8)	700 (14.4)	1712 (35.2)
Mixed forest	626 (12.9)	263 (5.4)	415 (8.5)
Oak forest	206 (4.2)	23 (0.5)	178 (3.7)
Plantation	24 (0.5)	- -	- -

nent quadrat was plotted. Successional tendency was interpreted by analysing changes of importance value and diameter (mature tree: using importance values for species with frequency values higher than 10%. We addressed the effect fire facilitating succession by comparing the growth rate of height and diameter of regenerating individuals.

Results and Discussion

Vegetation prior to fire

Before the fire, vegetation tended to be distributed in the following order, moving from the coast to the inland areas: pine forest, mixed forest of pine and oaks, and oak forests. Pine forest was mainly dominated by *Pinus densiflora*. Pine-oak mixed forest and oak forest were dominated by *P. densiflora* and *Quercus mongolica*, respectively. Agricultural land and residential areas were restricted to lowland near the coast and at stream sides. Table 1 presents the real extent of the different landscape elements.

P. densiflora forest, especially in rural regions, is a secondary forest, and it has been periodically managed for the production of *Tricholoma matsutaka*. In addition, periodical cutting and thinning to obtain wood, fuel, feed for livestock, and organic fertilizer, have also played an important role in maintaining this forest type (Nakagoshi 1987). With decreased human disturbance, pine forest commonly succeeds to oak forest (Lee 1989). Large patches of pine forest occur in the lowlands only near areas frequently disturbed by people. By contrast, oak forest (with *Quercus mongolica*) was found only in remote places.

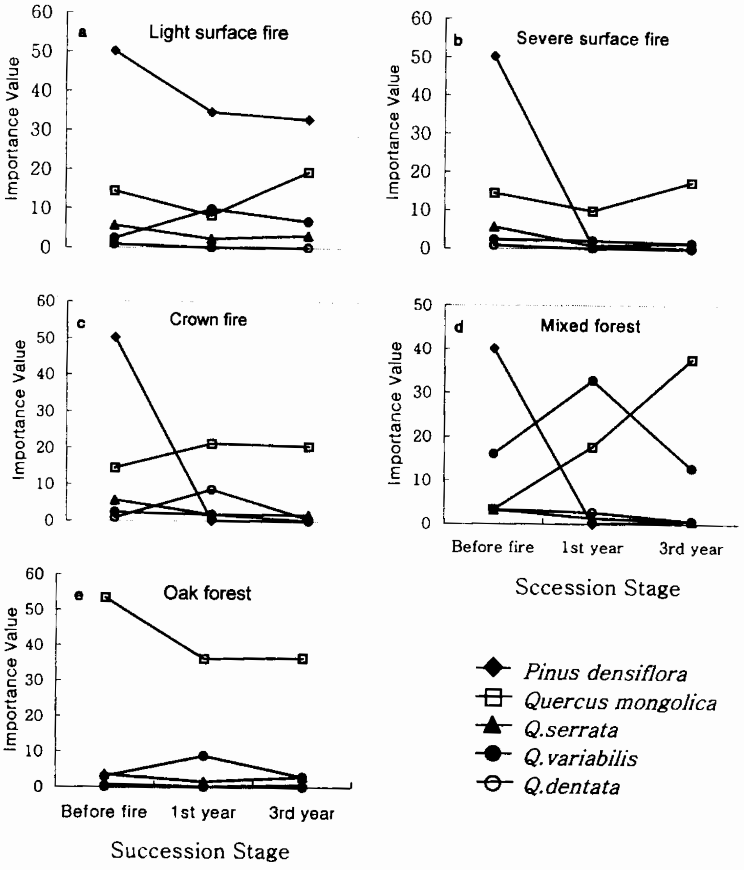

Fig. 1. Changes in importance values of dominant woody species with the lapse of years after fires at sites different in fire density and vegetation type. **a**, **b** and **c** are pine forests; **d** is mixed and **e** is oak forest; they were disturbed by severe and light surface fires, respectively.

Fire-disturbance types

The fire map showed that crown fire was mainly distributed in the eastern part of the study area, while light and severe surface fires of low intensity were found in the western part.

Fire types were different according to vegetation type (Table 2) (Johnson 1995; Whelan 1995). This is because fuel conditions govern the spread and intensity of fire and vary by vegetation type. In fact, most pine forests were disturbed by crown fire, while the ratio of light surface fire was the highest in the oak and mixed forests. We deduced that such a difference might be related to characteristics of bark of pine and oak which have different contents of flammable resins. Moreover, considering the fact that pine has a higher tolerance to water deficit than oak (Lee 1997), the higher intensity of fire in pine forests could be caused by a difference in moisture conditions. Consequently, the spreading of fire was likely determined by the synergism of the pine-dominated vegetation type and habitat conditions (e.g. wind, soil moisture).

The effect of fire on succession

In the pine forest disturbed by light surface fire, the importance value of *P. densiflora* somewhat decreased, while those of oaks tended to increase. In the pine forests disturbed by severe surface and crown fires, there was heavy mortality of *P. densiflora* and the importance value of oaks increased and became dominant (Fig. 1). In oak forest disturbed by light surface fire, the importance value of oaks more or less decreased but they remained the dominant species. Mixed forest and pine forest showed a similar pattern (Fig. 2). These results suggest that pine forest will be replaced by oak forest and oak forest will be maintained continuously.

The size distribution of the major tree populations helps us to describe succession (Barbour et al. 1987). Fig. 2 shows the size distribution of major woody species in the unburned pine (a), oak (b), and mixed (c) forests, and the burned pine, mixed, and oak forests that varied in fire intensity and time since fire (d-i). In all the pine and mixed forests, the *P. densiflora* population is composed of two groups: mature trees and young trees. From the size distribution, we see that seedlings and saplings of pine had been recruited before fire. This active recruitment of pine seedlings probably started after cutting of pine or undergrowth including oaks considering that *P. densiflora* is a shade-intolerant species.

Oaks in the unburned pine forest were composed of young trees less than 10 cm in diameter (Fig. 3). Their diameter was smaller than that of young pine trees but their density (7100/ha) was higher than that of young pine trees (2300/ha). These data show that pine tends to be replaced by oak during succession. By contrast, most oaks that occurred in both unburned and burned pine forests were sprouts that originated from cut stumps. From this we deduce that succession had been retarded by excessive artificial interference.

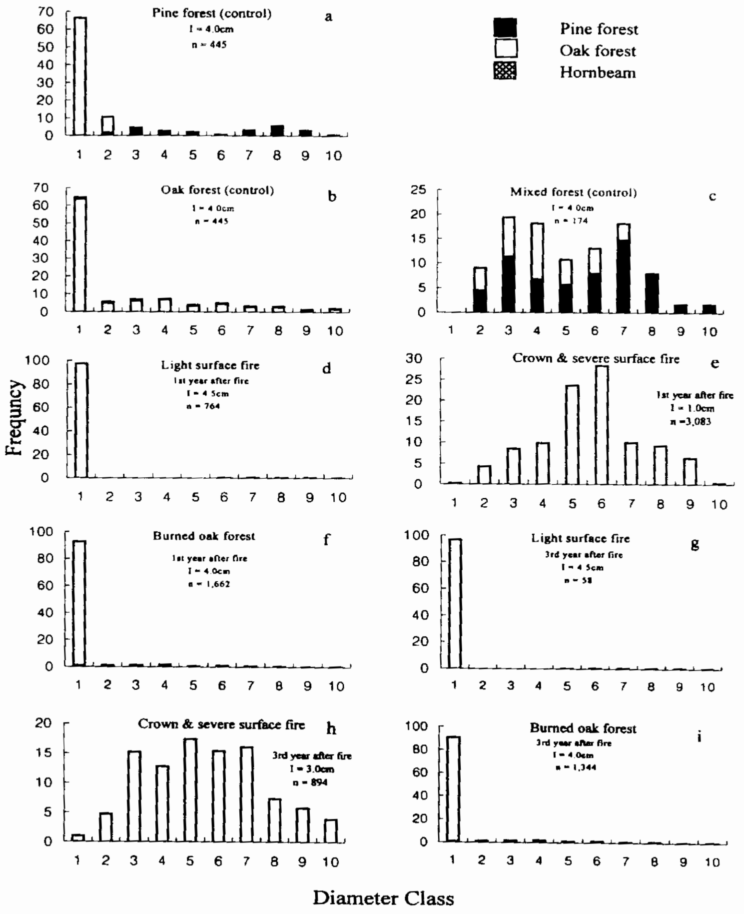

Fig. 2. Size class distribution of dominant woody species in permanent quadrats installed in sites different in fire intensity and vegetation type. **a**, **b** and **c** show the results in unburned forests and **d-i** show those in burned forests. *I* and *n* indicate the interval of diameter class and the number of trees surveyed.

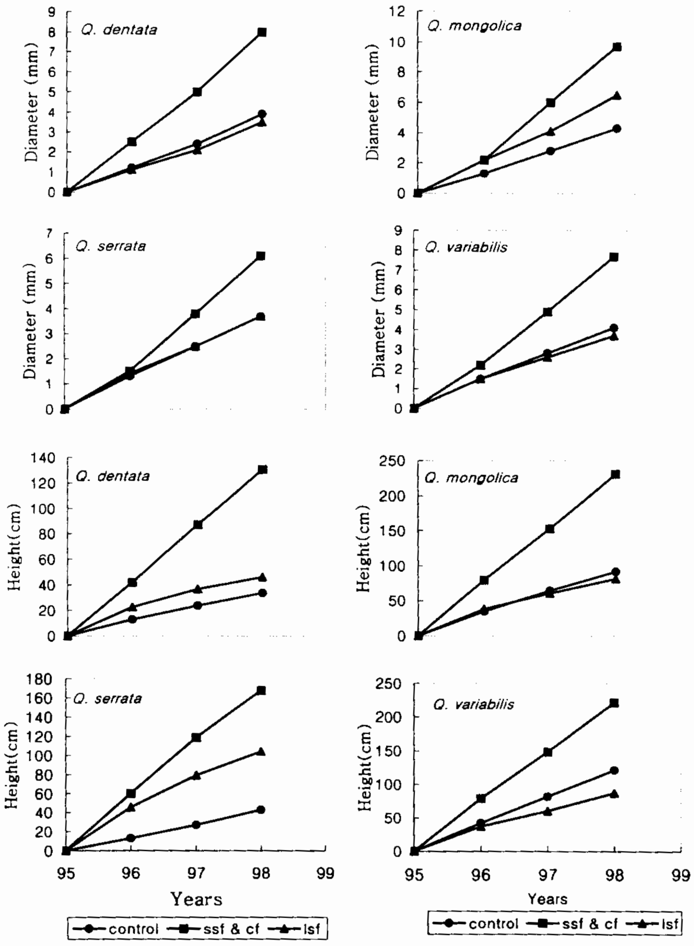

Fig. 3. Growth states of height and annual rings of some oak species, predicted as successors of pine in both unburned and burned pine forests. Control = unburned forest; ssf = severe surface fire; cf = Crown fire; lsf = Light surface fire.

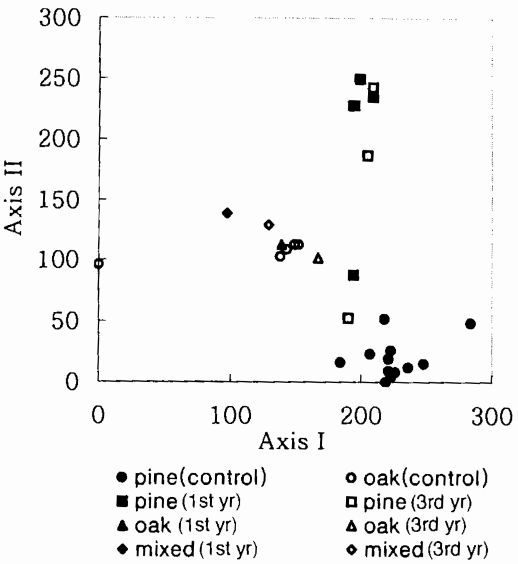

Fig. 4. Stand ordination of pine, oak and mixed forests. Control indicates unburned stands.

Most pine trees were killed by the fire except those in areas of light surface fire. The tops of young oaks under the pine canopy were killed but subterranean parts remained alive. Many plants have special life forms and survival strategies under the disturbance regime (Trabaud 1987). After the disturbance, many oaks sprouted from subterranean regenerative buds, forming young oak stands (Fig. 3). In the area of light surface fire, most pine trees were alive and pine forest continued to dominate. However, in these stands the density of oaks increased greatly (Fig. 3). Their density (77 000/ha) was higher and their growth was faster as compared with those under unburned pine forest (Fig. 3). From those results, we estimated that fire facilitated succession from pine forest to oak forests and consequently induced change of landscape pattern.

Changes of species composition in burned forests were analysed with DCA ordination (Fig. 4). Unburned pine stands are found at the right side of axis I and unburned oak and burned pine stands were at the left and central parts, respectively. Among the burned pine stands, those disturbed by light surface fire were located close to the unburned pine stands, while those disturbed by crown and severe surface fires were located far from them. On the other hand, burned oak and mixed stands were located close to the unburned oak stands. These results show that species composition of burned pine stands was changed and such a change was more remarkable under severe fire. In addition, species composition of oak stand disturbed by light surface fire was hardly changed and that of mixed forest disturbed by severe surface fire was changed similarly to that of oak stands. But changes of species composition with the lapse of years after fire were not striking.

Fire as a cause of landscape changes

Wood production from pine forest is the main goal of forestry in this region. A special use of the forests is the collection of the edible mushroom *Tricholoma matsutake*. However, most pine forest were burnt and mycelia of this mushroom were injured by the fire. Consequently, the mushroom can no longer be collected in this area. In this way, fire might be an important causal factor inducing drastic changes in the landscape system (Turner & Bratton 1987; Trabaud & Galti 1996). Many people who depended on the collection of mushrooms lost their valuable merchandise when the pine forest was destroyed.

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Species composition on tipup mounds and pits created by catastrophic windthrow in a Minnesota forest

McAlister, Suzanne D.[1*], Palmer, Michael W.[1], Arévalo, José Ramón[2] & DeCoster, James K.[3]

[1]*Oklahoma State University, Botany Department, 104 LSE, Stillwater, OK 74078-3013, USA;*
[2]*Departamento de Ecología, Universidad de La Laguna, 38206, La Laguna, Islas Canarias, Spain;*
[3]*South Florida Natural Resources Center, Everglades National Park, 40001 State Road 9336, Homestead, FL 33034, USA;*
Fax +14057447074; E-mail sdmca@osuunx.ucc.okstate.edu

Abstract. We recorded the presence of vascular plant species on microsites generated by the nearly complete windthrow of a *Pinus strobus* forest. We classified microsites as unaltered forest floor, old soil uplifted with the root mass, soil on the mound which was newly exposed, and the pit. Ruderal species (e.g. *Chenopodium album*, *Verbascum thapsus*, *Conyza canadensis*) were most frequent in the new soil microsites, but only once had > 10% frequency in the unaltered forest floor quadrats. Species composition of old soil microsites was intermediate between that of forest floor and new soil microsites. *Dryopteris carthusiana* and animal burrows were more frequent in the pits than in other microsites. Canonical Correspondence Analysis indicated that the species composition of the four microsites differed in the first years after the disturbance. 14 yr later, the communities on the microsites have converged to a similar species composition, which is distinct from the pre-disturbance forest floor community, and similar to the current forest floor community.

Keywords: Convergence; Disturbance; Habitat heterogeneity; Microsite; Topography.

Nomenclature: Kartesz (1994).

Introduction

Catastrophic windthrow of forest trees may create tipup mounds and pits, thus disturbing the ground layer and creating microsite heterogeneity (Foster 1988; Schaetzl et al. 1989b; Peterson et al. 1990). Vascular plant species have differential success on the different types of microsites (Ellison et al. 1993; Henry & Swan 1974; Putz 1983; Webb 1988; Peterson & Pickett 1990), due to differing physical and chemical processes/ properties operating therein (Beatty 1984; Schaetzl et al. 1989a; Peterson et al. 1990; Carlton & Bazzaz 1998a; Denslow et al. 1998). Differences in species composition among the microsites may remain over time as succession occurs on the site as a whole, or the microsites may converge in species composition due to increasing similarity in environmental conditions. There are few long-term studies on tipups beginning immediately after catastrophic windthrow, and processes occurring on recent tipups may be different from those on long-established tipups (Beatty 1984; Peterson & Campbell 1993).

We followed vascular plant species on pits and mounds and intact forest floor quadrats from two weeks until 14 yr after the storm event. We studied whether species responded to the type of microsite created by the uprooted trees and whether the species composition changed through time.

Methods

The study site, the Cedar Creek Natural History Area (CCNHA), is a U.S. National Science Foundation Long Term Ecological Research site in Anoka and Isanti Counties, Minnesota. On July 3, 1983, straight line winds associated with a large thunderstorm blew down portions of several forests in CCNHA. Before the storm, the forest was dominated by *Pinus strobus* and *Betula papyrifera*, with a total density of 1104 stems/ha, and a basal area of 42m^2/ha. The forest floor was essentially flat and no old tipups were visible (pers. obs.). It is likely that the trees colonized an old field. The storm reduced the forest to a density of 446 stems/ha, and a basal area of 12 m^2/ha. 14 yr later, the site had a few, large *Pinus* remaining, and the young canopy is dominated by *Fraxinus nigra*, *Quercus rubra* and *Prunus serotina* (Arévalo et al. this volume)

We established 120 randomly located quadrats (1 m × 1m) on the 'forest' floor within two weeks after the storm of July 1983. These were permanently marked in the two diagonal corners with iron reinforcement bars. As we could not guarantee the exact dates of revisits, we chose to record only the presence of vascular plant species. The quadrats were surveyed in July 1983, which is assumed to reflect pre-disturbance vegetation, and resampled in July of 1984, 1985, 1990, 1993 and 1997. The presence of vascular plant species rooted in the new and old soil of the 56 tipups was recorded beginning in 1984; the pit vegetation was sampled beginning in 1985. New soil encompassed all the disturbed soil above the level of the forest floor, and is equivalent to the 'mound + plate + under' of Carlton & Bazzaz (1998b), or the 'mound' of Peterson et al. (1990). Old soil was that portion of the forest floor which had been uplifted, often to near vertical, but retained its soil structure intact, at least at first, thus is equivalent to the 'TOP' of Carlton & Bazzaz (1998b). In the present study, pit included all exposed soil below the level of the forest floor, thus equivalent to the 'pit + wall' of Peterson et al. (1990).

The species data were ordinated with Canonical Correspondence Analysis (CCA; ter Braak 1987) using Canoco 4 for Windows (ter Braak & Šmilauer 1998). Explanatory variables were all dummy (1/0) variables representing the type of microsite (pit, new soil, old soil, forest floor quadrats), separated by year. These dummy variables are represented by their centroids, along with species scores, on ordination biplots.

Results

Canonical Correspondence Analysis indicated that in the early years of this study (top of Fig. 1), the microsites differed in species composition. Old soil plots were similar to the forest floor quadrats, and pits were more similar to old soil than new soil plots. The close positioning of all of the centroids from 1997 in the bottom of Fig. 1 indicates that the species composition of the microsites has converged through time. Species scores illustrate taxa typical of new soil in the upper right of Fig. 2, those most frequent in forest floor quadrats on the upper left, and those that increased in all microsites on the lower left.

Prior to the windthrow, *Amphicarpaea bracteata*, *Carex pensylvanica*, *Maianthemum canadense*, *Parthenocissus quinquefolia*, and *Rubus idaeus* all had > 35% frequency in the forest floor quadrats (Table 1). In the first two years after the storm, these species remained at about the same frequency, except *Maianthemum*, which doubled. CCA species scores for these species are located in the upper middle left portion of Fig. 2. Many of the less frequent species increased their frequency. In this period the new soil quadrats were dominated by ruderal species; vines (*Vitis riparia*, and *Parthenocissus*) and the clonal *Rubus ideaus* were also frequent.

Carex pensylvanica, *Chenopodium album*, *Conyza canadensis*, *Verbascum thapsus* and *Polygonum cilinode* all more than doubled their frequency in old soil plots by 1985. Two years after the storm, *Parthenocissus* and *Rubus* were present in more than half of the plots and *C. canadensis* was present in one third.

In 1990 and 1993 several species – *Urtica dioica*, *Hackelia deflexa* – increased strongly in frequency in all microsites, only to decline again by 1997. *Pinus strobus* seedlings also followed this pattern. CCA species scores of these taxa are in the lower middle of Fig. 2.

By 1997, two additional species – *Dryopteris carthusiana* and *Polygonum cilinode* – had joined the five common forest floor species in all four microsites (Table 1). They also had > 35% frequency.

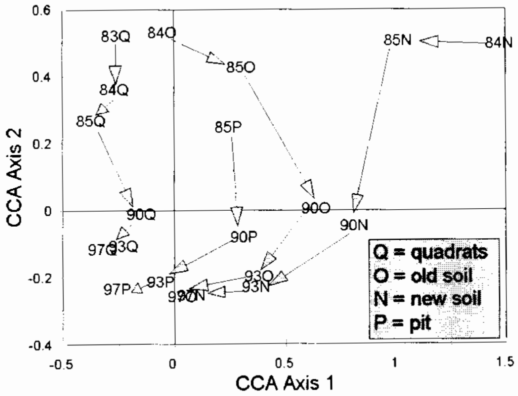

Fig. 1. CCA-diagram: centroids of microsite type, by year. The first two digits of the centroid label represent the year of study, and the letter represents the microsite type. Arrows connect subsequent sampling episodes.

Discussion

In the first two years after the storm the four microsite types had clear differences in species composition. As found by Carlton & Bazzaz (1998a), the initial type and amount of soil disturbance which occurred in the storm strongly influenced recruitment patterns. The bare mineral soil in the new soil plots was initially colonized by ruderal species (these may have been either from activation of the seed bank (Putz 1983) or from wind dispersal into the site (Nakashizuka 1989; Peterson et al. 1990)). Species composition in the old soil plots initially was similar to undisturbed forest floor quadrats. Species composition in pits was (unlike Carlton & Bazzaz 1998a), more similar to that of old soil than new. This is perhaps due to the sandy well-drained soil (preventing localized flooding as was found by Putz 1983; Cornett et al. 1997), to the dense shade hindering establishment of ruderals, and to vegetative ingrowth of forest floor plants.

The plant communities in these four microsites were

Table 1. Frequency (in percent) of species with at least 200 occurrences, by year and microsite type, in order of declining frequency.

	Forest Floor Quadrats						New Soil on Mounds					Old Soil on Mounds					Pits			
Species	1983	1984	1985	1990	1993	1997	1984	1985	1990	1993	1997	1984	1985	1990	1993	1997	1985	1990	1993	1997
Rubus idaeus	92.5	91.7	93.3	89.2	91.7	92.5	46.0	84.3	92.6	90.7	89.1	84.9	96.3	91.1	92.9	94.6	60.0	92.3	85.2	90.6
Parthenocissus quinquefolia	89.2	85.8	91.7	91.7	93.3	91.7	60.0	54.9	48.1	72.2	85.5	67.9	87.0	64.3	76.8	87.5	55.6	51.9	61.1	79.2
Amphicarpaea bracteata	60.8	51.7	64.2	74.2	71.7	70.8	14.0	5.9	9.3	48.1	60.0	32.1	35.2	30.4	41.1	48.2	17.8	30.8	59.3	58.5
Carex pensylvanica	37.5	38.3	39.2	54.2	55.8	43.3	10.0	21.6	44.4	55.6	49.1	13.2	35.2	50.0	66.1	58.9	15.6	40.4	40.7	28.3
Maianthemum canadense	32.5	42.5	59.2	55.8	60.0	66.7	0.0	2.0	16.7	29.6	38.2	20.8	38.9	25.0	33.9	41.1	6.7	23.1	37.0	41.5
Polygonum cilinode	0.8	8.3	8.3	52.5	68.3	68.3	10.0	7.8	44.4	63.0	72.7	1.9	14.8	57.1	66.1	76.8	13.3	40.4	55.6	67.9
Pinus strobus	26.7	13.3	18.3	67.5	62.5	29.2	12.0	9.8	77.8	70.4	40.0	5.7	11.1	50.0	53.6	28.6	2.2	61.5	42.6	22.6
Urtica dioica	15.0	21.7	19.2	22.5	40.0	31.7	8.0	5.9	33.3	48.1	45.5	13.2	20.4	19.6	60.7	46.4	22.2	23.1	37.0	28.3
Conyza canadensis	0.0	9.2	3.3	12.5	5.8	3.3	80.0	64.7	68.5	64.8	36.4	1.9	42.6	66.1	73.2	25.0	33.3	51.9	16.7	3.8
Arisaema triphyllum	3.3	25.0	28.3	41.7	47.5	45.8	0.0	0.0	5.6	18.5	27.3	7.5	9.3	10.7	12.5	25.0	11.1	21.2	35.2	45.3
Dryopteris carthusiana	0.0	12.5	12.5	14.2	25.0	34.2	0.0	0.0	9.3	55.6	65.5	0.0	1.9	10.7	50.0	66.1	15.6	30.8	48.1	54.7
Aquilegia canadensis	20.8	22.5	25.0	26.7	29.2	24.2	2.0	7.8	16.7	24.1	20.0	17.0	18.5	28.6	30.4	23.2	20.0	34.6	29.6	18.9
Vitis riparia	14.2	15.0	15.0	21.7	40.8	20.8	20.0	9.8	27.8	37.0	12.7	15.1	16.7	25.0	42.9	16.1	0.0	32.7	42.6	15.1
Toxicodendron radicans	13.3	22.5	22.5	27.5	30.8	31.7	0.0	0.0	9.3	14.8	18.2	11.3	11.1	14.3	23.2	25.0	6.7	19.2	24.1	26.4
Galium triflorum	21.7	40.8	33.3	14.2	35.0	29.2	6.0	5.9	1.9	14.8	16.4	3.8	7.4	0.0	17.9	10.7	15.6	5.8	20.4	18.9
Aralia nudicaulis	13.3	25.8	25.8	22.5	23.3	23.3	2.0	3.9	16.7	18.5	23.6	13.2	13.0	17.9	19.6	23.2	6.7	9.6	7.4	24.5
Hackelia deflexa	0.0	18.3	13.3	35.0	40.0	15.8	10.0	7.8	22.2	33.3	9.1	7.5	5.6	19.6	32.1	3.6	8.9	15.4	20.4	15.1
Quercus ellipsoidalis	17.5	20.0	15.8	25.0	29.2	29.2	0.0	0.0	1.9	7.4	12.7	0.0	1.9	1.8	12.5	26.8	2.2	5.8	7.4	24.5
Anemone quinquefolia	1.7	2.5	34.2	37.5	28.3	26.7	0.0	0.0	0.0	9.3	3.6	1.9	1.9	8.9	17.9	12.5	6.7	17.3	9.3	20.8

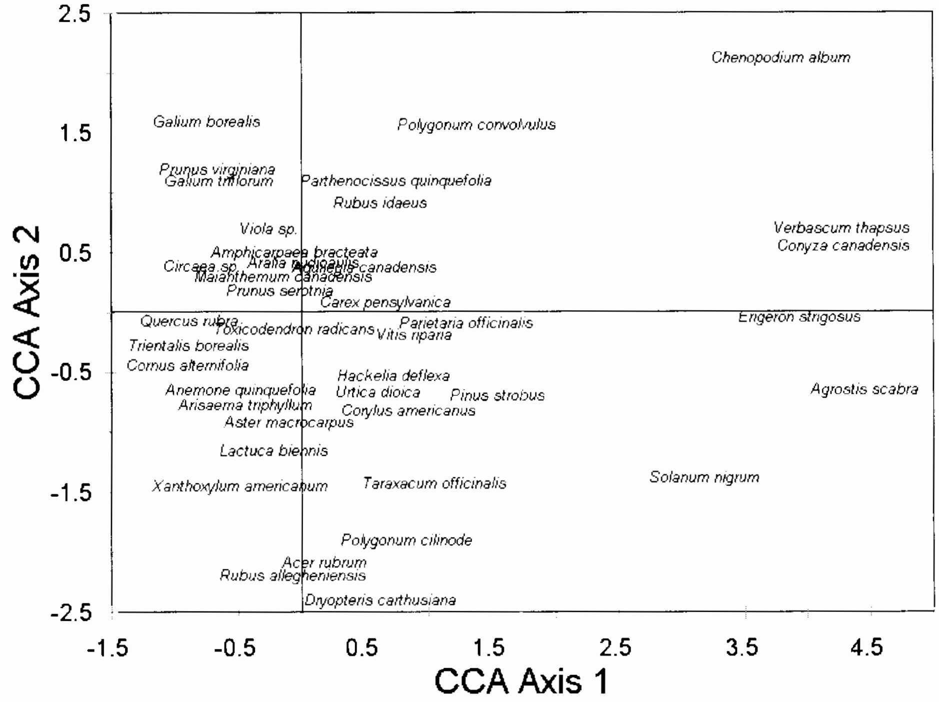

Fig. 2. CCA-diagram: species scores for the 40 most frequent species from the same ordination as in Fig. 1. Note difference in scale of the axes.

quite dynamic over the study period, particularly in the first 7-10 years. Rapid changes on tipups in the first few years were also found by Peterson et al. (1990), Putz (1983) and Núñez-Farfán & Dirzo (1988). Such dynamics are likely due to continue, albeit at a slower pace, as a result of erosion of the mounds, soil sloughing into pits, burrowing of animals, as well as successional changes (Jonsson & Esseen 1990; Peterson et al. 1990; Denslow et al. 1998).

After 1990 the microsite types began to converge, although they were distinct for several more years. By 1997 the initial differences in species composition among the microsites were nearly gone. Such convergence is perhaps explained by processes such as soil formation in the disturbed microsites (Carlton & Bazzaz 1998a; Denslow et al. 1998). This is somewhat contrary to most studies of older tipups in which differences in species composition remain for decades (Beatty 1984; Peterson & Campbell 1993). The extremely sandy nature of the soil in the present study may preclude large differences in soil moisture between pit and mound. Peterson & Pickett (1990) proposed that such moisture differences are primary determinants of species composition in tipup mound microsites.

Peterson & Pickett (1995) observed convergence of species assemblages in forest and blowdown areas within 7 - 8 yr after a tornado. Unfortunately, there are no intact pine forests in the vicinity, so we are not able to make a comparison. However, as evidenced by the CCA (Fig. 1), species composition is not (yet) returning to pre-disturbance conditions.

The intact forest floor seemed to be quite resistant to invasion by the ruderal species, (only once did any of the weedy species have > 10% frequency). Many of the existing forest floor species in these plots appeared to respond favorably to the new regime, particularly *Maianthemum canadense*, *Anemone quinquefolia* and *Arisaema triphyllum*. Thus they are tolerant of higher light, perhaps somewhat limited by light in the intact forest, and seemed to spread readily, after several years, to the other microsites.

The initial differences among the four microsite types have converged such that the current ground layer, while mounded and pitted, is remarkably similar in species composition. However, the forest floor has not returned to what it was, nor is it likely to, since the post-disturbance canopy will be likely dominated by hardwood species rather than pines (Arévalo et al. this volume). Accelerated canopy succession after a windstorm was found also by Dyer & Baird (1997) in other Minnesota forests. In the present study, the main differences from the predisturbance understory vegetation are a high frequency of *Polygonum cilinode* and *Dryopteris carthusiana*. We will continue to follow this forest to determine whether species composition on the different microsites will continue to converge through time, or diverge again.

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Population mosaic cycles in forest ecosystems

Smirnova, Ol'ga V.[1]*, Zaugol'nova, Lyudmila B.[1], Istomina, Irina I.[1] & Khanina, Larisa G.[2]

[1]*Centre of Forest Ecology and Productivity, RAS, Novocheremushkinskaya 69, Moscow 117418, Russia;*
[2]*Institute of Mathematical Problems in Biology, RAS, Pushchino 142290, Russia;*
**Fax +70953322917; E-mail smirnova@cepl.rssi.ru*

Abstract. We used a population-ontogenetic approach to study the structure and dynamics of forest vegetation. Our approach uses the following concepts: flow of generations, population mosaic, population element and population locus. Spatial-temporal parameters of population elements and population loci of the dominant tree species of the East-European temperate forests were investigated. The overstorey structure and dynamics of these old-growth forests were described through population mosaics of tree species. It was shown that gaps and tree falls were formed during forest development and that these produced high levels of biological diversity.

Keywords: Gap mosaic; Generation flow; Old-growth temperate forest; Population mosaic; Sustainable population; Tree ontogeny.

Introduction

Many ecologists have shown that the distinctive feature of old-growth forests is the gap mosaic, a mosaic of patches of different ages (e.g. Yamamoto 1981; Hibbs 1982; Shugart 1984). The main cause of gap formation is the fall of large trees due to age and disturbance. In this paper, the spatial-temporal parameters of gap mosaics are defined by the flow of generations of tree populations. This flow is realized in space at any given time as the population mosaic. A gap mosaic in a mono-dominant forest is a population mosaic of the dominant tree species. A gap mosaic in a multi-species forest is formed by superposition of population mosaics of different tree species.

We investigated population mosaics of trees in protected and managed forests in ca. 30 regions in the southern and central parts of the Russian Federation and in Ukraina. Results of these studies have also been reported on by Smirnova (1994), Popadiouk et al. (1995); Smirnova et al. (1995).

Methods

Biological age is defined as a stage of development in ontogeny. We distinguish juvenile (j), immature (im), virginal (v), reproductive or generative (g), and senile (s) ontogenetic stages. The reproductive stage is subdivided as follows: young (g1), middle (g2), and old (g3) individuals. Tree individuals at different ontogenetic stages need different volumes of resources for survival and development. Individuals at different stages also have a strong difference in shoot structure (morphology) as well as in their place and role in the community. For a detailed description of the features of each ontogenetic stage, see Gatzuk et al. (1980) and Smirnova et al. (1999).

A population locus is defined as a collection of plant individuals with the same biological age (Serebryakova & Sokolova 1977; Zaugolnova et al. 1988). We distinguish between (1) young loci consisting mainly of immature and/or virginal individuals; (2) mature loci consisting mainly of reproductive young and/or middle-aged individuals; and (3) old loci consisted mainly of reproductive old and/or senile individuals. We characterized population loci by the duration of the ontogenetic stages, and by the minimal area at which light requirements of individuals at these ontogenetic stages are met (Evstigneev 1988; Smirnova et al. 1990).

We also define a unit within the plant population mosaic for investigation: the elementary demographic unit (Smirnova et al. 1988; Zaugolnova et al. 1992). A population element is considered as a minimal set of individuals at different ontogenetic stages, which is sufficient for sustainable turnover of generations. The population element must include population loci in all age groups. We characterized a population element by species longevity and by the minimal area required for sustainable turnover of generations. The concepts described above are based on the population ontogenetic approach which has been developed in the Russian school of plant population demography under T.A. Rabotnov and A.A. Uranov.

To analyse the overstorey patterns and dynamics we studied parameters of population elements and of population loci of tree species in mono-dominant forest stands. Parameters of population elements and population loci were investigated in the above-mentioned forests; at each location one to three sample plots with an area of 2 - 12 ha were established.

The duration of the ontogenetic stages of tree species was calculated as the difference between absolute (calendar) ages of trees at the end and the beginning of the stages. Specimens of trees at each sample plot were taken for measurement of absolute age: 100 specimens of immature individuals, 25 specimens of virginal individuals, and 10 specimens of reproductive individuals. Absolute age was measured by year rings or by branch orders. Ontogenetic stages of individuals were defined by biomorphological characters (Smirnova et al. 1999) developed according to Serebryakov's approach (Serebryakov 1962; Serebryakova 1972). Duration of full ontogeny of species (species longevity) was calculated as the sum of duration of all ontogenetic stages of the species.

Areas of population loci of different ages of dominant tree species were determined by field measurements. Areas of population loci were measured either in mono-dominant uneven-aged forests or in poly-dominant forests, but loci formed by one species at a particular age or stage class were chosen for measurement. Boundaries of groups of individuals at the same or close biological ages were mapped at scale 1:100. Areas of the polygons were calculated. No less than 10 population loci of different ages for each species were measured.

Minimal areas of sustainable turnover of generations (areas of population elements) for dominant tree species were determined by both calculations and field measurements on tree populations in mono-dominant uneven-aged forests, notably in *Fagus* forests in the Carpathian Mountains and *Picea* forests in the Middle Ural. First, we determined the area of the population element from a plot in which a few mature individuals of the species occurred. The area of the plot is increased gradually until individuals of all ontogenetic stages are included. It is essential that the number of individuals at different ontogenetic stages be sufficient for sustainable turnover of species generations. That is, a ratio of individuals at different age stages must correspond to the ratio of these in the optimal ontogenetic spectrum of the species.

An ontogenetic spectrum is a graphic image of the distribution of individuals in different ontogenetic stages. The idea of an optimal ontogenetic spectrum was proposed by L.B. Zaugolnova (in Serebryakova 1976). The optimal ontogenetic spectrum depends on biological properties of the species such as life form, duration of ontogenetic stages, reproduction and settlement properties (Shorina & Smirnova 1985; Vorontzova & Zaugolnova 1985; Zhukova & Ermakova 1985). It was shown that the optimal ontogenetic spectrum of trees has a steep decline in density with age (Smirnova 1994). This corresponds with data from tree growth tables developed in forestry. Tree populations in man-disturbed forests usually do not have population loci of all age groups. Increasing the plot area in such cases does not lead to the determination of the population element and an approximate area for the population element must be compared with the square of the mean dispersal radius of the species' diaspores.

A calculation method was used for determining the areas of species population elements for trees which do not form mono-dominant uneven-aged forests in the study region. The minimal area should be sufficient for sustainable turnover of tree species generations and must be equal to the area sufficient for the simultaneous existence of population loci of all ages. Areas released by the death of old trees must be large enough for the development of young individuals if the populations are to persist. The period of formation of a new locus equals the sum of juvenile and immature stage duration ($t_j + t_{im}$). This period corresponds to the frequency of the appearance of new generations; therefore this frequency is necessary for the sustainable turnover of generations. Consequently, $T/(t_j + t_{im})$ (where T is a full ontogeny duration) is the duration of time for the formation of a young locus for sustainability. Suppose that each young locus goes through a full ontogeny and dies and that a new young locus appears in its place. The duration of age stages varies. We introduce a recounting coefficient, which normalizes the absolute time of stage duration according to the period of formation of a new young locus:

$$T_i / (t_j + t_{im}) \tag{1}$$

where T_i is a duration of stage *i*.

The area of the population element (S_p) is the sum of areas of loci of all age groups multiplied by the duration of each age stage expressed through the recounting coefficient:

$$S_p = \sum (S_j * T_i / (t_j + t_{im})) \tag{2}$$

Another formula was used for the calculation of tree population element areas. This area was calculated as a multiple of the area of the largest locus, formed by reproductive individuals (S_g), and the frequency of a new generation appearance $T / (t_{im} + t_j)$

$$S_p = S_g * T / (t_{im} + t_j) \tag{3}$$

Results and Discussion

The main difference in species longevity is the result of differences in the duration of reproductive periods of the species ontogeny (Table 1). One group of tree species with maximal species longevity and maximal duration of reproductive stage stands out. This group includes *Quercus robur*, *Fagus sylvatica*, *Fraxinus excelsior* and *Picea abies*. Maximal longevity of each generation provides these species with the possibility of holding the occupied area for a long time. The long duration of the reproductive period often permits the species to occupy new sites, thereby promoting the maintenance of populations in the community.

Other species have a shorter duration of full ontogeny and of reproductive stages. These species exist in old-growth forests owing to their various biological properties. First, some of these species are highly shade-tolerant and have a great capability for seed and/or vegetative propagation. These biological peculiarities allow some species with

Table 1. Mean values of temporal ontogenetic parameters of the main dominant tree species of the East-European temperate forests; a = age (yr); d = duration of ontogenetic stage (yr).

	Quercus robur		*Fagus sylvatica*		*Fraxinus excelsior*		*Tilia cordata*		*Acer platanoides*		*Acer campestre*		*Ulmus glabra*		*Carpinus betulus*		*Picea abies*		*Betula pendula*		*Pinus sylvestris*	
Ontogenetic stage	a	d	a	d	a	d	a	d	a	d	a	d	a	d	a	d	a	d	a	d	a	d
Juvenile	3	3	3	3	3	3	5	5	3	3	3	3	3	3	3	3	3	3	2	2	2	2
Immature	10	7	10	7	8	5	15	10	7	4	15	12	7	5	10	7	15	12	5	3	7	3
Virginal	30	20	30	20	25	17	30	15	20	13	20	5	25	18	20	10	30	15	15	10	20	13
Young reproductive	60	30	50	20	40	15	60	30	40	20	50	30	50	25	40	20	60	30	25	10	40	20
Mature reproductive	160	100	140	90	120	80	100	40	90	50	80	30	90	40	60	20	120	60	50	25	100	60
Old reproductive	300	140	250	110	200	80	160	60	160	70	140	60	150	60	100	40	220	100	90	40	200	100
Senile	350	50	280	30	250	50	220	60	200	40	160	20	180	30	130	30	250	30	100	10	240	40
Species longevity	380	30	300	20	280	30	250	30	220	20	180	20	200	20	160	30	280	30	120	20	260	20

Table 2. Age interval of trees in different ontogenetic stages.

	Quercus robur	*Fagus sylvatica*	*Fraxinus excelsior*	*Tilia cordata*	*Acer platanoides*	*Acer campestre*	*Ulmus glabra*	*Carpinus betulus*	*Picea abies*	*Betula pendula*	*Pinus sylvestris*
Ontogenetic stage											
Juvenile	1 - 10	1-15	2 - 15	2-7	1-20	1-15	1-15	1-15	2-10	1-10	2-10
Immature	3 - 20	3-65	3-25	2-40	2-25	3-35	2-40	2-25	4-30	2-20	2-20
Virginal	10-50	11-120	10-40	12-60	9 - 40	10-40	11-50	10-55	8 - 80	6-45	6-35
Young reproductive	25-110	40-150	20-60	30-80	25-60	30-70	25-70	30-70	20-90	15-70	15-65
Mature reproductive	55-160	90-200	50-130	50-100	50-110	45-120	40-110	50-100	40-160	50-90	40-120
Old reproductive	150-350	150-300	100-300	80-250	90-200	70-160	80-160	80-160	80-280	80-140	80-260
Senile	180-400	180-350	170-350	110-300	130-240	90-200	100-220	110-200	90-300	110-150	90-280

short ontogeny to succeed several generations during one generation of the longer-lived species. Among the other species, *Betula* is a pioneer, but it persists in old-growth forest through quick turnover of generations and very large seed productivity (2 - 3 × higher than other species). *Pinus* is even more light-demanding and also requires mineral soil for seedling establishment, but it can persist in multispecies mixed forests because of longevity and the long duration of its reproductive period.

There is a considerable variation in the interval of absolute ages of tree individuals in different ontogenetic stages (Table 2). Individuals in the same ontogenetic stage can have different absolute ages. This difference is defined by the vitality of individuals: individuals of low vitality are delayed in their development and have a higher absolute age than individuals of normal vitality in the same ontogenetic stage. There are individuals of different vitality in natural populations, so there is an interval of absolute ages of individuals at each ontogenetic stage. A large interval indicates a larger number of environmental conditions under which the species can exist. These intervals are estimations of species tolerance: they are smaller for more light-demanding species (*Quercus, Betula, Pinus*), and wider for shade-tolerant species (*Fagus*).

Thus different tree species have different longevities and different durations of ontogenetic stages. The duration of ontogenetic stages of one species also varies depending on environmental conditions. For these reasons we believe that only the biological age of trees provides the means to compare the demographic structure of populations of different species and for the analysis of the state of populations and their role in vegetation community.

Spatial parameters of population elements and population loci are presented in Tables 3 and 4. The areas of population loci of all species increase with an increase in the biological age of individuals forming the locus. We explain this with reference to the light demands of tree species, which are different for individuals at different biological ages (Ellenberg 1974; Evstigneev 1988). Light demands of tree species are highest in the reproductive ontogenetic stage (Evstigneev 1988). Young individuals cannot grow successfully under a canopy formed by parent individuals because of low light levels. Development of a new tree generation occurs in gaps and depends on gap size. Sustainable development is possible when the gap size is large enough so that light requirements of young trees are met.

We have found that the transition of individuals to the reproductive stage is impossible for any tree species in small gaps (< 300 m^2). Transition of individuals to the reproductive stage as well as the full ontogeny of shade-tolerant trees (*Fagus, Tilia*, *Acer platanoides*, *A. campestre*, *Ulmus*, *Carpinus*, *Picea*) are possible in gaps of middle size (400 - 600 m^2). Light-demanding species (*Quercus, Fraxinus*) require large gaps (1000 - 1500 m^2) for their full development.

The population structure of a shade-tolerant tree in a mono-dominant uneven-aged forest (*Picea abies*) is shown in Table 4. We can see that the number of immature individuals increases rapidly with plot area. This is because of their high shade-tolerance and ability to grow in small gaps. The number of virginal and young reproductive individuals increases more slowly with plot area because of their great light demands and their requirement for large gaps for development.

Calculated areas of population elements of tree species – minimal areas sufficient for sustainable turnover of species generations for the dominant trees are presented in Table 3. Note that the values calculated by the first and the second formulas are similar, and are close to the results obtained with field measurements (see Table 4). The areas

Table 3. Areas of population loci and population elements of the main dominant tree species.

	Quercus robur	*Fagus sylvatica*	*Fraxinus excelsior*	*Tilia cordata*	*Acer platanoides*	*Acer campestre*	*Ulmus glabra*	*Carpinus betulus*	*Picea abies*
Ontogenetic stage				Areas of population loci					
Immature	300	50	100	100	50	50	100	50	100
Virginal	600	200	300	300	300	100	300	100	200
Reproductive	1500	400	1000	600	500	300	600	400	600
				Area of population element					
Formula 1	4.95	1.045	2.8863	0.8	1.3464	0.2883	1.4157	0.455	0.91
Formula 2	5.7	1.2	3.5	1	1.5714	0.36	1.7143	0.64	1.12

Table 4. Results of field measurements of the area of population elements of *Picea obovata* in the reserve Sabarskii (Middle Ural).

Area of plot (m ×m)	im1	im2	v1	v2	g1	g2	g3	s	Sum
10 ×10	98	45				2	1		146
20 ×20	123	69	8			4	2		206
30 ×30	221	145	8	5	12	5	4	1	401
40 ×40	234	187	32	37	12	13	12	1	528
50 ×50	258	213	36	68	29	15	18	1	638
60 ×60	311	219	79	89	34	18	19	1	770
70 ×70	367	301	87	90	35	27	23	2	932
80 ×80	378	331	95	90	40	34	23	3	994
90 ×90	560	345	112	98	40	39	26	3	1223
100 ×100	612	356	142	102	45	47	26	3	1333
110 ×110	676	397	154	102	89	51	28	3	1500

of population elements were calculated for mono-dominant forests without regard to areas occupied by herbs and shrubs, where, as a rule, regrowth of trees is impossible (Smirnova 1994; Smirnova et al. 1995). We have calculated that the minimal areas, at which sustainable turnover of tree species generations is possible, range from 0.29 (0.36) to 4.95 (5.70) ha. In reality the minimal areas are larger because of the areas occupied by herbs and shrubs. Moreover, the areas in multispecies communities are 10 × larger by our estimations (Smirnova 1994; Smirnova et al. 1995). For example, in the Table 3 we show population elements of all broad-leaved trees at an area of 12 ha in the unique multispecies uneven-aged broad-leaved forests in the reserve Kaluzhskie zaseki (Kaluga region) by the method of plot area increase. However, it was clear that 12 ha is not sufficiently large for *Quercus robur.* Without a discussion of the 'oak-problem' here (Vera 1997; Smirnova 1998; Olff et al. 1999), we note that, in theory, it is possible to measure areas of population elements of tree species as well as the minimal area for sustainable existence of multispecies uneven-aged temperate forest, but it is very difficult to find such large areas in the eastern Europe.

A detailed analysis of the development of population loci of different species in gaps of different size in different forests (e.g. Chistyakova 1991; Popadiouk et al. 1995; Leonova 1999) have allowed us to deduce some general features of forest canopy dynamics.

A small gap in a forest canopy is formed as a result of the fall of one to two large trees. Light availability is increased, and some immature trees begin to grow in the gap. The gap is enlarged gradually as a consequence of the falling of surrounding old trees and the number of growing individuals is increased. Enlargement of the gap area leads to differences in light conditions within it. This leads to an unequal development of young individuals in the gap, which reinforces the difference in ecological conditions within the gap. It was shown for broadleaved forests in Central Russia that heterogeneity in light conditions occurs within gaps of more than 1000 m^2 but that this does not occur within gaps of smaller size (Smirnova 1994; Leonova 1999).

Diversity of ecological conditions in large gaps promotes simultaneous development of population loci of different trees. Species composition and ways of locus development are defined by speed of gap enlargement. Thus, gaps in multispecies temperate forests include individuals of one or several species, but most individuals are of the same biological age. Development of young individuals depends on light requirements, which implies that development is different in the gaps of different size and in different parts of gaps.

A comparison of the spatial-temporal parameters of population elements of tree species of temperate forests reveals a spatial and temporal continuum of population mosaics. The continuum provides the possibility of a sustainable existence of multispecies uneven-aged forests because of asynchronous development of population loci of different species.

Different tree species need different amounts of time and different sized areas for their development and for their full ontogeny. Light requirements of young trees of different species define the composition of young population loci. There are shade-tolerant tree species in small gaps, but both shade-tolerance and light-demanding tree species can develop in large gaps. Therefore, in East Europe, uneven-aged forests consist of shade-tolerant species (*Picea, Fagus, Carpinus*), but uneven-aged forests consist only of light-demanding species (*Betula, Pinus, Quercus*).

The dynamics of tree population loci are determined by the light requirements of the tree species. Specific environmental conditions occur below tree crowns and these define the composition and structure of lower strata. Environmental conditions are changed drastically with tree fall – different microsites appear (log, hillock and pit), where seedlings of trees and shrubs, moss and herb species of different ecology can develop. Thus, the creation of gaps provides conditions for forests with a high level of biological diversity.

We consider an old-growth temperate forest as a hierarchy of population mosaics of species differing in areas and in turnover time of their elements. Population mosaics of tree species have the largest spatial-temporal dimensions in the forest community, and population mosaics of other species are determined by the trees. Because of this, the sustainability and development of forest ecosystems are regulated by the population mosaic cycles of tree species.

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Progress towards North American vegetation classification at physiognomic and floristic levels

Barbour, Michael[1]*, Glenn-Lewin, David[2] & Loucks, Orie[3]

[1]*Environmental Horticulture, University of California, Davis, CA 95616, USA;* [2]*Fairmount College of Liberal Arts and Sciences, Wichita State University, Wichita, KS 67260, USA; Fax 316-978-3234; E-mail: dglennle @twsuvm .uc.twsu.edu;* [3]*Dept. of Zoology, Miami University, Oxford, OH45056, USA; Fax 513-529-6900; E-mail: loucks@msmail .muohio.edu;* **Fax +15307521819;*
E-mail: mgbarbour @udavis.edu

Abstract. In late 1994, the Ecological Society of America created a Panel on Vegetation Classification. Its objective was to facilitate the creation of a standardized, scientifically credible vegetation classification for the United States. The Panel – 20 regional and national vegetation scientists – is a neutral forum for the review of goals and standards for nomenclature, hierarchy, and methodology. It also identifies areas for research and encourages broad public, governmental, and scientific participation. The Panel has cooperated with an inter-agency group, the Federal Geographic Data Committee, in beginning to create national standards for a vegetation classification system at physiognomic levels. A document deal-ing with these upper levels of classification was formally endorsed by the Secretary of the Interior in 1997. In 1998, the Panel completed a draft document dealing with proposed minimum standards for lower floristic levels. The terms "alliance" and "association" are employed somewhat differently from their use by traditional phytosociologists. Following its wide distribution for comment, the ESA will publish a final version of the document.

Keywords: Alliance; Association; Canada; Ecological Society of America, Federal Geographic Data Committee; Mexico; Nature Conservancy; Panel on Vegetation Classification.

Introduction

United States vegetation ecologists have made significant progress toward nationally con- sistent standards for vegetation sampling and vegetation classification over the past 6 yr. For the first time, there has been a national effort to accomplish this standardization: an effort by academics through the Ecological Society of America (ESA), by government scientists through the Federal Geographic Data Committee (FGDC), and by conservationists through The Nature Conservancy (TNC), a non-profit, non-governmental organization.

The motivation to seek a national consensus has been conservation – a need to identify and protect representative examples of all plant communities natural to the United States (and eventually to Canada and Mexico, thus inclusive of all of the North American land area). With conservation ecology as a driving force, there has been a resurgence of interest in vegetation sampling, data archiving and analysis, classification, and mapping in North America. US phytosociology has been in a state of lethargy for several decades, ever since the ascendence of the individualistic/continuum theory over the association-unit theory in the 1950s (Barbour 1995, 1996; Mucina 1997) and the replacement of a 'nature in balance' paradigm with a 'nature in flux' paradigm in the 1970s (Botkin 1990). Vegetation classification and mapping, however, are essential and eminently practical to serve the purposes of resource management, conservation, and restoration. Classification and mapping approaches can be used to good advantage, while recognizing that they over-simplify the landscape.

The participants: individuals and entities

This resurgence was apparent at a well-attended classification workshop sponsored by the ESA in August, 1993. The workshop was jointly convened by Robert Peet of the University of North Carolina and Dennis Grossman of TNC. At that time, TNC was the only entity in the United States attempting to derive a national vegetation classification system at both floristic and physiognomic levels, and it had just been awarded a contract by the US National Park Service to map and classify vegetation in all of the national parks. At the same time, other federal agencies were pursuing their own independent national classifications (e.g. Forest Service, Bureau of Land Management, Fish and Wildlife Service). The potential for chaos among different classifications was very high.

As a consequence of that successful workshop, Peet and Grossman wrote a letter to then-President of the ESA Jerry Franklin, asking that he appoint a special committee on vegetation classification so that members of ESA might have some positive role to play – at least having an avenue to voice scientific opinions – about the nascent classifications. Within a few months, President Franklin did create such a committee, which was to report back to ESA within a year with recommendations on how ESA might proceed in this area. Michael Barbour was asked to be Chair because of his recent experience chairing a similar state effort in California (Keeler-Wolf 1993; Sawyer & Keeler-Wolf 1995). He was joined by 15 others, including regional academic experts and agency ecologists already involved in classification work. The special committee met in mid-1994 and created a mission, work plan, initial roster of members, budget needs, and objectives (Table 1) for a recommended entity called a Panel on Vegetation Classification. The Panel would be administered by ESA, but membership would not be restricted to ESA ecologists.

In late 1994, the new President of ESA, Judy Meyers, and the ESA Council ap-proved of the special committee's recommendations and gave the Panel a 3-yr period of life. Orie Loucks of Miami University (Ohio) was appointed Chair, Michael Jennings of the US Geological Survey (Biological Resources Division) as Vice Chair, and 18 others

Table 1. Initial objectives of the Panel on Vegetation Classification, 1995.

1. Provide a neutral forum for the review and discussion of vegetation classification.
2. Assure broad public access to the process of creating a standardized, credible classification system for the United States.
3. Set standards for hierarchical structure, nomenclature, data acquisition, and data archiving for United States vegetation classification.
4. Establish an ongoing process of review for future modification of standards.
5. Adopt standardized named units of vegetation.
6. Provide for an ongoing process of review for modifications to, and additions of, named units.
7. Identify areas for further research relative to classification and encourage research in those areas.

as members (Table 2). Members included ecologists from academia, federal agencies, and conservation organizations. A budget sufficient to support Panel meetings, a small staff, and outreach activities was provided by grants from several federal agencies.

The Panel met for the first time in mid-1995 in conjunction with the 38th meeting of IAVS at Rice University, Texas. At that meeting, the Panel met its first timely challenge: to comment on national vegetation terminology being developed by an inter-agency entity called the FGDC. The FGDC had been created in 1990 to promote a coordinated development and shared use of geographic data. One of its several sub-committees is called Vegetation and it is charged with developing and implementing uniform standards of data collection, archiving and interpretation of vegetation data. The FGDC had just completed a draft document, 'Standards for vegetation classification: assumptions, principles, definitions, and hierarchical classification categories', which it was circulating for review. The ESA's Panel made many substantial suggestions regarding terminology and these were later incorporated by the FGDC. Interior Secretary Bruce Babbitt formally endorsed the revised document in October of 1997 (Anon. 1996). As Chair Loucks wrote in an editorial in the Bulletin of the ESA (Loucks 1996), the importance of the Panel's review "can hardly be over-emphasized...[because] all federally funded projects will be affected, including much academic research and agency work... These standards will influence the direction of ecosystem- and landscape-scale ecology for decades."

Table 2. Members of the ESA Panel on US National Vegetation Classification, 1995-1998.

Member	Affiliation
Abrams, M.	Pennsylvania State University
Barbour, M.	University of California, Davis
Berg, K.	Bureau of Land Management
Brown, D.	Arizona State University
Dammon, A.	University of Connecticut
Glenn-Lewin, D.[1]	Wichita State University
Grossman, D.	The Nature Conservancy
Hartshorn, G.	World Wildlife Fund/Duke University
Hemstrom, M.	Forest Service
Jennings, M.[2]	Geological Survey/Biological Resources Division
Loucks, O.[3]	University of Miami
MacMahon, J.[4]	Utah State University
Peet, R.	University of North Carolina
Phister, R.	University of Montana
Shaw, D.	Environmental Protection Agency
Spaeth, K.	Agricultural Research Service
Talbot, S.	Fish and Wildlife Service
Udvardy, M.[5]	California State University, Sacramento
Waggoner, G.	Geological Survey/Biological Resources Division
Walker, J.	Forest Service
Walker, M.	University of Colorado, Boulder

[1]Chair, 1998-; [2]Vice Chair, 1995-; [3]Chair, 1995-1997; [4]Ex-officio, President of ESA; [5]Deceased

The FGDC document addressed vegetation classification at physiognomic levels,visible and mappable from aerial photographs and remotely sensed images (Table 3). The definitions of the physiognomic levels class, group, and formation are based on earlier work by Anon. (1973) and Driscoll et al. (1984). These categories include information on overall dominant growth form, ground cover percentage, overstory plant height, leaf traits (including phenology), climate, and topographic position.

Definitions of alliance and association

The FGDC document did not address in detail the lower, more local, floristically-based categories, but it did propose names and brief definitions for them: alliances and associations (Table 3). Both – in the tradition of North American phytosociology – are based more on diagnostic species that may include dominant species, rather than the narrower definition of characteristic taxa *sensu* Braun-Blanquet. The association is developed through analysis of the total floristic composition in all vegetation strata. The alliance emphasizes the composition of the vegetation in the dominant, uppermost stratum. An alliance, thus, can be mapped from remotely sensed data, a trait highly desired by resource agencies that manage large areas.

An association, the lowest unit in the US national vegetation classification hierarchy, has a definite floristic composition (several species having high constatncy) and a consistent physiognomy, and it occupies a repeated, predictable environment. (The classification will recognize that rarely an association can be a singularity, occuring only once.) It is characterized by diagnostic species deetermined from numerical analysis of overstory and understory species. Successional communities can be recognized as associations. Associations are named with the Latin binomials of overstory/understory diagnostic species (see examples in Table 3).

An alliance, in the words of the Panel's draft document, "is made up of a phys-iognomically uniform group of plant associations that share one or more dominant or diagnostic species that – as a rule – are found in the uppermost vegetation stratum. The alliance is determined both by floristic patterns of the associations it contains and by the physiognomic-ecologic characteristics of the vegetation formation it represents."

Hierarchically, an alliance is an aggregation of syntaxonomically related associations. This concept of the alliance is similar to that defined in recent US Forest Service documents (J. Fites & B. Bingham, pers. comm.) and the

Table 3. Hierarchical levels and examples of vegetation classification, at physiognomic and taxonomic levels, proposed by the FGDC and adopted by the United States Department of Interior in 1997.

Hierarchical level	Forest example	Scrub example	Herbaceous example
Division	Vegetated	Vegetated	Vegetated
Order	Tree-dominated	Shrub-dominated	Herb-dominated
Class	Open tree canopy	Dwarf shrubland	Herbaceous
Subclass	Deciduous	Evergreen	Perennial graminoid
Group	Cold-deciduous	Microphyllous	Temperate
Subgroup	Natural	Natural	Natural
Formation	Upland	Cushion	Temperate tall dense sod grassland
Alliance	*Quercus garryana*	*Cassiope mertensiana*	*Andropogon gerardii-Panicum virgatum*
Association	*Quercus garryana-Quercus kelloggii/Rhus diversiloba*	*Cassiope mertensiana-Phyllodoce empetriformis*	*Andropogon gerardii-Panicum virgatum-(Spartina patens)*

Canadian Committee on Ecological Land Classification (Strong et al. 1990).

An alliance is synonymous with the categories 'series', 'cover type' and 'consociation' of various agencies, and also with cateories V and VI of the Canadian system. The FGDC document states that alliances are named with the Latin binomial of the dominant species. For example, in the montane mixed conifer forest of the western United States, are the *Pinus ponderosa* alliance (a single dominant), a *Pinus ponderosa-Calocedrus decurrens* alliance (two dominants separated by a hyphen), or a *Pinus ponderosa-(Pinus flexilis)* alliance (parenthetical species not consistently present), among many other possibilities. The Canadian system uses common names for alliances (e.g. pondererosa pine).

At the present time, there are no minimal sampling or analysis criteria for the definition of alliances or associations, nor for formal publication of names. Using the North American definitions given above, TNC in 1994 reported that their ecologists had recognized approximately 1200 alliances and 2800 associations (Anon. 1994) in the United States. (TNC staff; Grossman 1998 and pers. comm.) estimate that these numbers had doubled by the end of 1998.)

Despite the North American flavor of definitions for alliance and association by the FGDC, the Panel attempts to be as inclusive as possible with regard to methodologies. Among those methods is the releve approach to sampling. TNC has adopted the releve approach to sampling vegetation, and there has been some recent movement among other agencies and academic ecologists to do the same, including members of the Panel. In California, for example, State Department of Fish and Game staff, responsible for quantifying and defining rare vegetation types (Sawyer & Keeler-Wolf 1995), typically gather releve-type samples in the field to document vegetation. A series of major publications, using both the releve approach and traditional syntaxonomy, has appeared in the last half-dozen years for western North American scrub and forest vegetation (Peinado et al. 1997, 1995a, b, 1994; Rivas-Martinez 1997, 1999) and eastern North American forests (Miyawaki et al. 1994). These authors' works did not appear completely *de novo*, but were built upon earlier and continuing traditional phyto-sociological research conducted at more local levels by such North Americans as Adolf Češka, Henry Conard, Antony Damman, M. Grandtner, Karel Klinka, Vera Komarkova, V. Krajina, Jack Major, Henry Oosting, Marcel Rejmánek, and Steve Talbot, as well as their students and collaborators. So, the answer is "no" to Moravic's rhetorical question, posed only seven years ago (Moravec 1992): "Is the Zurich-Montpellier approach still unknown in vegetation science of the English-speaking countries?"

The next few years: a standards publication and new directions

Under a renewed 3-yr lifespan granted by ESA to the Panel in 1998, and with David Glenn-Lewin as Chair, the Panel has focussed on preparing for publication a standards document for United States vegetation classification. It will consist of half a dozen chapters that will endorse sampling and analysis methods, propose archiving and oversight review procedures on data and nomenclature, and assign categories of confidence to the plot data used to define any particular association.

Draft documents have already been discussed at two annual meetings of the ESA. A proposed final draft was more widely circulated for review in 1999. After a comment period, the document will be published and made available for general sale by the ESA. The document is not intended to freeze vegetation classification in the United States, but rather to encourage its evolution in a thoughtful, structured way. The Panel expects that there will be future edited iterations of the standards document, much as there have been repeated 'approximations' of a soils classification document by the United States' Soil Survey Staff (Anon. 1975).

As the standards document nears completion, the ESA Panel is turning its attention to the problems of implementation. The Panel is seeking to form a consortion of itself, TNC, FGDC, and the US National Biological Information infrastructure, to oversee both the implementation of standards and their future evolution. It is laying out a plan for publicizing their availability and educating the user community about them. At this time, the Panel envisions a series of workshops for this purpose. The Panel is also involved in broad discussions among its members and with others about database needs and development. The Panel will also seek funding mechanisms for the implementation of the classification, the maintenance of data bases, and outreach activities.

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Application of the species-group method to the data base of calcareous grasslands in Germany

Jandt, Ute

Albrecht-von-Haller-Institute for Plant Sciences, Department of Vegetation Science & Population Biology, Univ. Göttingen. Untere Karspüle 2, D-37073 Göttingen, Germany;
Fax +49551392287; E-mail ujandt@gwdg.de

Abstract. According to traditional approaches, calcareous grassland communities in Germany are classified in two phytosociological orders and about five alliances according to their position within the subatlantic-continental climatic gradient and available water supply. In the last few decades, several synoptic tables have been published to support this view. Although there is a general agreement on the main frame of phytosociological arrangement of communities within the *Festuco-Brometea* class, details vary considerably depending on the authors.

During the last several years, large vegetation data bases have been established which easily allow numerical classifications. In most cases, synoptic tables are not suitable for the application of classifications to data bases, mainly because of the lack of large-scale differential species and the lack of allocation criteria. The species-group method is presented, which enables computation of original vegetation data in large data bases. The use of this method allows retention of the broadly accepted traditional Braun-Blanquet scheme, but in addition supplies clear and reproducible allocation criteria for classification.

In the present study about 7700 relevés of calcareous grasslands from Germany have been compiled from the literature. Based on maximization of fidelity, groups of differential species were extracted. These groups can be equivalently used to subdivide the data set.

Classification was performed by combining species groups using formal logic. The resulting units were evaluated and optimized in respect to their correspondence to the traditional phytosociological alliances.

Keywords: Braun-Blanquet system; Classification; *Festuco-Brometea*; Large-scale vegetation survey.

Nomenclature: Ehrendorfer (1973) for phanerogams; Frahm & Frey (1987) for mosses; Wirth (1980) for lichens.

Introduction

Since the beginning of phytosociology, relevés have been made of *Festuco-Brometea* communities, which occur over large areas of Central Europe and adjacent regions. Tens of thousands of relevés from these communities have been published. Synoptic tables have proved of little value in applying classifications to data bases mainly because of the lack of large-scale differential species and the lack of allocation criteria. The aim of the present study was to find out whether this vast data collection allows for detecting differential species to characterize vegetation units on a large scale. The second objective was to use these differential species to produce a classification which corresponds to the existing Braun-Blanquet system as much as possible, but in addition, supplies clear allocation criteria for each vegetation unit.

Phytosociological background

Traditionally, in Central Europe the class *Festuco-Brometea* is subdivided into two geographically separated orders, the *Festucetalia valesiacae* and the *Brometalia* (Oberdorfer & Korneck 1978; Royer 1991). These orders comprise several alliances, which are widely accepted by phytosociologists, but for the details of assignment and contents of each alliance various opinions exist. Also lower vegetation units have been created using different phytosociological methods, yielding numerous associations that often are not comparable, although they sometimes even share the same names.

As an example, Table 1 lists all associations that different authors have described as belonging to the *Festucion valesiacae* in Germany. Each column represents one author, each row contains synonymous or similar associations. The application of different phytosociological methods as well as the size of the investigation areas of the different authors has led to various subdivisions of the alliance.

The main associations of the *Festucion valesiacae* are the *Potentillo-Stipetum* in the east, the *Festuco-Stipetum* in the centre and the *Allio-Stipetum* in the south of Germany, but these three communities can be more easily geographically distinguished than floristically.

The *Allio-Stipetum* and the *Potentillo-Stipetum* have been established using character species and following the Zürich-Montpellier method (Braun-Blanquet 1964); whereas the *Festuco-Stipetum* is based on diagnostic species groups of the Eberswalde method (Mahn 1965; Scamoni & Passarge 1963: 65 a.f.; Dierschke 1994: 338).

The main problem with the flood of associations is that most of them lack clear allocation criteria and are often based on subjective opinions. Serious differences in classification are also caused by the fact that normally one researcher investigates only a restricted area; this results in a survey which is only valid for this special area. Such geographically restricted surveys do not allow extrapolation of results to larger areas. Therefore, it is necessary to establish a vegetation classification with emphasis on clear and reproducible allocation criteria, covering the whole distribution area of the vegetation type considered. This conception also matches the aims of the Working Group on European Vegetation Survey of the International Association for Vegetation Science (IAVS) (Mucina et al. 1993; Rodwell et al. 1995).

Table 1. Associations of the alliance *Festucion valesiacae* according to different sources.

<table>
<tr><td>author</td><td>Royer 1991</td><td>Oberdorfer & Korneck 1978</td><td>Pott 1992</td><td>Preising et al. 1997</td><td>Mahn 1965</td><td>Schubert 1974</td><td>Schubert, Hilbig, Klotz 1995</td><td>Krausch 1961</td><td>Passarge 1964</td><td>Dengler 1994</td></tr>
<tr><td>area</td><td>Central Europe (selection)</td><td>Southern Germany</td><td>Germany</td><td>Lower Saxony (Central Germany)</td><td>Central Germany</td><td>Southeastern Germany</td><td>Central and Northeastern Germany</td><td>Brandenburg (Northeastern Germany)</td><td>Northeastern Germany</td><td>Brandenburg (Northeastern Germany)</td></tr>
<tr><td>order</td><td colspan="10">Festucetalia valesiacae Br.-Bl. et Tx. 1943</td></tr>
<tr><td>suborder</td><td>Stipo-Festucenalia valesiacae Royer</td><td colspan="9"></td></tr>
<tr><td>all.</td><td>Festucion rupicolae Soo (1929) 1940</td><td colspan="3">Festucion valesiacae Klika 1931</td><td colspan="2">Astragalo-Stipion Knapp 1944</td><td>Festucion valesiacae Klika 1931</td><td>Festuco-Stipion capillatae (Klika 1931) Krausch 1959</td><td>Festuco-Stipion Krausch 1959</td><td>Festucion valesiacae Klika 1931 em. Klika 1955</td></tr>
<tr><td>suball.</td><td>Eu-Festucenion rupicolae Soo 1971</td><td colspan="9"></td></tr>
<tr><td>ass.</td><td colspan="2"></td><td>Festuco valesiacae-Stipetum capillatae (Libb. 1931) Mahn 1959</td><td>Stipetum capillatae (Hueck 1931) Krausch 1960</td><td>Festuco valesiacae-Stipetum capillatae Mahn 1959</td><td>Festuco-Stipetum Mahn 1965</td><td>Festuco valesiacae-Stipetum capillatae (Libb. 1931) emend. Mahn 1959</td><td>Stipetum capillatae (Hueck 1931) Krausch 1960</td><td>Festuco-Stipetum capillatae (Libb. 1936) Mahn 1959</td><td></td></tr>
<tr><td>ass.</td><td>Geranio-Stipetum Mahn 1965</td><td colspan="3"></td><td colspan="2">Geranio-Stipetum capillatae Mahn 1965</td><td rowspan="2">(incl. Geranio-Stipetum
and Teucrio-Stipetum)</td><td rowspan="3">(incl. Festuco-Stipetum
and Potentillo-Stipetum)</td><td colspan="2" rowspan="2"></td></tr>
<tr><td>ass.</td><td>Teucrio-Stipetum Mahn 1965</td><td colspan="3"></td><td colspan="2">Teucrio-Stipetum capillatae Mahn 1965</td></tr>
<tr><td>ass.</td><td>Potentillo arenariae-Stipetum capillatae Libbert 1933</td><td></td><td>Potentillo-Stipetum capillatae Libb. 1933</td><td colspan="3"></td><td>Potentillo arenariae-Stipetum capillatae (Hueck 1931) Krausch 1961</td><td>Potentillo-Stipetum capillatae Libb. 1933</td><td>Potentillo arenariae-Stipetum capillatae (Hueck 1931) Libb. 1933</td></tr>
<tr><td>ass.</td><td colspan="3">Allio sphaerocephali-Stipetum capillatae (Knapp 1944) Korneck 1974</td><td colspan="2"></td><td>Erysimo-Festucetum valesiacae Klika 1932</td><td colspan="4"></td></tr>
<tr><td>ass.</td><td colspan="2">Genisto-Stipetum tirsae Korneck 1974</td><td>Genisto pilosae-Stipetum stenophyllae Korn. 1974</td><td colspan="7"></td></tr>
<tr><td>ass.</td><td>Festuco-Silenetum otitis Libbert 1933</td><td colspan="9"></td></tr>
<tr><td>ass.</td><td>Festuco valesiacae-Stipetum capillatae Sillinger 1931</td><td colspan="9"></td></tr>
</table>

Vegetation data base

The working group in Göttingen has started to establish a vegetation data base actually containing about 7700 relevés from various authors, mainly belonging to the Festuco-Brometea.

The map of Germany (Fig. 1) illustrates the origin of the relevés in the data base, classified by landscape units (Meynen et al. 1953-1962). The map shows that plots of calcareous grasslands incorporated in the data base are not evenly distributed, but concentrated in northern and central Germany. In the current state of the data base, relevés from southern Germany have been included only accidentally. Consequently the data base is far from complete, but it represents the calcareous grasslands of central Germany quite well. (All readers are kindly requested to contribute to the database by sending electronic versions of *Festuco-Brometea* relevés, provided that geographical references are included.)

Determination of species groups

In order to obtain groups of differential species from the vegetation database, own software, developed in our department (Bruelheide 1995; see also Bruelheide & Jandt 1995, 1997) was used. The algorithm makes use of the distribution of all species in the entire data base. Starting groups of species are selected which subsequently are tested and optimized independently. Two examples are given in Table 2.

The species groups are used to form groups of relevés that show the property to have a minimum number of species of the group of differential species. The composition of the species group, the number of species belonging to the group and the required minimum number are derived by a process of optimization based on statistical criteria. The species groups are formed independently of each other. This entails that different groups may have one or more species in common.

Classification by species groups

To obtain vegetation units from the species groups, a classification was established using formal logic (Bruelheide

Table 2. Examples of species groups resulting from independent optimization processes.

***Salvia pratensis* group**: Two out of eight species required	***Leontodon hispidus* group**: Eight out of 16 species required
Salvia pratensis	*Leontodon hispidus*
Festuca rupicola	*Briza media*
Achillea pannonica	*Carex flacca*
Eryngium campestre	*Carex caryophyllea*
Filipendula vulgaris	*Koeleria pyramidata*
Bupleurum falcatum	*Thymus pulegioides*
Potentilla heptaphylla	*Ranunculus bulbosus*
Adonis vernalis	*Plantago lanceolata*
	Cirsium acaule
	Plantago media
	Scabiosa columbaria
	Linum catharticum
	Lotus corniculatus
	Carlina vulgaris
	Festuca ovina
	Potentilla neumanniana

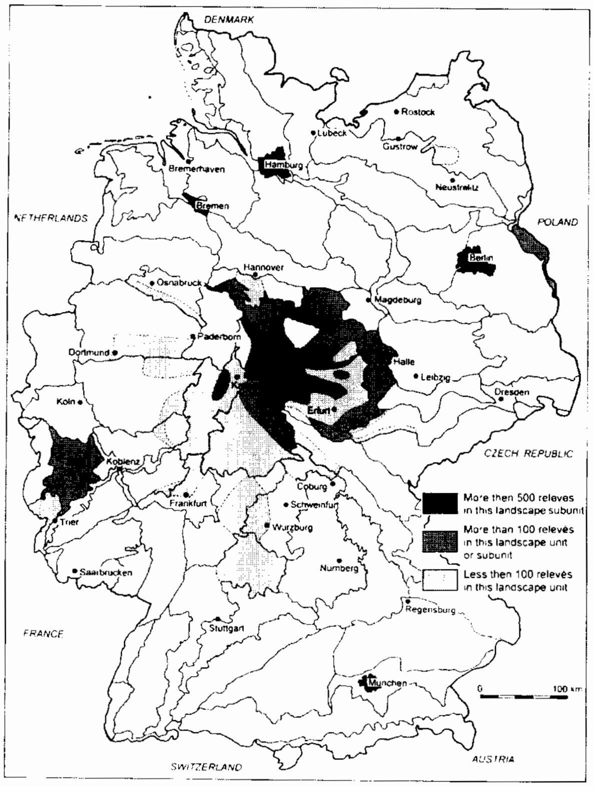

Fig. 1. Origin of the relevés in the database.

Table 3. Alliances encountered in the data base using the species-group method. English names according to Ellenberg (1988).

alliance	number of relevés
Festucion valesiacae (Continental arid swards)	640
Cirsio-Brachypodion (Continental fairly dry swards)	935
Xerobromion (Suboceanic arid swards)	457
Mesobromion (Suboceanic fairly dry swards)	3412
Festucion pallentis (Pale fescue rocky outcrop comm.)	159
Koelerio-Phleion (Acid-soil fairly dry swards)	156
Arrhenatherion (Oatgrass meadows)	411
Alysso-Sedion (Stonecrop calcareous wheathered rock comm.)	107
Geranion sanguinei (Bloddy cransebill fringe comm.)	77
Koelerion glaucae (Blue green hairgrass sandy swards)	81
Sesleria varia communities (Blue moorgrass slope comm.)	582

1997). The initially equivalent species groups are weighted subjectively in order to obtain a hierarchical classification. The resulting classification should reflect traditionally used vegetation units with practical importance as much as possible. Therefore, the alliances of the Braun-Blanquet system were chosen as references. As was said above, the associations known from literature lack comparable assignment criteria and cannot serve as basic units for comparisons.

For the formal definition referring to species groups three possible cases are considered: a species group is (1) required to define an alliance, (2) allowed to occur without any relevance for the definition of the considered alliance or (3) not tolerated within the alliance. Alliances are defined either by presence of one species group or by combinations of several species groups. In addition, they are arranged hierarchically. For example, the first criterion for definition of the *Mesobromion* is presence of the *Leontodon hispidus* group (Table 2). Yet this criterion is applied only if certain other species groups, such as the *Salvia pratensis* group (Table 2) are not present. Altogether, using species groups, 11 different allliances were distinguished in the data base (Table 3). Some further alliances are represented by few relevés only. Furthermore, these alliances can be subdivided into lower vegetation units using species groups. For more details see Jandt 1999.

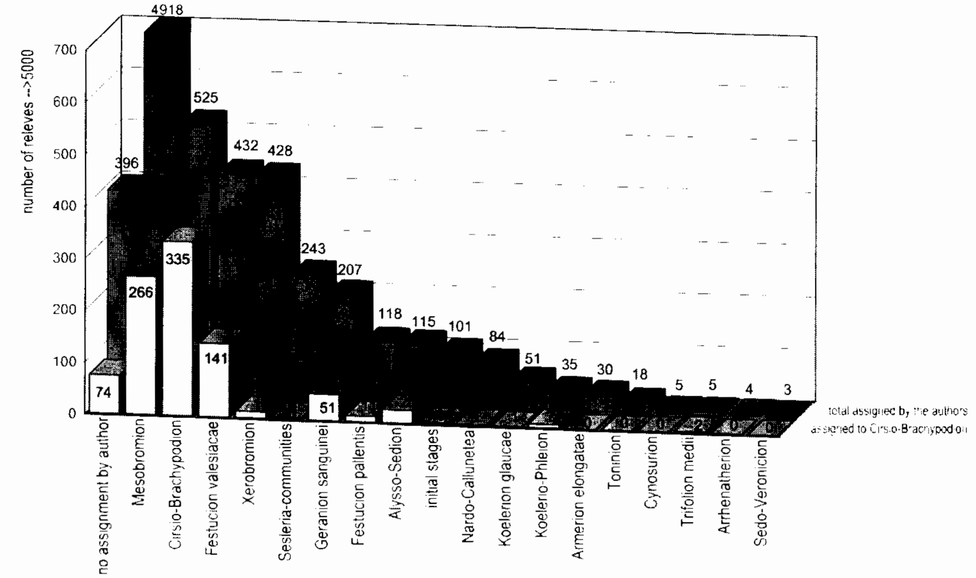

Fig. 2. Assignment of relevés to the *Cirsio-Brachypodion* using species groups in comparison with the original authors' opinion.

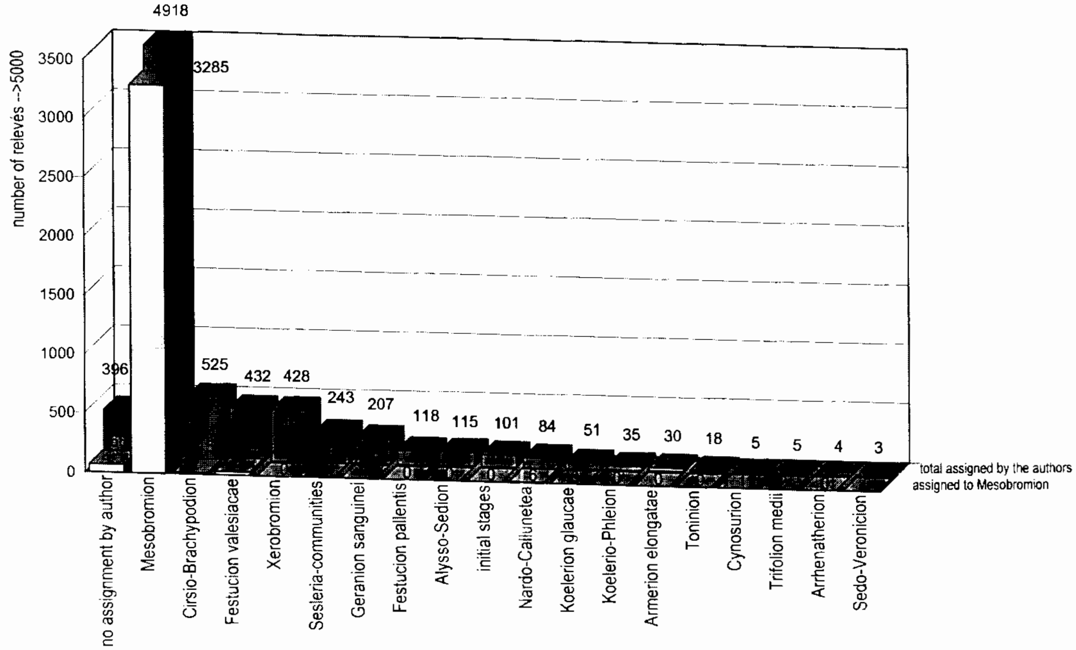

Fig. 3. Assignment of relevés to the *Mesobromion* using species groups in comparison with the original authors' opinion.

Evaluation

The formal definition of alliances was compared with the original authors' opinion, to check the correctness of the assignment of relevés to a certain vegetation unit. For this purpose each relevé in the database was supplied with the information of its original assignment on the alliance level.

The evaluation of the *Cirsio-Brachypodion* is illustrated in Fig. 2. The front columns shown in pale grey shading show the degree of assignment of relevés in the data base to the *Cirsio-Brachypodion* when the species-group method and the previously described formal allocation scheme is applied. Background columns in dark grey represent the total number of relevés present in the database, assigned to the different alliances according to the opinion of the original author. There are 335 out of a total of 525 relevés of the *Cirsio-Brachypodion* that have been congruently assigned. A further 266 relevés were allocated to the *Cirsio-Brachypodion*, which had originally belonged to the *Mesobromion* as well as 141 relevés originally described as belonging to the *Festucion valesiacae*. Only a few other alliances also contribute to the *Cirsio-Brachypodion*.

Obviously, the species-group assignment does not exactly match the individual authors' opinions. This outcome was to be expected, because it reflects the lack of universally valid allocation criteria and the variety of personal opinions.

Fig. 3 shows the same pattern of assignment for the *Mesobromion*. In this case the number of relevés that originally did not belong to the *Mesobromion* is quite low. The relatively high number of relevés (1633) originally described as the *Mesobromion*, but not assigned to it in this study, mostly includes species-poor initial forms.

Outlook

The species-group method yields subdivisions of the data set comparable to alliances of the Braun-Blanquet system. Further subdivision results in lower vegetation units comparable to associations, subassociations and so on. Vegetation units obtained by the species-group method can be presented as synoptic tables, to which phytosociologists are accustomed. Therefore, the method unifies the advantages of traditional vegetation units that have been approved in practice, with those of a reproducible and objective computer analysis supplying clear allocation criteria. Although the method is incorruptible in treating species and relevés equivalently, personal judgements and experience may be incorporated. For other examples of application of the species-group method see Bruelheide (1995), Burkart (1998), Jandt (1999), Pflume (1999) and Baumann (2000).

It should be noted that this classification, as it is a geographically restricted classification, is not the ultimate solution for some alliances that occur at the periphery of their distribution area in Germany. Nevertheless, within the considered area, the allocation scheme is generally valid. Another important achievement of the species-group method is, that it is applicable on a local scale as well as on national scale and perhaps, in the future, on European scale.

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Ecological classification of shrubs and semi-shrubs in temperate deserts of Eurasia

Safronova, Irina N.

Vegetation Geography and Cartography Department, Komarov Botanical Institute of the Russian Academy of Sciences, 197376 St.-Petersburg, Russian Federation; Fax +78122344512; E-mail irinasaf@is1189.spb.edu

Abstract. Shrubs and semi-shrubs give a peculiar appearance to the temperate deserts of Eurasia. The ecology of these species, which are widespread on the plains between the Caspian and Aral Seas, is described. The desert shrubs and semi-shrubs were divided into four ecological groups: petrophytes, psammophytes, halophytes, and eurytopic shrubs and semi-shrubs. Petrophytes (shrubs: *Caragana grandiflora*, *Rhamnus sintenisii*: semi-shrubs: *Astragalus turcomanicus*, *Salsola arbusculiformis*) grow exclusively on stony-gravelly shallow soils developed over different rocks, such as limestone, sandstone, chalk (with the exception of Tertiary carbonate clays). Psammophytes (shrubs: *Calligonum aphyllum*, *C. caput-medusae*, *C. leucocladum*, *Haloxylon persicum*; semi-shrub: *Astragalus karakugensis*) are found only on sandy soils and sand massifs. Halophytes (shrubs: *Nitraria schoberi*, *Tamarix elongata*, *T. gracilis*, *T. hispida*, *T. hohenackeri*, *T. laxa*, *T. ramosissima*) are found on saline soils of different texture. The eurytopic species occur in a wide range of habitats: *Calligonum junceum* and *Haloxylon aphyllum* are common species of salt-laden sands and soils with a strong concentration of gypsum; shrubs: *Atraphaxis replicata*, *Salsola arbuscula*, *Calligonum junceum*, *Haloxylon aphyllum*, and semi-shrubs *Convolvulus fruticosus*, *Krascheninnikovia ceratoides* grow on limestone, sandstone, chalk as well as on sands with a depth of 50-80 cm.

Keywords: Ecological group; Eurytopic species; Halophyte; Petrophyte; Psammophyte.

Nomenclature: Czerepanov (1995).

Characteristics of temperate deserts

In Eurasia the temperate deserts are distributed from the Ergeni Mountains in the west (45° E) to Dzungaria in the east (85° E) and from the southern boundary of the steppe area in the north from 48° N (crossing the Caspian Lowland, Sub-Ural Plateau, Mugodzhary Mountains and Kazakh Hummocky Plain) to the mountains of Central Asia (Kopet Dagh, Pamir-Alaj, Tien-Shan) in the south (38° N).
This area is characterized by the large annual and summer daily amplitudes of air temperature, low precipitation (50 - 250 mm) and high evaporation (3 - 4 × precipitation). The coldest month is January with an average monthly temperature of –5 to –15° C (minimum –46° C). The average monthly July temperature is +25 to 29° C (maximum +47 °C). The temperature sum of temperatures above +10 °C is 3400 - 4600 °C. The predominating soils are brown and grey-brown desert soils, while salty soils (solonetz, solonchak), sands and takyrs occur often in the Temperate Desert area. Solonetz is characterized by dense surface and dense salty horizon with a columnar or prismatic structure in the lower part of the profile. Solonchak is a hydromorphic soil with a high concentration of water-soluble salts in the surface layer, forming salt efflorescence. Takyr is a primitive shallow desert soil, mainly loamy, with dense and smooth surface cracked in polygons (Rachkovskaya et al. 1990).

Various plant growth forms characterize the vegetation of the deserts, with dwarf semi-shrubs dominating. Shrubs are plants with woody stems and branches throughout and taller than 50 cm. Semi-shrubs are also taller than 50 cm but have partly ligneous annual shoots, the upper part of which die off every autumn. Dwarf semi-shrubs are similar to semi-shrubs, but with smaller stems and lower height (30 - 40 cm) (Nechaeva 1973).

Dwarf semi-shrubs (notably *Artemisia*, *Anabasis*, *Salsola*, *Atriplex*) form plant communities in diverse environments and determine the physiognomy of most of the landscapes in the region. Shrubs and semi-shrubs are indicators of a more favourable soil water status, particularly on sands (which have a low evaporation because of the low water capacity and suboptimal capillary action of soil water), stony-gravelly substrates of various lithology condensing water, and saline (solonchak) depressions with high ground water levels.

Shrubs and semi-shrubs are a particular characteristic of the biome of the Eurasian Temperate Deserts. They attain a height of 1 to 1.5 m on average (minimum 0.5 - 0.8 m; maximum 2 - 2.5 m) and show various horizontal patterns ranging from nearly even to clumped distributions, they can form dense mono-dominant or oligo-dominant communities.

Ecological groups of shrubby desert species

Communities characterized by shrubs and semi-shrubs occupy large areas. Their significance in the vegetation is obvious in the 1 : 2 500 000 'Vegetation map of Kazakhstan and Central Asia' from 1995, and in the 'Map of reconstructed vegetation of Central and Eastern Europe' (same scale) from 1996. In the map legends 40 shrub and semi-shrub species from 11 families are mentioned.

The four most important families – as far as the number of species is concerned – are *Polygonaceae* (12), *Fabaceae* (10), *Tamaricaceae* (8) and *Chenopodiaceae* (6). Other families include the *Convolvulaceae* and *Ephedraceae* with two species and five families with one species (Table 1).

This short survey is limited to those shrubby species which served as a basis for delimitation of mapping units of plain deserts in the legend of the vegetation map of Kazakhstan and Middle Asia (Ladygina et al. 1995). The desert shrubs and semi-shrubs are divided into four ecological groups: petrophytes, psammophytes, halophytes and eurytopic species (Safronova 1996).

1. *Petrophytes* grow on cobble hill-slopes, on plateau stone terraces, in canyons with rock outcrops of various lithological composition. They are *Salsola arbusculiformis*, *Malacocarpus crithmifolius*, *Rhamnus sintenisii* and *Crataegus ambigua*.

Salsola arbusculiformis is a North-Turanian species and a main dominant of plant communities on the Bet-Pak-Dala Plateau. Its range spreads through the Ust'urt Plateau up to the mountains of the Mangyshlak Region; its eastern distribution limit is found in the Alashan' Desert (Grubov 1955; Petrov 1966) with a gap in the eastern part of Chinese Dzungaria and Kashgaria and in central parts of the Gobi Desert (Lavrenko 1962).

Rhamnus sintenisii is a West-Turanian species. It is widely distributed throughout the Mangyshlak Region. It is a solitary large branched shrub of 1.5 to 2 m tall and inhabits precipices, deep canyons, and rarely occurs on rolling hills with outcrops of limestone and sandstone. The species is especially abundant on the precipices of the Tjub-Karagan Peninsula. On the Kinderli-Kayasan Plateau it is scattered along dry streams with stony bottoms.

Malacocarpus crithmifolius is a West-Turanian species. It forms stands on stony slopes and screes, but it is rare and listed as an endangered species (Bikov 1981).

Crataegus ambigua is an endemic species of the Western Turan. Its solitary shrubs are not uncommon in canyons of the Mangyshlak mountains and on plateau precipices. It is included in the Red Book of Kazakhstan (Bikov 1981).

2. *Psammophytes* occur on sands (with different kind of relief such as dune, bump, barkhan, etc.). This is the largest group with 20 species. Among those, the Sahara-Gobi genus *Calligonum* predominates (nine species). The centre of the distribution of this genus is found in sand deserts of Turan (Lavrenko 1962; Musaev 1969). *C. aphyllum*, *C. caput-medusae* and *C. leucocladum* are the Turanian species; *C. aphyllum* is the only representative of this genus which is widely spread on the sands of the Caspian Lowland. *C. murex* is a Central-Turanian species. *C. microcarpum*, *C. setosum* are South-Turanian elements. *C. dubijanskyi* and *C. plicatum* are East-South-Turanian species.

Astragalus brachypus and *A. karakugensis*, both Turanian elements, are widespread. The other species of the genus *Astragalus* – one of the species-richest genera in the world, and especially well-differentiated in Central Asia (Kamelin 1973) – have smaller distribution ranges: *A. ammodendron* occurs on the sands of Western Turan; *A. paucijugus* is common eastward of the Aral Sea and *A. unifoliolatus* is a South-Turanian species.

The South-Turanian psammophytes *Salsola richteri*, *Ephedra strobilacea*, *E. lomatolepis*, the Turanian *Eremosparton aphyllum* and the Irano-Turanian *Haloxylon persicum* and *Mausolea eriocarpa* play an important role in the plant cover of the sand massifs of the Turan.

Psammophytes form mono-dominant communities of *Haloxylon persicum* and oligo-dominant communities of *Calligonum* species or communities dominated by *Astragalus*, *Calligonum*, *Salsola*, *Ephedra*, *Mausolea eriocarpa* or *Eremosparton aphyllum*.

Table 1. Basic ecological and taxonomic data on the shrubs and semi-shrubs occurring in Temperate Deserts of Eurasia. Legend: Growth-form codes: S = shrub (plant with woody stems and branches throughout and > 50 cm); SS = semi-shrub (> 50 cm and woody stems and branches which are dead for most of the year). Family abbreviations: AST = *Asteraceae*; CHE = *Chenopodiaceae*; CON = *Convolvulaceae*; EPH = *Ephedraceae*; FAB = Fabaceae; ZYG = *Zygophyllaceae*; PEG = *Peganaceae*; POL = Polygonaceae; RHA = *Rhamnaceae*; ROS = *Rosaceae*; TAM = *Tamaricaceae*. Ecological group codes: EU = eurytopic species; PS = psammophyte; P = petrophyte; H = halophyte; Latitudinal distribution at the limits of the Temperate Desert Zone in Eurasia with dominant dwarf semi-shrubs (plant similar to semi-shrubs, but with smaller wooden stems and height 30 - 40 cm), semi-shrub- and shrub communities: n = northern deserts (subzone between 47° and 48°N); m = middle deserts (subzone between 43° and 47°N); s = southern deserts (subzone between 38° and 43°N); Floristic elements (according to Lavrenko 1962): SG = Saharo-Gobian; ITG = Irano-Turano-Gobian; TG = Turano-Gobian; IT = Irano-Turanian; T = Turanian; NT = North Turanian; ST = South Turanian; CWT = Caucasian-West Turanian; WT = West Turanian; WST = West-South Turanian; CT = Central Turanian; ET = East Turanian; EST = East-South Turanian.

Species name	Fam	Growth form	Ecol. group	Lat. distr.	Flor. elem.
Ammodendron eichwaldii	FAB	S	EU	s	WT
Astragalus ammodendron	FAB	SS	PS	n, c, s	WT
A. brachypus	FAB	SS	PS	n, c, s	T
A. karakugensis	FAB	SS	PS	n, c, s	T
A. paucijugus	FAB	SS	PS	c, s	ET
A. turcomanicus	FAB	SS	EU	c, s	WT
A. unifoliolatus	FAB	SS	PS	s	ST
A. villosissimus	FAB	SS	EU	s	EST
Atraphaxis replicata	POL	S	EU	n, c, s	IT
Calligonum aphyllum	POL	S	PS	n, c, s	T
C. caput-medusae	POL	S	PS	c, s	T
C. dubijanskyi	POL	S	PS	s	EST
C. junceum	POL	S	EU	c, s	TG
C. leucocladum	POL	S	PS	n, c, s	T
C. microcarpum	POL	S	PS	s	ST
C. murex	POL	S	PS	c, s	CT
C. plicatum	POL	S	PS	s	EST
C. setosum	POL	S	PS	s	ST
Caragana grandiflora	FAB	S	EU	c, s	CWT
Convolvulus erinaceus	CON	SS	PS	n, c, s	IT
C. fruticosus	CON	SS	EU	n, c, s	T
Crataegus ambigua	ROS	S	P	c	WT
Ephedra lomatolepis	EPH	S	PS	s	ST
E. strobilacea	EPH	S	PS	s	ST
Eremosparton aphyllum	FAB	S	PS	n, c, s	T
Haloxylon aphyllum	CHE	S	EU	n, c, s	IT
H. persicum	CHE	S	PS	c, s	IT
Krascheninnikovia ceratoides	CHE	SS	EU	n, c, s	SG
Malacocarpus crithmifolius	PEG	S	P	c	WT
Mausolea eriocarpa	AST	SS	PS	s	IT
Nitraria schoberi	ZYG	S	H	n, c, s	T
Reaumuria fruticosa	TAM	S	EU	c, s	WST
R. oxiana	TAM	SS	EU	s	EST
Rhamnus sintenisii	RHA	S	P	c, s	WT
Salsola arbuscula	CHE	S	EU	n, c, s	ITG
S. arbusculiformis	CHE	SS	P	n, c	NT
S. richteri	CHE	S	PS	s	ST
Tamarix elongata	TAM	S	H	n, c, s	TG
T. gracilis	TAM	S	H	n, c, s	TG
T. hispida	TAM	S	H	n, c, s	TG
T. hohenakeri	TAM	S	H	n, c, s	ITG
T. laxa	TAM	S	H	n, c, s	ITG
T. ramosissima	TAM	S	H	n, c, s	ITG

3. Halophytes are connected with saline habitats: solonchaks, solonetz and saline soils of different texture. Almost all of them (six species) are *Tamaricaceae*, one species belongs to the *Zygophyllaceae* (*Nitraria schoberi*, a Caspian-Turanian species). The *Tamaricaceae* are represented by the Saharo-Gobian genus *Tamarix* with most species widely spread throughout the whole Turan, e.g. *T. elongata* and *T. gracilis* (Table 1).

4. Eurytopic species cover a large range of habitats as compared with the other groups. The group includes four species of *Fabaceae* and three *Chenopodiaceae*, two *Polygonaceae*, two *Tamaricaceae* and one *Convolvulaceae*. *Caragana grandiflora* is a Caucasian-West-Turanian species, occurring in the Aral region and on the Ust'urt Plateau, it has the phytocoenotic optimum in the Mangyshlak Region. *C. grandiflora* communities are distributed on rocks of various lithology, but preferably on chalk and occasionally on deep (compact) saline sands.

Astragalus turcomanicus a West-Turanian species widespread in the Mangyshlak Region on eroded slopes and rocky habitats of various lithological composition (limestone, sandstone, chalk, deep sands), being codominant in shrub-semi-shrub communities.

Astragalus villosissimus is an East-South-Turanian species. It plays a significant role in vegetation of the Kyzylkum sands and on stony-cobble soils of the Syr-Darya Karatau Lowland.

Ammodendron eichwaldii is a West-Turanian species growing on stony-gravelly soils and sands, and forming mono-dominant plant communities, or it is a component of oligo-dominant shrub communities and *Haloxylon aphyllum* communities.

Haloxylon aphyllum is an Iran-Turanian species. It is one of the main dominants of the Turan Deserts. *H. aphyllum* communities occupy large sandy areas. It is a frequent component of oligo-dominant psammophyte desert plant communities and also occurs as separate shrubs on steep stony slopes, precipices and screes. *H. aphyllum* tolerates high salt contents quite well and grows on gypsum soils as well.

The eurytopic group includes one *Calligonum* species, *C. junceum*. This species is found mainly on saline sands, but also grows on gypsum soils and on Tertiary (often variegated) clays.

Atraphaxis replicata (Iran-Turanian), *Convolvulus fruticosus* (Turanian), *Krascheninnikovia ceratoides* (a continental species with an extensive range), *Salsola arbuscula* (a Gobi-Iran-Turanian species), widely spread in Temperate Deserts, are found both on stony-gravelly soils over various bedrocks and on shallow sand deposits. They form three mono-dominant communities and several oligo-dominant communities, which are characteristic of the West Turan (especially of the Mangyshlak Region).

Two species of the Saharo-Gobian genus *Reaumuria* (*Tamaricaceae*), *R. fruticosa* and *R. oxiana* belong to the eurytopic group as well. The former species has a West-South-Turan range; the range of the latter one is included in the Kyzylkum Desert. Both species prefer saline habitats with gypsum clays, saline sands, solonchak and takyrs.

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Preliminary syntaxonomic scheme of vegetation classes for the Central Bushveld of South Africa

Winterbach, R.[1,2], Bredenkamp, G.J.[1]*, Deutschländer, M.S.[1] & Mucina, L.[1,3]

[1]*Department of Botany, University of Pretoria, Pretoria 0002, Republic of South Africa;* [2]*Present address: Chobe National Park, Botswana;* [3]*Present address: Department of Botany, University of Stellenbosch, Private Bag X1, Stellenbosch 7602, South Africa;*
* *Fax +271243625099; E-mail gbredenk@scientia.up.ac.za*

Abstract. Data from 29 vegetation studies done in the so-called Central Bushveld, South Africa (a large region N and NW of Pretoria), were subject to syntaxonomic synthesis using TWINSPAN and further refined with traditional table-sorting procedures of the floristic-sociological approach to classification of vegetation. The analysis revealed four major groups of communities, interpreted at this stage as zonal vegetation classes which we preliminarily name: *Commiphoro mollis-Colophospermetea mopani*, *Panico maximi-Acaciatea tortilis*, *Terminalio sericeae-Combretetea apiculati* and *Englerophyto magalismontani-Acacietea caffrae*.

Keywords: Syntaxonomy; TWINSPAN.

Nomenclature: Arnold & De Wet (1994), except for *Englerophytum magalismontanum* (Sond.) T.D. Penn.

Introduction

The Central Bushveld of South Africa can be defined as the bushveld of the North West Province (N of the Magaliesberg) and the Northern Province. The area is situated between the Kalahari in the west (the Botswana border) and the Lowveld, east of the Great Escarpment (Fig. 1). Several vegetation studies have been conducted in the Central Bushveld. These include published studies (e.g. Schmidt et al. 1993; Schultze et al. 1994; Brown et al. 1996) as well as unpublished reports (e.g. by G.J. Bredenkamp in 1978 and Q. Nel in 1997). These studies were confined to farms or nature reserves, scattered throughout the Central Bushveld. The syntaxonomy and synecology of the vegetation of a part of the North West Province (van der Meulen 1979) are also included in this study.

The present general knowledge of the vegetation of this area is based on descriptions by Acocks (1988) and Low & Rebelo (1996). Their classifications of broad vegetation types were however not based on phytosociological data.

The aim of this study is to present a preliminary syntaxonomic synthesis of the available relevés in order to identify the major zonal vegetation types that may represent phytosociological classes. Relevés from azonal vegetation (e.g. wetlands, synanthropic vegetation) were disregarded.

Material and Methods

Results of classification efforts of 29 phytosociological vegetation studies (Table 1) performed in the region of the Central Bushveld, published as well as those presented in unpublished works, are summarized in 39 phytosociological tables and descriptions of many savanna communities. Relevés from azonal and intra-zonal communities were removed. The resulting data set had 2907 relevés with 1369 taxa. As a first step, we constructed a synoptic vector for each community from each table. Every community, representing zonal vegetation from the 39 phytosociological tables, was thus summarized into a single column in a single synoptic table. In total 378 plant communities representing local tables (sensu Westhoff & van der Maarel 1978) were re-analysed using programme TWINSPAN (Hill 1979). A final synoptic table was constructed, and major community groups, each interpreted preliminarily as a zonal vegetation class, were recognized. The final synoptic table (Table 2) contains the constancy values of the species, traditionally given in Roman numbers (I - V) representing 20% intervals.

Results

Four major groups of savanna plant communities were recognized. The first TWINSPAN division separated the Mountain Bushveld communities from the other communities. The second division separated communities from the Mopane Veld and the Arid Sweet Bushveld (Acocks 1988). A further division of the remainder resulted in two groups, one representing Broad-Leaved Bushveld (Werger & Coetzee 1978), dominated by *Combretum* species, while the other group is the Microphyllous Thorny Bushveld dominated by *Acacia* species (Cole 1986).

This suggests that the Central Bushveld may be divided into four classes, which we give the preliminary names:
Commiphoro mollis-Colophospermetea mopani;
Panico maximi-Acacietea tortilis;
Terminalio sericeae-Combretetea apiculati;
Englerophyto magalismontani-Acacietea caffrae.

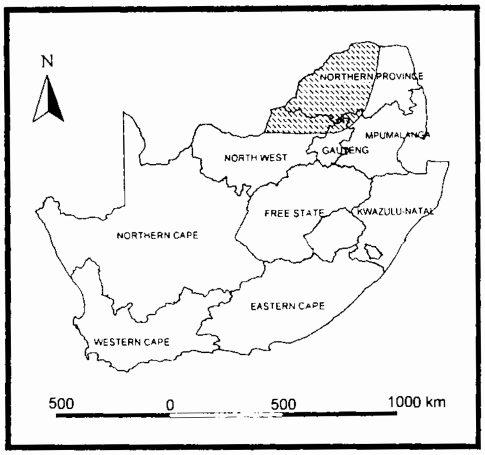

Fig.1. Location of the Central Bushveld, South Africa.

Table 1. Sources of phytosociological data used in re-analysis of the classification scheme for the Central Bushveld of South Africa.

Author	Year	Location	Rels.
Botha	1994	Waterberg Wildsentrum	104
Bredenkamp	unpubl.	Pietersburg Nature Res.	81
Bredenkamp & van Vuuren	1977	Turfloop Dam, Pietersburg	19
Brown & Bredenkamp	1994	Borakalalo Nature Res., Brits	82
Brown et al.	1995	Borakalalo Nature Res., Brits	137
Brown et al.	1996	Borakalalo Nature Res., Brits	132
Coetzee	1975	Rustenburg Nature Res.	191
Coetzee et al.	1976	Nylsvley, Nylstroom	161
De Frey	1993	Loskopdam, Groblersdam	10
De Kock et al.	1977	Wonderboom, Pretoria	41
Dekker & van Rooyen	1995	Messina Experimental Farm	148
Fourie	1994	Kwalata Game Ranch, Ellisras	63
Fourie	unpubl.	De Boveneinde, Vaalwater	27
Hattingh	1994	Warmbaths Nature Reserve	33
Kruger	1990	Mabalingwe, Warmbaths	107
Nel	unpubl.	Rustenburg Nature Res.	283
Pauw	1988	Atherstone Nature Res., Thabazimbi	43
Purchase	1994	Vlakpan, Marblehall	40
Schmidt et al.	1993	Rhino Ranch, Ellisras	43
Schultz et al.	1994	Imberhe Game Ranch, Ellisras	39
Smith	1992	Doornpoort, Pretoria	58
Turner	1995	Mokolo, Ellisras	85
van der Meulen	1979	North West Province	514
van Essen	1993	Bosveld Rentmeesters, Roedtan	25
van Rooyen	1983	Roodeplaat, Pretoria	70
van Schalkwyk	1993	Mabula Game Res., Warmbaths	87
Visser et al.	1996	Honnet Nature Res., Tsipise	54
Westfall	1978	Silkaatsnek, Pretoria	74
Westfall	1985	Groothoek, Thabazimbi	156

Commiphoro mollis-Colophospermetea mopani

The communities of the *Commiphoro-Colophospermetea mopani* occur in the far northern part of the study area and are well-known as the Mopane Veld. The tree *Colophospermum mopane* is usually the sole spectacular dominant in this sparse-woodland community. It grows on fine-grained, usually deep soil that varies from sandy to loamy and clayey (Werger & Coetzee 1978).

Character species of this class include the woody species *Colophospermum mopane, Combretum mossambicense, Boscia albitrunca, Acacia erubescens, A. nigrescens, A. senegal, Grevia bicolor, Kirkia acuminata* and *Terminalia prunioides.* The most important diagnostic forbs are *Acalypha villicaulis, Sida ovata* and *Tribulus terrestris* accompanied by prominent grasses *Stipagrostis uniplumis, Eragrostis lehmanniana, Aristida adscensionis, Cenchrus ciliaris, Enneapogon cenchroides* and *Tragus berteronianus. Grewia bicolor* and *Enneapogon cenchroides* were revealed as the most important indicator species at the division level separating the *Commiphoro-Colophospermetea mopani* from the *Panico-Acacietea tortilis* and the *Terminalio-Combretetea apiculati.*

Panico maximi-Acacietea tortilis

This microphyllous Thorny Bushveld is considered as an Arid Bushveld (Huntley 1982, 1984) and it occurs in the Transvaal Plateau Basin, comprising the flat Bushveld Basin and the Waterberg, Soutpansberg and Pietersburg Plateaus (Cole 1986). It is characteristic of the dark, clayey soils often developed over basalt in the low lying areas.

The *Panico-Acacietea tortilis* gives way to deciduous broad-leaved savanna in upland areas with sandy soils underlain by granite, thus forming an extensive mosaic with the *Terminalio-Combretea apiculati.*

Diagnostic species for this class include trees and shrubs such as *Acacia karroo, A. robusta, A. nilotica, A. mellifera, Rhus lancea, R. pyroides* as well as grasses *Eragrostis rigidior, E. superba, Cymbopogon plurinodis.* Alien herbs such as *Tagetes minuta* and *Bidens bipinnata* are also very abundant and appear to have a diagnostic value.

The TWINSPAN analysis indicated that only one woody species can be considered as indicator: *Terminalia sericea.* This tree is usually associated with sandy soils of the *Terminalio-Combretetea apiculati.* It is possibly an indicator of some of the *Panico-Acacietea tortilis* plant communities occurring on the relatively sandy side of a soil texture ecocline within the *Panico-Acacietea tortilis* (Winterbach 1997). Other indicator species include *Eragrostis rigidior, Tagetes minuta, Aristida stipitata* and *Waltheria indica.*

Terminalio sericeae-Combretetea apiculati

The vegetation of this class occurs on sandy loam underlain by granite, quartzite and dolomite. It is considered by Huntley (1982, 1984) to be a moist savanna. On the Springbok Flats in the Bushveld Basin, where vertic clay soils are formed from underlying basalt, this vegetation is only found on sandy sediments and on aeolian sands (Werger & Coetzee 1978). In the slightly undulating landscape, this broad-leaved sparse woodlands form a mosaic with the *Panico-Acacietea tortilis*, where the former is found on the upland sandy areas whereas the latter occupies lower lying clayey areas.

The *Terminalio-Combretetea apiculati* are characterized by the woody *Diplorhynchus condylocarpon, Croton gratissimus* and *Pseudolachnostylis maprouneifolia.* Diagnostic forbs and grasses are *Rhoicissus revoilii, Tephrosia longipes, Aristida diffusa, Eragrostis chloromelas* and *Schizachyrium jeffreysii.* Other prominent species include trees and shrubs, e.g. *Ziziphus mucronata, Terminalia sericea, Vitex rehmannii, Dombeya rotundifolia, Combretum molle, C. zeyheri and Acacia caffra*, forbs, e.g. *Phyllanthus parvulus, Commelina africana* and *Solanum panduriforme* and grasses, e.g. *Brachiaria nigropedata, Panicum maximum, Digitaria eriantha, Aristida congesta* ssp. *congesta, Loudetia simplex, Schizachyrium sanguineum* and *Melinis repens.*

The indicator species derived from the TWINSPAN analysis for this class are *Combretum molle, Burkea africana, Diplorhynchus condilocarpon, Rhoicissus revoilii* and *Loudetia simplex.*

Englerophyto magalismontani-Acacietea caffrae

This mountain is found on the slopes of the Waterberg and the bushveld Magaliesberg, Witwatersrand and Suikerbosrand. It occurs mainly on sandy soils underlain by solid rock of various geology.

Table 2. Synoptic table for the vegetation classes of the Central Bushveld. Only very diagnostic or very frequent species were selected.

1: *Commiphoro-Colophospermetea mopani*
2: *Panico-Acacietea tortilis*
3: *Terminalio-Combretetea apiculati*
4: *Englerophyto-Acacietea caffrae*

Class	1	2	3	4
Number of communities	32	192	37	90
Group A: diagnostic species of the *Commiphoro-Colophospermetea mopani*				
Enneapogon cenchroides	V			
Grewia bicolor	V			
Aristida adscensionis	IV			
Terminalia prunioides	IV			
Stipagrostis uniplumis	IV			
Acacia nigrescens	III			
Acacia senegal	III			
Tribulus terrestris	III			
Aptosimum lineare	III			
Combretum mossambicense	III			
Acalypha villicaulis	III			
Boscia albitrunca	III			
Brachiaria deflexa	III			
Achyranthes aspera var. *sicula*	III			
Pavonia burchellii	III			
Monechma divaricatum	III			
Hibiscus micranthus	III			
Hermannia odorata	III			
Cenchrus ciliaris	III			
Gisekia africana	III			
Group B: diagnostic species of the *Panico-Acacietea tortilis*				
Acacia karroo	.	III		
Eragrostis rigidior	.	III		
Group C: species common to Classes 1 and 2				
Eragrostis lehmanniana	IV	II		
Grewia flava	III	III		
Acacia tortilis	III	III		
Evolvulus alsinoides	III	II		
Tragus berteronianus	III	II		
Kyphocarpa angustifolia	II	II		
Urochloa mosambicensis	II	II		
Aristida congesta ssp. barbicollis	II	II		
Group D: diagnostic species of the *Terminalio-Combretetea apiculati*				
Diplorhynchus condylocarpon	.	.	IV	
Rhoicissus revoilii	.	.	IV	
Tylosema fassoglense	.	.	III	
Croton gratissimus	.	.	III	
Asparagus africanus	.	.	III	
Gardenia volkensii	.	.	III	
Hexalobus monopetalus	.	.	III	
Euclea natalensis	.	.	III	
Mundulea sericea	.	.	III	
Pterocarpus rotundifolius	.	.	III	
Pseudolachnostylis maprouneifolia	.	.	III	
Strychnos pungens	.	.	III	
Tephrosia longipes	.	.	III	
Group E: species common to Classes 2 and 3				
Ziziphus mucronata	.	III	II	
Terminalia sericea	.	II	IV	
Brachiaria nigropedata	.	II	IV	
Vitex rehmannii	.	II	IV	
Eragrostis gummiflua	.	II	III	
Dombeya rotundifolia	.	II	III	
Ehretia rigida	.	II	II	
Perotis patens	.	II	II	
Pogonarthria squarrosa	.	II	II	
Monsonia angustifolia	.	II	II	
Merremia tridentata	.	II	II	
Lantana rugosa	.	II	II	
Limeum viscosum	.	II	II	
Enneapogon scoparius	.	II	II	
Cleome maculata	.	II	II	
Aristida stipitata	.	II	II	
Trichoneura grandiglumis	.	II	II	
Waltheria indica	.	II	II	
Aerva leucura	.	I	I	
Group F: species common to Classes 1, 2 and 3				
Panicum maximum	III	IV	III	
Dichrostachys cinerea	III	IV	II	
Digitaria eriantha	II	IV	IV	
Aristida congesta	II	IV	IV	
Phyllanthus parvulus	II	II	IV	
Combretum apiculatum	II	II	IV	
Schmidtia pappophoroides	II	II	II	
Grewia monticola	III	.	II	
Group G: diagnostic species of the *Englerophyto-Acacietea caffrae*				
Senecio venosus	.	.	.	III
Indigofera comosa	.	.	.	III
Bulbostylis burchellii	.	.	.	III
Trachypogon spicatus	.	.	.	III
Group H: species common to Classes 3 and 4				
Burkea africana	.	.	V	II
Loudetia simplex	.	.	IV	III
Lannea discolor	.	.	IV	II
Ozoroa paniculosa	.	.	IV	II
Pellaea calomelanos	.	.	III	IV
Englerophytum magalismontanum	.	.	III	III
Andropogon schirensis	.	.	III	III
Tapiphyllum parvifolium	.	.	III	II
Maytenus tenuispina	.	.	III	II
Oldenlandia herbacea	.	.	III	II
Asparagus suaveolens	.	.	III	II
Ochna pulchra	.	.	III	II
Melinis nerviglumis	.	.	II	IV
Vangueria infausta	.	.	II	III
Faurea saligna	.	.	II	II
Setaria lindenbergiana	.	.	II	II
Eragrostis racemosa	.	.	II	III
Group I: species common to Classes 2, 3 and 4				
Themeda triandra	.	III	III	IV
Heteropogon contortus	.	III	III	III
Diheteropogon amplectens	.	II	III	IV
Combretum molle	.	II	V	II
Combretum zeyheri	.	II	IV	II
Brachiaria serrata	.	II	III	III
Schizachyrium sanguineum	.	II	III	III
Setaria sphacelata	.	II	II	III
Lippia javanica	.	II	III	II
Elionurus muticus	.	II	II	II
Commelina erecta	.	II	II	II
Acacia caffra	.	II	II	II
Osyris lanceolata	.	I	I	I
Eustachys paspaloides	.	I	I	I
Chamaecrista mimosoides	.	II	.	II
Diospyros lycoides	.	II	.	II
Eragrostis curvula	.	II	.	II
Rhus leptodyctia	.	II	.	II
Celtis africana	.	I	.	I
Hyperthelia dissoluta	.	I	.	I
Nuxia congesta	.	I	.	I
Group J: species common to all classes				
Melinis repens	III	III	IV	II
Commelina africana	II	III	III	III
Solanum panduriforme	II	III	II	II
Rhynchosia totta	II	.	II	II
Chaetacanthus costatus	I	I	I	I
Rhus magalismontana	I	.	I	I

The tree *Protea caffra*, the forbs *Indigofera comosa, Selaginella dregei* and *Bulbostylis burchellii* and the grasses *Panicum natalense, Bewsia biflora, Digitaria diagonalis, Cymbopogon validus, Brachiaria serrata* and *Trachypogon spicatus* are diagnostic species. Constantly present woody species include *Englerophytum magalismontanum, Faurea saligna, Ozoroa paniculosa* and *Ochna pulchra*. Further frequent prominent forbs include *Pellaea calomelanos, Commelina africana, C. erecta* and *Chamaecrista mimosoides*, while dominant grasses include *Loudetia simplex, Melinis nerviglumis, Eragrostis racemosa, Themeda triandra, Heteropogon contortus* and *Diheteropogon amplectens*.

Melinis nerviglumis, Pellaea calomelanos and *Bulbostylis burchellii* were identified as the indicator species separating the Mountain Bushveld from other savanna types of the studied region. Indicator species for further divisions within the class include *Englerophytum magalismontanum, Celtis africana, Nuxia congesta* and *Rhus magalismontana*.

Discussion and Perspective

This is the first attempt to identify zonal phytosociological classes for the South African savanna from relevé data. We acknowledge that the names of these classes are not validly described according to the Code for Phytosociological Nomenclature (Barkman et al. 1986). The formal descriptions accompanied by full necessary documentation will be presented elsewhere.

We have identified the Mountain Bushveld as a very diverse vegetation type comprising many different communities. Further study may reveal that this class might be divided into various units interpretable as classes. This expectation is enhanced by complex topography of the rugged Waterberg and Magaliesberg mountain ranges, resulting plethora of habitat types and a complicated phytogeographic set-up.

TWINSPAN placed the majority of the Arid Sweet Bushveld (Acocks 1988) communities into the *Commiphoro-Colophospermetea mopani*, even when *Colophospermum mopane* was missing. Some of the communities are, however, grouped together with those of the *Panico-Acacietea tortilis*. This result suggests that the Arid Sweet Bushveld could be divided into two distinct vegetation types.

The species composition of the *Panico-Acacietea tortilis* suggests an *Acacia*-dominated vegetation on clay soils, as well as on sandy deposits, overlying the clay. The occurrence of species such as *Acacia mellifera, Kyphocarpa angustifolia, Tribulus terrestris, Eragrostis lehmanniana, Stipagrostis uniplumis* and *Aristida adscensionis* in these communities may indicate an affinity with the Kalahari dry savanna (van Rooyen et al. 1988).

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Main latitudinal and longitudinal characters of Russian mire vegetation

Yurkovskaya, Tat'yana K.

Vegetation Geography and Cartography Department, Komarov Botanical Institute of the Russian Academy of Sciences, Popov St. 2, RU-197376 St. Petersburg, Russian Federation;
Fax +78122344512; E-mail carta@map.bin.ras.spb.ru

Abstract. Regional features of mire vegetation are controlled by its latitudinal and longitudinal position. Latitudinal position is related to vegetation structure, peculiarities of dominating synusiae, and replacement of plant species groups with different types of latitudinal distribution. Changes in mire vegetation along the latitudinal gradient follow a sequence of zones and sub-zones involving tundra, taiga, and broadleaved forest. Along the west-east (oceanity-continentality) gradient the essential changes are reflected in the replacement of differentiating species. Throughout the area of middle taiga in Russia, from the west to east, forest formations are subjected to replacement of differentiating tree dominants (*Picea abies*, *P. obovata*, *Abies sibirica*, *Pinus sibirica*, etc.). On raised bogs *Sphagnum fuscum* retains dominance throughout the entire middle taiga. Still several co-dominants and also species with different types of longitudinal range replace each other so that different regional types of raised bogs can be distinguished. Analogous consecutive series can be also traced in palsa mires. The zonal distribution patterns of most types of mires are different in Europe and Asia.

Keywords: Azonality; Intrazonality; Meridional changes; Mire massif; Sub-zone; Vegetation structure; Zonality.

Nomenclature: Czerepanov (1981) for vascular plants and Savich-Lyubitskaya & Smirnova (1968) for *Sphagnum*.

Introduction

The main aim of this communication is to discuss the results of a long-term mire vegetation research, performed by the author and earlier mire scientists in different parts of Russia. The book by Osvald (1923) entitled 'Die Vegetation des Hochmoore Komosse' can be considered the first modern description of mire vegetation. This work was of essential importance for the development of mire science in Russia (Bogdanovskaya-Guiheneuf 1928). At present a huge amount of data is available, which needs to be summarized, especially facts concerning the effects of zonal and longitudinal location on floristic composition and vegetation structure of mires. Both of the latter usually display regional peculiarities.

As to vegetation units used for consideration of the geographical distribution of mires, the principles of two-line classification (Sochava 1979) are applied. Along one line homogeneous units (phytocoenomeres) are classified according to the concepts of the Russian geobotanical school (Shennikov 1964) or the floristic-sociological school (Braun-Blanquet 1964). Along another line heterogeneous units (phytocoenochores) are classified. For mires they are mire complex (mire site), mire massif, system of mire massifs, etc. For example, mire complexes are united into 'mire complex types' and these in turn in 'mire complex type groups'. Mire massifs have been classified (Yurkovskaya 1992, 1995) hierarchically as 'mire massif types', 'mire massif type groups' and 'mire massif type classes'.

Zonality in mire vegetation

Regional features of mire vegetation are controlled by its zonal and meridional location. Zonal position is being reflected in vegetation structure, the peculiarities of dominating synusiae, and also the replacement of plant species groups with different types of latitudinal distribution (arctic, hypoarctic, boreal, etc.) along the north-south gradient. The highest subdivisions of mire vegetation (at the level of classes of types of mire massifs) change from the north southwards. Such changes are commensurable with the replacement of a zonal or sub-zonal vegetation types, such as tundra, taiga, broadleaved forest, or steppe.

The views presented in this paper are to a considerable extent in contradiction with Heinrich Walter's zonality/intrazonality concept (Walter 1973). It is my belief that not only so-called zonal (placor) vegetation but also all other types of vegetation (intrazonal, azonal and extrazonal ones) are subordinated to the rule of geographical zonality. In other words, they bear characters of their belonging to a peculiar zone: floristic composition of plant communities (the set of latitudinal 'zonal' geoelements of flora); their structure (height, density, number of layers etc.) and so on. Walter (1979) in his 'Vegetation und Klimazonen' contradicts himself to some extent, for instance by differentiating the mires of the boreal zone as a particular zonal category, which agrees with my point of view. I have revealed the latitudinal regularities in mire distribution and emphasize the relations between mires and the zonal vegetation. Polygonal mires form such a case since their distribution is connected with the tundra zone and the region of continuous permafrost. South of this region, palsa mires are distributed. Their range is connected with the region of sporadic permafrost.

In the southern part of the tundra and the northern part of the taiga aapa mires (string fens, ribbed fens) are spread. The ascertainment of continuous pan-boreal range of aapa mires in Eurasia essentially changed the idea of their distribution only through a set of several isolated localities. The entire taiga zone is well-suited for the development of raised bogs. The distribution of forest swamps is mostly connected with boreal and nemoral zones. The mire zonality is reasonably well depicted in the analytic map of the mire vegetation of East Europe (Yurkovskaya 1980).

I show that vegetation of the herb mires (poor and also rich fens) in Eastern Europe displays a distinct zonal character as well (all the previous investigators considered them azonal). Several types of such mires consistently replace one another from the North to the South. In the North these are low-herb (10 - 20 cm height) communities where arctic and hypoarctic species predominate – hypoarctic species are distributed in the south of the tundra and in the north of the taiga zones (Yurtsev 1966); the term is used in modern Russian botanical-geographical literature. In the taiga zone plant height varies from 10 to 15 cm in small-sedge mires up to 70 - 80 cm in large-sedge mires, where boreal species predominate. In the nemoral zone the herb layer may attain a height of 1 m and is characterized by the participation of boreal-nemoral species. In the steppe zone the large-sedge and tall-grass communities (2 - 4 m tall) prevail, the southern amphibious herbaceous and (sub)-cosmopolitic species being among the most prominent.

The syntaxonomy of mires is supposed to change along the north-south gradient as well, but unfortunately, this subject is poorly known in Russia. Hence I shall only present some examples here. In the tundra zone, the *Alnetea glutinosae*, the *Phragmitetalia* and related syntaxa are absent. There are many specific tundra associations and therefore a new alliance - the *Caricion stantis* – was described by Matveyeva (1994). Associations of the *Oxycocco-Sphagnetea*, dominating the mires of the taiga zone, are entirely absent in the tundra. In the steppe zone they are presented by only a few associations. The azonal *Scheuchzerio-Caricetea fuscae* is also represented by different associations in several zones and sub-zones.

Finally, some thoughts are presented on the difference between Walter's (1968, 1979) and the Russian concepts of zonality and intrazonality. According to the Russian concept, the vegetation of placors (loamy watershed plains) and zonal vegetation are not synonyms. Both placor, slope, and valley (as well as mire) vegetation may be subject to zonal change. However on placors this change is most dependent on climate, which results in vegetation characters, typical of zone (sub-zone) as a whole (Sukachev 1928; Shennikov 1964; Alexandrova 1980 and others).

Longitudinal changes in mire vegetation

The essential longitudinal changes of mire vegetation can be observed also along the oceanity-continentality gradient. For example, in the middle taiga sub-zone these changes are similar to those in forests. Whereas in forests tree dominants replace each other from west to east (*Picea abies*, *P. obovata*, *Abies sibirica*, *Pinus sibirica*, etc.) in raised bogs the changes involve only co-dominant species and also differentiating species of various longitudinal ranges (Atlantic, Subatlantic, East-European, Eurosiberian, etc.). *Sphagnum fuscum* retains dominance throughout the entire sub-zone.

The areas of distribution of raised bog types are well delineated. Five regional types were distinguished within the group of types of the liverwort-lichen-peatmoss raised bogs. These types include:

1. *Calluna vulgaris*, *Trichophorum cespitosum*, *Rhynchospora alba*, *Sphagnum magellanicum* and *S. rubellum* along the Baltic Sea coast;
2. *Calluna vulgaris*, *Empetrum nigrum*, *Trichophorum cespitosum*, *Carex rariflora* and *Sphagnum lindbergii* along the White Sea coast;
3. *Chamaedaphne calyculata* and *Pinus sibirica* in the north and middle taiga of West Siberia;
4. *Empetrum nigrum* and *Carex middendorfii* in West Kamchatka;
5. *Sphagnum fuscum* and *S. lenense* on the Sakhalin Island.

In palsa mires one can observe an analogous consecutive series, such as

1. Mires with *Betula nana*, treeless in North Europe;
2. *Betula nana* and *Pinus sibirica* in West Siberia;
3. *Betula exilis* and *Larix gmelinii* in East Siberia;
4. *Larix gmelinii* and *Sphagnum orientale* in the Far East.

Geographically differentiating species provide a tool for distinguishing and outlining the regional types of mires, which is used for mapping at small scale.

The zonal distribution patterns of most types of mires is different in Europe and Asia (asymmetry). Polygonal mires in Northeast Europe are exclusively connected with the north tundra sub-zone, but in Asia they are spread over the arctic, north (typical) and south tundra sub-zones. Palsa mires are confined to the south tundra and forest-tundra in Europe but to the forest-tundra and the north taiga in West Siberia and eastward. The aapa mires (string fens) in Europe are mainly found from the forest-tundra to the middle taiga, whereas in Siberia they spread from the tundra to the south taiga. In Asia the northern and the southern boundaries of the raised bogs shift to the South (Table 1).

Table 1. Asymmetry in the latitudinal distribution of mires in European and Asian Russia. E = Europe; A = Asia.

Zone	Arctic								Boreal								Nemoral					
Subzone	Arctic tundra		North tundra		South tundra		Forest-tundra		North taiga		Middle taiga		South taiga		Sub-taiga		Broad-leaved		Forest-steppe		Steppe	
	E	A	E	A	E	A	E	A	E	A	E	A	E	A	E	A	E	A	E	A	E	A
Mire massif type class																						
Polygonal	-	+	+	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Palsa	-	-	-	-	+	-	+	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Aapa	-	-	-	-	-	+	+	+	+	+	+	+	-	+	-	-	-	-	-	-	-	-
Raised bog	-	-	-	-	-	-	-	-	+	-	+	+	+	+	+	+	+	+	-	+	-	+

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Land-cover types in central Argentina based on Landsat TM and phytosociological data

Zak, Marcelo R. & Cabido, Marcelo

Instituto Multidisciplinario de Biología Vegetal, CONICET – Universidad Nacional de Córdoba, Casilla de Correo 495, 5000 Córdoba, República Argentina;
Fax +54 351 4332104; E-mail marcezak@com.uncor.edu

Abstract. Landsat TM satellite imagery appears as a very useful tool for classifying and mapping vegetation at intermediate scale in a short time. Complemented with field surveys, it can provide floristic and structural information of the existing land-cover types and their present spatial patterns. In the present study we identified the spatial patterns of eight different land-cover types (which vary from halophytic open shrublands to mountain woodlands) in the northern part of the Province of Córdoba, central Argentina, using Landsat TM imagery (30 m × 30 m ground resolution) and multivariate analysis of phytosociological field data. In this manner we integrated two different scales which provide details of land-cover structure and patterns. Previous information on the area reveals that the extent of stable communities has been substantially reduced and most of the remaining natural and semi-natural vegetation consists of secondary xerophytic forests and shrublands. The areas that retained stable communities are related to some kind of constrain for agriculture.

Keywords: Remote sensing; Spatial pattern; Vegetation classification.

Nomenclature: Zuloaga & Morrone 1999; Zuloaga et al. 1994, 1996.

Introduction

There are many attempts to use Landsat Thematic Mapper to study land cover types (mainly forests) at the intermediate scale (Horler & Ahern 1986; Sader et al. 1990; Curran & Foody 1993; Tuomisto et al. 1994; Riaza et al. 1998). Potential uses for such land-cover data are many and varied and include assessing ecosystem status, modelling nutrient cycling and runoff, understanding spatial patterns of biodiversity and land-use planning (Vogelman et al. 1998). An emerging conclusion of many such studies is that even though Landsat TM spectral data appears as a very useful tool for purposes of classifying and mapping vegetation at intermediate scale, it must be complemented with field surveys, which provide floristic and structural information of the existing land-cover and vegetation types (Howard et al. 1996).

Field surveys and satellite imagery are at different ends of a continuum (Howard et al. 1996); while satellite images can be used to gather information from broad geographical areas in a short time, the level of detail is limited. Through field surveys, every element down to a single vegetation patch or even an individual plant can be identified, but when a large geographic area is involved, this method becomes more expensive and time consuming. Hence, there is a need to investigate appropriate methods oriented to integrate approaches at variable scales in order to provide specific details of land-cover and vegetation structure and patterns.

The vegetation classifications of the Province of Córdoba (Central Argentina) in use nowadays are based in phytogeographical parameters (Kurtz 1904; Luti et al. 1979) which only show the potential vegetation. Recently, floristic and physiognomic studies of the province's vegetation have been made (Cabido 1985; Cabido & Acosta 1985; Menghi et al. 1989; Cabido et al. 1993; Cantero et al. 1996), but although these studies contribute to the interpretation of the mechanisms responsible for vegetation changes, they show deficiencies in describing and interpreting those changes at a regional scale. Satellite information may be used to overcome this problem, because it covers large areas at regular intervals, with a spectral resolution that can be related to parameters from which the structure and physiognomy of vegetation can be derived (Gates et al. 1965).

Despite the need for current land-cover data, much of the intermediate-scale land-cover data now available for most of central and northwestern Argentina are outdated, incomplete and of questionable accuracy. Although this data set is probably still adequate for some applications, many land-cover changes have occurred since the different data sets were compiled.

In this study, we aim at identifying the spatial patterns of the different land cover types in the northern part of the Córdoba Province, central Argentina, using Landsat TM imagery (30 m × 30 m ground resolution) and classifying their vegetation through multivariate analysis of phytosociological field data.

Material and Methods

Study area

The Province of Córdoba, located in the centre of Argentina, covers 168000 km^2 (Fig. 1). Its climate is temperate to

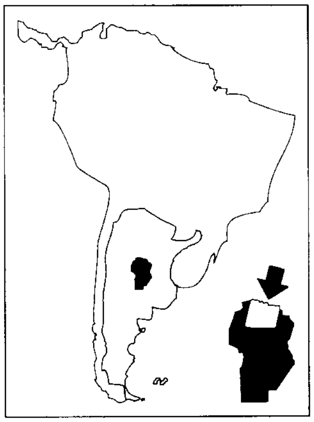

Fig. 1. Location of the Córdoba Province and of the study area.

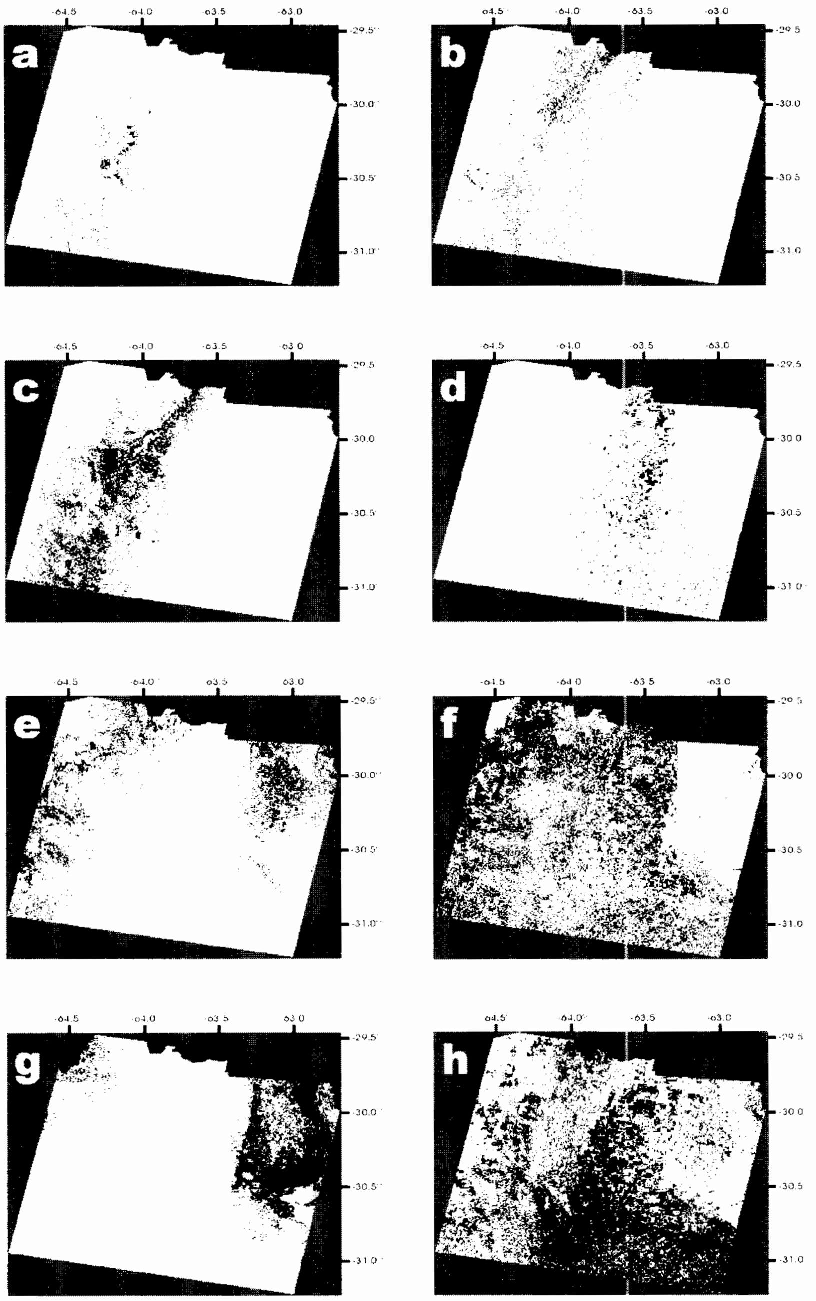

Fig. 2. Community level land-cover type map derived from Landsat TM. Cover types are shown separately to improve visualisation. **a.** *Lithraea* woodland; **b.** *Trithrinax* palm woodland; **c.** *Acacia* and *Heterothalamus* shrublands; **d.** *Aspidosperma-Schinopsis* forest; **e.** *Aspidosperma-Stetsonia* forest; **f.** *Acacia* shrubland; **g.** halophytic communities; **h.** cultural landscapes. In all the figures water bodies are shown in light grey.

warm temperate, with a mean annual temperature increasing from 16 °C in the east-southeast to 19 °C in the northwest; mean annual rainfall decreases in the same direction from more than 800 to 400 mm. These variations explain the water deficit in the northern and western parts of the territory.

Our study area, located in the northern part of the Córdoba Province (belonging to the Chaco Phytogeographical Province), was selected as the training area for the study of the whole provincial territory due to its pronounced east to west geomorphological and climatic gradient, comprising a striking diversity of plant communities. The study area is crossed in its central part by a north-to-south mountain range with plains filled by quaternary sediments to the east and west of the range.

Selection and processing of satellite imagery

A Landsat 5 TM digital image free of clouds (Path 229/ Row 081) of 14 November 1997 was selected. Maximum spectral variability of a false colour composite image obtained using bands 3, 4 and 5 (blue, green and red respectively) was analysed and evaluated through an Unsupervised Classification technique using the ISODATA routine

(Ball & Hall 1965) for the generation of spectral signatures. It gave a first sight of the mappable units present in the image. The different clusters were then used as a reference from which the locations of the various field surveys were determined. The surveyed locations chosen and other areas selected using field experience served as training sites for the generation of spectral signatures for the Supervised Classification of the image. This classification was performed through a Maximum Likelihood routine using the seven bands of the TM scene. The final product of this process was a classified image in which eight different classes of known floristic composition are clearly defined. This image was then geo-referenced.

Collection and classification of vegetation data

116 sites of ca. 300 m × 300 m (corresponding to homogeneous sites of 10 × 10 Landsat TM pixels) distributed in the northern part of the Province were selected. The sites were chosen on the basis of the clusters obtained through the unsupervised classification of the TM image in order to represent a wide range of plant physiognomical types and climatic, geomorphological and edaphic conditions. In each site, the vegetation was described according to the Braun-Blanquet method. Data from each site were used for ordination of the vegetation through DCA (Gauch 1981).

Results

Land-cover types

Eight clearly differentiated vegetation cover types were derived from the patterns defined by the TM image and field surveys. A community level vegetation type map was derived from Landsat TM (Fig. 2).

According to the available data (Sayago 1969) and to unpublished information, changes in vegetation cover have occurred in most of the area. The extent of stable communities has been substantially reduced and most of the remaining natural and semi-natural vegetation consists of secondary xerophytic forests and shrublands.

The first DCA axis discriminates mountain, lowland and halophytic communities. Different altitudinal belts are differentiated in the mountain vegetation through the second ordination axis (Fig. 3).

Mountain cover types

Lithraea woodland. This community covers 1 % (ca. 16 180 ha) of the study area (Fig. 2a) and is distributed as isolated patches along the slopes of the low mountain ranges. It is dominated by the evergreen tree *Lithraea ternifolia*, accompanied by the deciduous trees *Condalia montana* on eastern, wetter slopes and *Schinopsis haenkeana* on drier north and west facing slopes. *Ruprechtia apetala* and *Croton sarcopetalus* are the most frequent and abundant shrubs. This cover type used to form a continuous vegetation belt but has been substantially reduced by fire and logging, and replaced by shrublands and man made grasslands.

Trithrinax palm woodland. This community occurs in low longitudinal valley bottoms within the mountainous region, with a cover of 2 % (ca. 53 330 ha) (Fig. 2b). Its physiognomy is characterized by an open tree stratum dominated by the native palm *Trithrinax campestris* on a dense grass matrix with *Stipa tenuissima*, *S. eriostachya* and *Paspalum notatum* as dominants.

Acacia and Heterothalamus shrublands. These communities cover the 8 % (ca. 245 400 ha) of the study area and occur as discontinuous patches on disturbed sites previously covered by *Lithraea ternifolia* and *Trithrinax* palm woodlands (Fig. 2c). The physiognomy of the *Acacia* shrublands, which extend on the lower parts of the mountain range, is that of a low open shrub stratum on a herb matrix. Its dominant shrub is *Acacia caven*, accompanied by *Eupatorium buniifolium*, *Colletia spinosissima*, *Flourensia campestris* and *Croton sarcopetalus*. The herbaceous stratum is dominated by different species of *Stipa*, *Tagetes minuta*, *Bidens subalternans* and many C_4 grasses.

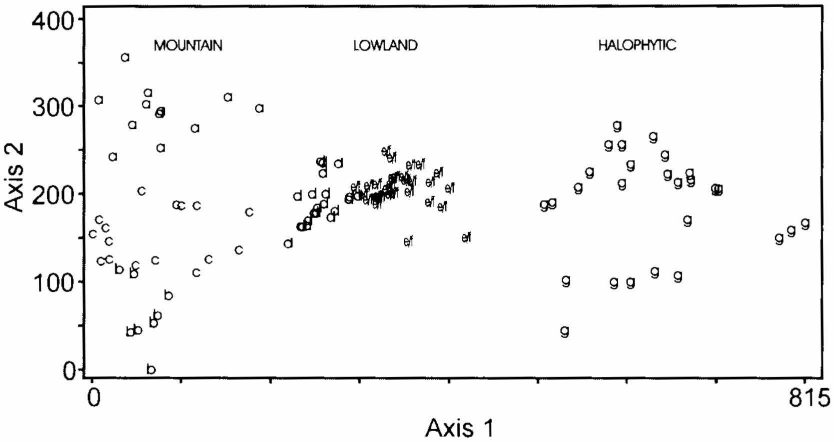

Fig. 3. Detrended Correspondence Analysis (DCA) of 116 inventories in northern Córdoba Province, central Argentina. **a.** *Lithraea* woodland; **b.** *Trithrinax* palm woodland; **c.** *Acacia* and *Heterothalamus* shrublands; **d.** *Aspidosperma-Schinopsis* forest; **e/f.** *Aspidosperma-Stetsonia* forest and *Acacia* shrubland; **g.** halophytic communities. (Letters correspond to the cover types in Fig. 2)

The physiognomy of the *Heterothalamus* shrublands is similar to that of the preceding but lower and more open. It is dominated by *Heterothalamus alienus* accompanied by *Acacia caven*, *Colletia spinossisima*, *Croton sarcopetalus* and different species of *Baccharis*, *Eupatorium* and *Vernonia* in the shrub stratum. This, as well as the *Acacia* shrubland community, shows some representative species of the mountain woodlands, such as *Lithraea ternifolia* and *Ruprechtia apetala*.

Lowland cover types

Lowland Chaco forests. This land-cover type is distributed through the flat territories of the study area (Fig. 2d and 2e) with a cover of 10 % (ca. 286990 ha). It comprises mostly secondary forests with only small patches of mature forests. The secondary forests are dominated by several xerophytic trees including *Aspidosperma quebracho blanco*, *Acacia praecox*, *Zizyphus mistol* and species of *Prosopis*. Some relic communities, mainly located to the east of the mountain range in the study area (Fig. 2d: *Aspidosperma-Schinopsis* forests), show a higher frequency of *Schinopsis lorentzii* (severely logged for extraction of tannin and production of railroad ties) and *Prosopis kuntzei* (from which posts were made) that dominated these communities until the beginning of this century. The forests located in the more arid plains, mainly to the west of the mountain range and in elevated patches of the saline depressions (Fig. 2e, *Aspidosperma-Stetsonia* forests), show an understory dominated by xerophytic shrubs including *Larrea divaricata*, *Mimozyganthus carinatus* and *Cercidium australe* which belong to the Monte phytogeographical province (Cabrera 1976), characterized by semi-desert shrublands. The cover-abundance values of *Stetsonia coryne* are high, the percentage cover of bare soil also being high; the abundance of *Selaginella sellowii*, dominating the moss layer, is striking.

This land cover type formerly covered the whole flat territories of the study area. After fire, logging and the expansion of agriculture it has been substantially reduced, and most of its past range is now occupied by cultural landscapes (Fig. 2h).

Acacia shrubland. This community covers 27 % (ca. 785 440 ha) of the study area and occurs on disturbed sites previously covered by lowland Chaco forests (Fig. 2f). The dominant species of the woody layer is *Acacia caven*, a deciduous shrub broadly distributed through the whole country and known by its marked invading ability. The composition of this community is not much different from that of the lowland forests, but its structure has been modified by logging, fires and overgrazing, showing an open shrubland physiognomy.

Halophytic community. This land cover type occurs on saline depressions present to the eastern and western extremes of the study area (Fig. 2g). It is a mosaic of halophytic communities dominated by succulent species (mostly *Chenopodiaceae*, *Cactaceae* and *Portulacaceae*). Non-halophytic species are severely constrained by high soil salt concentrations. The main physiognomic type is an open shrubland that alternates with slightly elevated small patches covered by fragments of forest communities with a reduced number of species. It comprises also *Spartina* grasslands in sectors that are subject to brief floods. This land-cover type covers 13 % (ca. 374940 ha) of the territory (including salty bare soils).

Cultural landscape. In this cover type we include all the land which has been in agricultural use in the near past (less than 10 yr after abandonment) and at present. As seen in Fig. 2h, this is the most extended cover type in the study area, covering 37 % (ca. 1 086 180 ha) of the territory, indicating a high intensity of disturbance and fragmentation of the original land cover.

Concluding remarks

In this study we show that the combined use of Landsat TM and field data allowed us to identify land cover types and to describe its spatial patterns, structure and composition. Thematic Mapper images showed a qualified mapping capability for vegetation communities and land-cover types.

The patterns derived from Landsat TM data and field surveys clearly identify the areas with primary, secondary and cultural vegetation, providing basic information for the assessment of the temporal evolution of land cover types since the first description of the vegetation of the study area in the beginning of the century (Kurtz 1904).

The areas that retained stable communities are related to some kind of constrain for agriculture. Well-preserved areas are highly determined by geomorphology: abrupt relief or saline depressions, which protect them from human activities such as farming. By contrast, the lowlands with quaternary sediments are mostly subjected to agriculture and post-agricultural cattle grazing. Only isolated patches of primary Chaco forests still remain, and most of the woody vegetation in the lowlands comprises secondary forests and shrublands.

Future research in the area should focus on a comparative analysis between previous maps (Kurtz 1904; Sayago 1969) and the maps based on TM imagery and new field surveys presented in this paper. This comparison will permit the construction of new maps showing the trends of change in plant communities and land cover types, their expansion or retraction, and their ranges in relation to logging, grazing, farming and abandonment.

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Ecogeographical differentiation of beechwoods in the Southern Balkans

Dzwonko, Zbigniew & Loster, Stefania

Institute of Botany, Jagiellonian University, ul. Lubicz 46, 31-512 Kraków, Poland;
Fax +48 12 4230949; E-mail ubdzwonk@cyf-kr.edu.pl

Abstract. A set of 607 phytosociological relevés from southeastern Serbia, F.Y.R. Macedonia, and Greece was subjected to numerical classification and ordination. The results obtained were used as the basis for a syntaxonomic analysis of beech, beech-fir and beech-maple woods of the southwestern part of the Balkan Peninsula. The *Doronico columnae-Fagenion* suballiance, which comprises associations from Serbia, F.Y.R. Macedonia and high altitudes in north Greece, and the *Doronico orientalis-Fagenion* suballiance, with associations from north and central Greece were confirmed. These suballiances belong to the alliance *Aremonio-Fagion* (order *Fagetalia*, class *Querco-Fagetea*). The results of ordination showed that the main directions of variation among the types of communities were most strongly correlated with latitude, altitude, and with the indicator values for nutrient and temperature.

Keywords: *Aremonio-Fagion*; Balkan Peninsula; Numerical method; *Querco-Fagetea*; Syntaxonomy.

Introduction

In the southern part of the Balkan Peninsula a natural beechwood zone occurs most frequently from 800 to 1700 m a.s.l., but in some places beechwoods form the timberline above 1900 m. However, these woods were considerably less known than the communities of beechwoods of Central and West Europe. At first all mesophilous beechwoods occurring in the area from the southeastern Alps to Albania and Greece were included in the *Fagion illyricum* (cf. Soó 1964). The distinct geographical differentiation of the associations of this alliance was noted by Borhidi (1963, 1965), who distinguished the association and geographical variants of some associations occurring in the southern part of the Balkans. Horvat et al. (1974) classified the beech, beech-fir and beech-maple woods occurring in the southern and middle parts of the Balkan Peninsula into a separate alliance – the *Fagion moesiacae*. In this alliance they placed only four broadly conceived zonal associations. Török et al. (1989), who carried out a numerical revision of the *Fagion illyricum* alliance, found a clear distinctness of two associations from southeastern Serbia and assigned them to the *Fagion moesiacae*. These authors also proposed a new, correct name for the *Fagion illyricum* – the *Aremonio-Fagion*.

Numerous phytosociological relevés of beechwoods in the former Yugoslav Republic of Macedonia and Greece were made during the last 20 yr. These new data make it possible to conduct a more complete classification of woods in the southern Balkans.

Material and Methods

A set of 607 relevés performed following the Braun-Blanquet approach was considered. They were made by different authors in the area from SE Serbia to central Greece – along ca. 500 km long geographical gradient. All relevés comprised 690 species and subspecies of vascular plants.

The relevés were numerically classified using the unweighted pair-group method (UPGMA, SYN-TAX 5.0; Podani 1993) both with presence/absence data and with cover-abundance values on the Braun-Blanquet scale (the symbol + was replaced by 0.5). Dissimilarities between relevés were calculated using Jaccard and Ružička formulas, respectively. Relevé groups were distinguished by comparing the two dendrograms obtained. All clusters composed of the same relevés in the two dendrograms were considered. Only groups consisting of at least five relevés were taken into account in the syntaxonomic analysis. The basis for the final classification of communities was 33 groups made up of 513 relevés.

For analysing the geographical differentiation of communities the numbers of species of six phytogeographical groups (chorotypes) were calculated for all the relevés. The mean characteristic indicator values (Landolt 1977) were calculated for all relevés to characterize the environmental conditions of the communities. Moreover, altitude, latitude, and aspect were taken into consideration.

Canonical variates analysis (CVA, CANOCO; ter Braak 1988) was used to identify patterns of environmental and geographical variation between the groups of relevés identified by numerical classification. Forward selection and associated Monte Carlo permutation tests were applied to select those variables that explain most of the variance in the data.

Results and Discussion

A classification of communities based on the results of the numerical analysis is presented in App. 1. Beechwoods communities from northeastern and central Greece were placed in the *Doronico orientalis-Fagenion*, which had been proposed by Raus (1980; cf. Bergmeier 1990). This suballiance is differentiated mainly by Subbalkan and Balkan species. The opposite group represents associations of beech, beech-fir and beech-maple woods from southeastern Serbia, F.Y.R. Macedonia, and high altitudes in north Greece (Fig. 1). For these associations we proposed a new suballiance, *Doronico columnae-Fagenion* (Dzwonko et al. 1999), with Submediterranean, Mediterranean and Balkan differential species. It may be supposed that also the beechwood associations occurring in Albania and western Bulgaria belong to this suballiance. For the mesophilous beechwood association which most frequently occurs in F.Y.R. Macedonia and southeastern Serbia the name *Doronico columnae-Fagetum* was suggested (Dzwonko et al. 1999). Only two associations from Serbia and F.Y.R. Macedonia represent the *Epimedio-Fagenion* and the *Ostryo-Fagenion*.

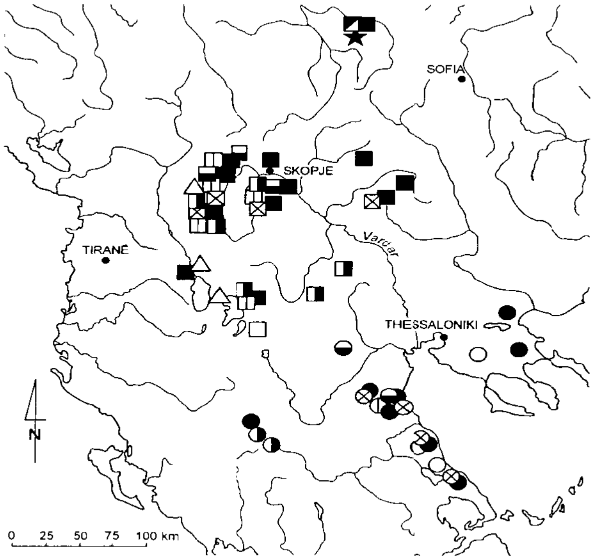

Fig. 1. Distribution of the associations and communities included in this study. Upper half filled square: *Hyperico umbellatae-Fagetum*; filled squares: *Doronico columnae-Fagetum*; lined squares: *Campanulo-Fagetum*; lower half filled squares: *Aceri heldreichii-Fagetum*; right half filled squares: *Abieti-Fagetum*; open square: *Adoxo moschatellinae-Fagetum*; crossed squares: *Luzulo-Fagetum*; right half filled circles: *Geranio striati-Fagetum*; lower half filled circles: *Physospermo-Fagetum*; filled circles: *Lathyro alpestris-Fagetum*; crossed circles: *Orthilio secundae-Fagetum*; lined circle: *Fagus-Satureja grandiflora* community; open circles: *Fagus moesiaca* communities; star: *Helleboro odori-Fagetum*; triangles: *Aceri obtusati-Fagetum*.

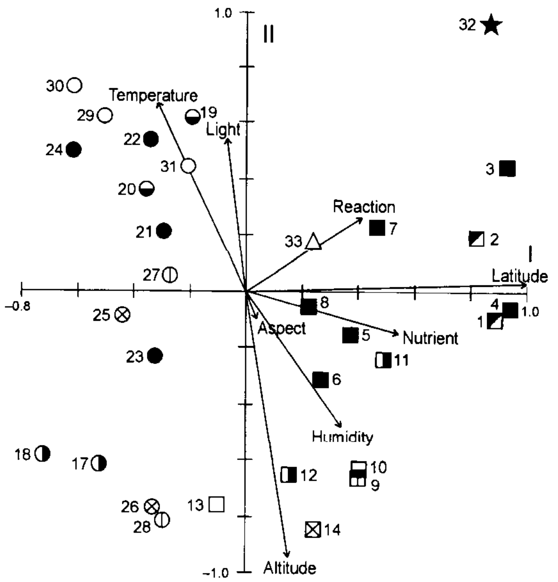

Fig. 2. Ordination of the relevé groups along the first two CVA axes in relation to geographical variables and ecological indicator values. Numbers indicate communities listed in App. 1. Symbols as in Fig. 1.

The CVA results indicate a very clear geographical and environmental pattern of differentiation between the distinguished types of communities. All eight variables taken into consideration (latitude, altitude, aspect, indicator values for nutrient, reaction, light, temperature and humidity) are significant ($P < 0.01$). The first CVA-axis distinctly separates the associations of the *Doronico orientalis-Fagenion* from the associations and communities of the *Doronico columnae-Fagenion* (Fig. 2). This axis is strongly correlated with latitude ($r = 0.99$) and the indicator values for nutrient ($r = 0.54$). The second CVA-axis is most closely correlated with altitude ($r = -0.95$) and indicator values for temperature ($r = 0.67$), and separates the associations, variants and communities of both suballiances from higher and lower altitudes, while they are characterized by the lowest and highest indicator values for temperature.

The clear floristic differences between the two suballiances under comparison are due to changes in the flora of beechwoods, proceeding from the north southwards. Euro-Siberian, Euro-Asiatic, European and Central-European species are more numerous in the communities of the *Doronico columnae-Fagenion*, while Submediterranean, Mediterranean, Subbalkan and Balkan species occur more frequently in the communities of the *Doronico orientalis-Fagenion* (Table 1). This suggests classification of beechwood associations into regional suballiances using phytogeographical species groups rather than ecological species groups.

The presented classification is subject to future refinement, because not all the types of beech and beech-fir woods of the southern Balkans have been equally well examined, and intensive research is needed to obtain complete data.

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Table 1. Chorological spectra of the suballiances. Figures are mean species numbers in relevés. SB: Subbalkan and Balkan; SM: Submediterranean and Mediterranean; CE: Central European; E: European; ES: Euro-Siberian and Euro-Asiatic; C: Circumpolar.

Suballiance	SB	SM	CE	E	ES	C
Doronico columnae-Fagenion	3.2	3.7	6.1	6.1	7.3	3.6
Doronico orientalis-Fagenion	5.1	5.6	3.2	4.4	3.6	2.7
Epimedio-Fagenion	1.8	7.5	6.6	8.4	10.1	6.1
Ostryo-Fagenion	5.6	7.1	5.7	6.9	6.4	1.7

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App. 1. Syntaxonomic classification of beechwoods in the south-western part of the Balkan Peninsula. Authors of relevés are given in parentheses. 1: Barbero & Quézel (1976); 2: Bergmeier (1990); 3: Dzwonko et al. (1999); 4: Em (1961); 5: Em (1974); 6: Gamisans & Hebrard (1980); 7: Habeck & Reif (1994); 8: Jovanović (1955); 9: Karagiannakidou (1993); 10: Quézel (1967); 11: Quézel & Contandriopoulos (1965); 12: Raus (1980); 13: Rizovski & Džekov (1990).

Group number	Name of community	No. of relevés and authors
All. *Aremonio-Fagion* (Horvat 1938) Török, Podani et Borhidi 1989		
Suball. *Doronico columnae-Fagenion moesiacae* Dzwonko et al. 1999		
	Ass. *Hyperico umbellatae-Fagetum* (Jovanović 1955) Borhidi 1963	
1	*typicum* (*Piceo-Fagetum serbicum* Jovanović 1955)	12 (8)
2	*luzuletosum* (*Abieti-Fagetum serbicum luzuletosum* Jovanović 1955)	11 (8)
	Ass. *Doronico columnae-Fagetum moesiacae* (Jovanović 1955) Borhidi ex Dzwonko et al. 1999	
3	*phyllitetosum* (*Fagetum montanum serbicum calcicolum* Jovanović 1955)	13 (8)
4	*poëtosum* (*Abieti-Fagetum serbicum poëtosum* Jovanović 1955)	21 (8)
5	*typicum*	46 (3, 4, 13)
6	*calaminthetosum*	15 (13)
7	*cardaminetosum*	7 (3)
8	*festucetosum*	5 (13)
9	Ass. *Campanulo trichocalycinae-Fagetum moesiacae* (Em 1961) Dzwonko et al. 1999	8 (4)
10	Ass. *Aceri heldreichii-Fagetum moesiacae* Jovanović 1957	10 (3)
	Ass. *Abieti-Fagetum moesiacae* Horvat, Glavač et Ellenberg 1974	
11	*cardaminetosum*	9 (5)
12	*vaccinietosum*	11 (5)
13	Ass. *Adoxo moschatellinae-Fagetum* Quézel 1967	6 (10)
	Ass. *Luzulo luzuloidis-Fagetum moesiacae* Horvat, Glavač et Ellenberg 1974	
14	*vaccinietosum*	5 (3, 4)
15	*galietosum*	6 (13)
16	*typicum*	8 (3)
Suball. *Doronico orientalis-Fagenion moesiacae* Raus 1980		
	Ass. *Geranio striati-Fagetum* Quézel et Contandriopoulos 1965	
17	variant of Southern Pindos	10 (11)
18	variant of Sterea Ellas	11 (1)
	Ass. *Physospermo-Fagetum* Quézel 1967	
19	*euphorbietosum epithymoidis*	8 (10)
20	*juglandetosum regiae*	9 (1)
	Ass. *Lathyro alpestris-Fagetum* Bergmeier 1990	
21	variant of North Central and North East	55 (2, 6)
	variant of Mt. Olimbos	
22	form with *Physospermum cornubiense* and *Hedera helix*	23 (7)
23	form with *Corallorhiza trifida*	12 (7)
24	variant of East Central	12 (12)
	Ass. *Orthilio secundae-Fagetum* (Barbero et Quézel 1976) Bergmeier 1990	
25	low altitude variant	58 (1, 2, 6, 12)
26	high altitude variant	10 (7)
	Fagus sylvatica-Satureja grandiflora community	
27	low altitude variant	21 (2)
28	high altitude variant	15 (7)
29	*Fagus moesiaca* community on moister soils	6 (12)
30	*Quercus frainetto-Fagus moesiaca* community	8 (12)
31	*Fagus moesiaca-Rubus canescens* community	25 (9)
Suball. *Epimedio-Fagenion* Marinček et al. 1993		
32	Ass. *Helleboro odori-Fagetum* (A.O. Horvát 1959) Soó et Borhidi in Soó 1962 (*Fagetum montanum serbicum silicicolum* Jovanović 1955)	10 (8)
Suball. *Ostryo-Fagenion* Borhidi 1963		
33	Ass. *Aceri obtusati-Fagetum* Fabijanić, Fukarek et Stefanović ex Fukarek, Stefanović et Fabijanić 1967	27 (3, 13)

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Distribution of forest floor species in a fragmented landscape

Graae, Bente Jessen

Department of Plant Ecology, University of Copenhagen, Øster Farimagsgade 2D, DK-1353 København K, Denmark; Fax +4535322321; E-mail bentej@bot.ku.dk

Abstract. The occurrence of forest floor plant species was recorded on 68 forest sites, half of them on diluvial sand in Jutland and half of them on clayey moraine on the island of Zealand, Denmark. Species numbers were smaller in Jutland than on Zealand. On Zealand, species numbers were higher in forests originating from before 1768 compared to forests established in the 19th century, whereas such differences were not visible among the Jutland sites. However, in both regions ancient and recent forests showed differences with respect to categories of seed dispersal. Recent forests had more long-distance adapted species whereas ancient forests had more species without such adaptations. The present study suggests that one of the most important factors affecting forest species richness in Danish deciduous forests is continuity and proximity to ancient forests. It has been possible to identify quite common species as good indicators of forest continuity, though these seem more reliable in the eastern part of Denmark where soils are less sandy than in the western part, and where the landscape has been more intensively exploited over centuries than in Jutland. Analyses using seed dispersal types have also been shown to be valuable, and it seems that seed dispersal may be extremely important in determining potential species composition and richness of recent forests. Although data from whole stands were used to assess the response of species to isolation, there was a close relationship between stand level and quadrat level results. This suggests that surveys using 25 m × 25 m quadrats may be sufficient to draw conclusions about forest continuity, at least on soils which potentially may hold a rich flora.

Keywords: Forest continuity; Fragmentation; Seed dispersal; Species diversity.

Nomenclature: Hansen 1981.

Introduction

Forest continuity and landscape fragmentation have been shown to be important for many forest vascular plant species in countries neighbouring Denmark: Great Britain (Peterken & Game 1984); Belgium (Hermy & Stieperaere 1997); Poland (Dzwonko & Loster 1989); Sweden (Brunet 1993); The Netherlands (Grashof-Bokdam 1997) and Germany (Wulf 1997), but no such studies have so far been reported from Denmark itself. Denmark is quite special in this respect, because the deciduous forests have had a high degree of continuity and stability over the last two centuries. Existing forest boundaries were largely established in 1804, and so the forests have occupied the same sites for 200 yr and probably much longer. There has been an increase in total forest cover from 2% to 12% in the last 200 yr, but this is predominantly due to plantations of introduced conifers. As the rest of northwestern Europe, the forest landscape is highly fragmented and local populations of forest species are presumed to be quite isolated from each other. However, almost all forests in Denmark are intensively managed, which makes it likely that management has had as much influence on the flora as have landscape scale processes. This study aims to describe the role of landscape fragmentation on forest vascular plant species in two regions of Denmark, and to identify any effects of landscape fragmentation on the forest flora.

Material and Methods

Forests in two regions (one in Himmerland in Jutland, the other in Hornsherred on Zealand) were surveyed for 220 forest species (species having forest as their main habitat according to Hansen 1981), each species was assigned a frequency from 1 to 5 in both a quadrat of 25 m × 25 m and in the entire stands (sizes ranging from 1 - 20 ha), and environmental variables were measured in the field or read from maps. Ancient forests in this study were taken as those recorded on maps from the late 18th century; recent forests have originated since then (all of them originated in the beginning of the 19th century). Detrended Correspondence Analysis (DCA) was used to elucidate factors of major influence to the vegetation, and type of dispersal and lateral spread have been applied to the data set to detect the role of species traits on their distribution in the fragmented landscape.

Results

Ordination

There were large differences between the two regions, and the data were processed separately. On Zealand, only edaphic variables were important at the scale of 25 m × 25 m; at the stand level, edaphic parameters were strongly correlated with DCA-axis 1 while the isolation and fragmentation variables were correlated with DCA-axis 2 (Table 1). Species number was also correlated with axis 2 and showed close correlations with the isolation and forest size measures. Ancient and recent forests were divided into two groups along axis 2, as did stands on morainic clay and glaciofluvial sand, and it has proved difficult to separate the effects of these two factors. As there were only six recent forests included and even these on different soil types, it was not possible to divide the data set. A new study will elucidate the relative roles of soil parent material and forest continuity.

In the Jutland data the ordination showed no differences between the two levels investigated (quadrats and stands), and there was no obvious separation of edaphical variables and landscape related variables onto different axes at the stand level (Zealand). DCA-axis 2 seems to reflect differences in tree species composition: the *Fagus*-dominated stands in the densely forested area (Rold Skov)

Table 1. Significant correlations (Spearman rank correlation coefficient) between environmental and isolation variables and the first two axes of two DCA ordinations on the different scales of the Zealand data set; results are given at both quadrat and stand levels. Significant differences in groupings along the axes between ancient and recent forests and between those on clayey moraine and glaciofluvial sands/gravels are also indicated (* = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$; Mann Whitney's *U*). Correlations with Ellenberg values have been tested on the basis of species distributions in the ordination. The columns to the right show correlations between the measured variables and with species numbers in quadrats and stands. - No significant correlation or difference.

Quadrats		Stands				
DCA1	DCA2	DCA1	DCA2			
0.337	0.199	0.175	0.113	Eigenvalue	Correlation	
3.208	2.353	1.862	2.053	Axis length	Species number/	
11.7	18.6	13	21.4	Cum. % Variance	Quadrat	Stand
0.46	-	0.55	0.43	Dist. to forest complex	−0.50	0.66
				Dist. to ancient forest	−0.62	−0.63
-	-	-	−0.44	Deciduous forest size	0.46	0.50
-	-	-	-0.38	Topography		
0.68	−0.36	0.57	0.37	pH		
				Fagus		
				Quercus		
				Acer		
-	-	-	−0.47	Species no. Quadrat		0.75
-	-	-	−0.56	Species no. Stand	0.75	
-	-	-	***	Diff. ancient - recent forests		
-	-	-	**	Diff. clay - sand		
				Ellenberg-Light		
0.41	-	0.55	-	Ellenberg-Temperature		
-	-	-	-	Ellenberg-Continentality		
-	-	-	-	Ellenberg-Moisture		
0.38	-	0.27	-	Ellenberg-Reaction		
0.35	-	0.41	-	Ellenberg-Nitrogen		

Table 2. Significant correlations (Spearman rank correlation coefficient) between environmental and isolation variables and the first two axes of two DCA ordinations on the different scales of the Jutland data set. For further explanation see Table 1.

Quadrats		Stands				
DCA1	DCA2	DCA1	DCA2			
0.420	0.340	0.316	0.188	Eigenvalue		
3.170	4.423	2.267	2.095	Axis length	Species number	
12.6	22.1	16.6	26.5	Cum. % Variance	Quadrat	Stand
0.68		0.63	0.52	Dist. to forest complex		
	0.35		0.36	Dist. to ancient forest	−0.40	−0.38
−0.69		−0.63		Forest size		
−0.68		-0.62		Deciduous forest size		
				Topography	0.43	0.34
				pH		
			− 0.56	*Fagus*		
0.36		0.36	0.39	*Quercus*		
0.35			0.49	*Ulmus*		
0.38		0.35		*Acer*		
				Fraxinus		
0.37			0.49	*Corylus*		
				Sambucus		
	0.42		0.37	*Populus*		
				Sorbus		
				Species no. Quadrat		0.49
				Species no. Stand	0.49	
*			*	Diff. ancient - recent forests		
				Diff. recent forest - scrub		
			**	Diff. ancient forest - scrub		
				Ellenberg-Light		
				Ellenberg-Temperature		
				Ellenberg-Continentality		
	0.36			Ellenberg-Moisture		
0.44		0.40		Ellenberg-Reaction		
0.45		0.37		Ellenberg-Nutrients		

were situated at one extreme, whilst small *Quercus*-scrubs with various other tree species were at the other. These had often a limited continuity, but recent forests contained both beech plantations and stands derived from natural regeneration. Table 2 shows that distance to ancient forest was correlated with species number for each stand. The correlation between topography and species number can also be interpreted in a historical context, as it is more likely that hilly areas were deforested to a lesser degree than flat areas. Former scrubs were more similar to recent forests than to ancient ones.

Seed dispersal and clonality

The species number in the stands was markedly lower in recent than in ancient forests in the Zealand data set, but this did not apply to the forests in Jutland ($p = 0.22$; Mann Whitney *U*). However, abundances for species with clonal growth had higher values in ancient forests than in recent forests in both regions (Zealand: $p = 0.027$; Jutland $p = 0.025$; Wilcoxon Signed Rank Test), whereas species without clonal growth did not show a significant difference (Zealand: $p = 0{,}970$; Jutland: $p = 0.19$; Wilcoxon Signed Rank Test). This indicates that, although many species with clonal growth were able to colonize the recent forests, they have not yet reached the same abundance as in the old forest, where they have had more time for clonal growth.

A clear tendency for both regions is also obvious when comparing species with different types of adaptations to seed dispersal (Table 3). Species which are assumed to disperse over long distances by adhesion to animals (epizoochorous) or by wind (WINDm) do not have a significantly lower species number in the recent forests, whereas species regarded to be short distance dispersers as the myrmecochores, unspecialized and short distance wind (WINDc) dispersed species are significantly fewer. This would be expected if seed dispersal distance is the main factor responsible for colonization of recent forests. Endozoochorous species show a significant difference on Zealand but not in Jutland. In this study, all plants with fleshy fruits are considered endozoochorous; they are often considered as bird-dispersed and hence long-distance dispersed. The main difference in the Zealand data, however, is due to *Lonicera periclymenum*, *Majanthemum bifolium* and *Polygonatum multiflorum* (in 43% of the ancient and 17% of the recent forests). The latter two are probably not dispersed by birds, and may instead be species which are adapted to dispersal by mammals which are not far-ranging. Mueller-Schneider (1977), for example, points out that

Table 3. Minimum, maximum and mean number of species belonging to each type of dispersal group. Unspecialized species show no adaptations for dispersal by animals or wind; WINDc are wind-dispersed plants but usually over short distances; WINDm are wind-dispersed with minute seeds. The last column indicates significant differences between means (* = $p<0.05$, ** = $p<0.01$, *** = $p<0.001$; paired t-test where possible, otherwise Wilcoxon Signed Rank Test). For information on categories, see Text.

		Ancient			New			
	n	Min.	Max	Mean	Min.	Max.	Mean	Diff.
Zealand								
Species number	88	16	41	30.00	10	19	14.50	***
Epizoochorous	14	2	10	6.93	3	7	5.17	
Endozoochorous	16	1	9	3.39	0	2	1.17	**
Myrmecochorous	20	2	10	6.32	0	4	2.00	***
Unspecialized	16	2	10	6.39	1	4	3.00	**
WINDc	7	1	4	2.79	0	1	0.33	**
WINDm	14	1	8	3.68	1	6	3.00	
Aquatic dispersal	1	0	1	0.64	0	0	0.00	
Jutland								
Species number	90	9	40	23.42	12	28	19.20	
Epizoochorous	13	1	6	3.11	1	6	2.8	
Endozoochorous	13	1	8	4.47	2	6	4	
Myrmecochorous	17	1	9	3.42	1	3	1.8	**
Unspecialized	18	2	8	3.32	0	3	1.6	**
WINDc	7	1	4	2.11	0	2	1	*
WINDm	20	1	11	5.11	2	7	5	
Aquatic dispersal	2	0	1	0.05	0	0	0	

we do not know any dispersers for *Majanthemum bifolium*. These species do not show any affinity to ancient woodland in Jutland, though they are all quite common (*Polygonatum multiflorum* occurs in 53% of the ancient and in 40% of the recent forests). This seems to contradict the explanation that these species do not disperse well, but for *Lonicera* and *Majanthemum* an alternative explanation may lie in their ability to persist in non-intensively managed areas (heathlands and grasslands): the region in Jutland has had less intensive agriculture for centuries than that on Zealand.

Carex pilulifera, *Milium effusum*, and *Trientalis europaea* which are normally thought of as short distance dispersers seem to be independent of forest continuity in both regions; an explanation for this may be found through new investigations of dispersal strategies of forest plants. Only the results from stand level are shown here, but the same differences were seen at the quadrat level.

Table 4. Species found in more than 50% of the ancient forests (Anc) and less than 25% of the recent forests (Rec), or in more than 33% of the ancient forests and none of the recent forests. Dispersal type is determined from seed morphology. The table gives % for stands, but species which are common enough to show the same pattern at the quadrat level are marked with an asterisk. Hydro = Hydrochorous dispersal; for other abbreviations, see Table 3. For information on categories, see Text.

		Zealand		Jutland	
		Anc	Rec	Anc	Rec
	n	28	6	19	5
	Dispersal type	%	%	%	%
Melica uniflora	Myrm.	93	17	26	0
Oxalis acetosella	Unspec.	89	17	95	60
Stellaria holostea	Unspec.	86	17	95	20
Viola riviniana	Myrm.	68	17	11	0
Mercurialis perennis	Myrm.	64	17	11	20
Carex remota	Hydro.	64	0	5	0
Rumex sanguineus	Unspec.	64	0	16	0
Scrophularia nodosa	WINDc	61	0	21	20
Vicia sepium	Unspec.	57	0	11	0
Roegneria canina	Epizoo.	54	0	11	0
Gagea lutea	Myrm.	46	0	21	0
Hordelymus europaeus	Epizoo.	43	0	0	0
Lonicera periclymenum	Endozoo.	43	0	63	60
Majanthemum bifolium	Endozoo.	43	0	74	80
Ranunculus auricomus	Myrm.	36	0	32	0
Primula elatior	WINDc	36	0	0	0
Veronica montana	Unspec.	36	0	0	0
Luzula pilosa	Myrm.	36	0	84	60
Adoxa moschatellina[1]	Myrm.	21	0	37	0
Galium odoratum	Epizoo.	93	100	42	0

[1] Müller-Schneider (1977) suggested that *Adoxa moschatellina* is dispersed by snails; this species has been added to the myrmecochores instead of endozoochores.

Indicators of long forest continuity

More species characteristic of ancient forests were found on Zealand than in Jutland. Part of the reason for this is that the stands in Jutland were generally more species-poor than those on Zealand. However, the less intensive agricultural use of the Jutland region with larger heathland and meadow systems preserved compared to the Zealand region may also play a crucial role to species survival outside their natural habitat - the forest - when the areas were deforested. None of the recent forests contained *Stellaria holostea* or *Melica uniflora* in the quadrats, stressing their potential as evaluation tools for forest continuity. *Anemone nemorosa*, which by many authors has been described as a good ancient forest indicator (Hermy 1994) did not show any affinity to ancient forest when looking at presence/absence data in this study. However, the abundances of this species were markedly higher in the old forests on Zealand compared to the new ones, which indicates that the cover of *Anemone nemorosa* is a better indicator of forest continuity in Denmark than the presence of this species. This is in accordance with Swedish studies demonstrating the slow colonization rate of *Anemone nemorosa* (Brunet & Oheimb 1998).

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Xerothermic grassland: habitat island in an agricultural landscape

Kotańska, Malgorzata[1]*, Towpasz, Krystyna[1] & Mitka, Józef[2]

[1]*Institute of Botany, Jagiellonian University, ul. Lubicz 46, PL-31-512 Kraków, Poland;* [2]*Botanic Garden, Jagiellonian University, ul. Kopernika 27, PL-31-501 Kraków, Poland;*
**Fax +48124230949, E-mail kotanska@jetta.if.uj.edu.pl*

Abstract. Preliminary results of studies on the floristic and community diversity of xerothermic grassland on the Proszowice Plateau (Malopolska Upland, southern Poland) are presented. This area has been subject to anthropogenic pressure since the Neolithic. Stands of xerothermic grassland cover less than 5% of the area under study. They form habitat islands (refugia) among agricultural fields with a very rich flora, including rare and endangered species of various relic geographical elements, e.g. Pontic-Pannonian, Irano-Turanian and Mediterranean. Their existence is conditioned by specific site conditions and extensive management, especially burning.

Keywords: Braun-Blanquet method; *Festuco-Brometea*; Geographical element; Habitat condition; Human intervention; Numerical method.

Nomenclature: Mirek et al. (1995) for plants; Pawlowski et al. (1966) for syntaxa.

Introduction

In connection with the man-made, rapid changes in the vegetation cover of Central Europe in the last 30 yr (e.g. Fukarek 1979; Kornaś 1983), and a general decrease in biological diversity in various ecosystems on the scale of the whole world (e.g. Anon. 1992; McNelly 1992), regional surveys of biodiversity have become an urgent task. The Proszowice Plateau (Malopolska Upland, southern Poland) is a region of ancient human settlement and intensive agriculture dating back to the Neolithic (Kruk et al. 1996). In this area, severely deforested and now mainly covered by fields, stands of xerothermic grassland, i.e. secondary plant communities supported by human intervention, occur as islands in the agricultural matrix. They are refugia for many plants (and animals), some of them rare or endangered and representing interesting geographical elements.

Since the share of xerothermic grassland in the agricultural landscape is small, and its biotic significance disproportionally high, we wish to know the factors maintaining its diversity, phytosociological and geographical variability, and floristic composition. The aim of this study was to find relationships between the typological variation of xerothermic grassland and natural site conditions (substratum, exposure and declination), often modified by man's management practices.

Material and Methods

The investigations were carried out in an area hitherto not well studied, neither floristically nor syntaxonomically. The Proszowice Plateau is situated near Kraków (Fig. 1), in the zone of the Old Hills and Highlands (Malopolska Upland). This area of 770 km^2 has features typical of an agricultural landscape. Its wide and unforested hills of an altitude of up to 300 m consist of Miocene deposits overlain by loess (Kondracki 1978). Fertile chernozem on loess made this region one of the earliest settlement centres and a place of intensive agriculture in Poland (Kruk et al. 1996). The slopes and gentle hillock summits are covered by arable fields, occupying ca. 80% of the area, while in the wide and shallow stream valleys moist meadows predominate (13%). Isolated stands of xerothermic grassland occur in places not used for agriculture: on steep escarpments between fields, stream banks, and the steep slopes of hills and gullies.

The floristic composition of plant communities was investigated in 1997 in representative stands of xerothermic grassland occurring on various geological substrata, using the Braun-Blanquet (1964) approach. In total, 100 phytosociological relevés (of sample plots of 50 m^2) were made. Associations were determined on the basis of the observational-comparative method and numerical classification, i.e. minimum variance clustering based on Euclidean distance (MULVA 4 by Wildi & Orlóci 1990), following rules elaborated by Wildi (1989). The results of classification were imposed on a relevé ordination diagram obtained with Principal Component Analysis (CANOCO package; ter Braak 1988, see also Gauch 1982).

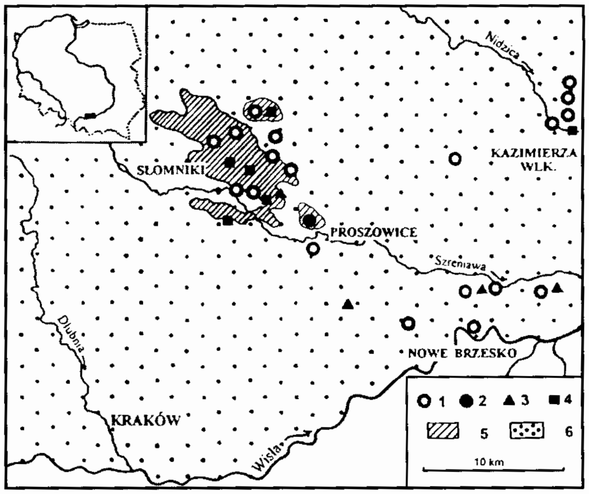

Fig. 1. Map of the Proszowice Plateau and distribution of xerothermic grasslands: 1 = *Thalictro-Salvietum pratensis*; 2 = *Sisymbrio-Stipetum capillatae*; 3 = *Brachypodietum pinnati*; 4 = *Inuletum ensifoliae*; 5 = Cretaceous marls and limestone; 6 = loess.

Results and Discussion

On the basis of the phytosociological survey three xerothermic associations of the *Festuco-Brometea* and one plant community dominated by *Brachypodium pinnatum* were distinguished. The associations are: *Sisymbrio-Stipetum capillatae*, *Thalictro-Salvietum* and *Inuletum ensifoliae* (Fig. 2a). The community with *Brachypodium pinnatum* has an intermediate character between the *Thalictro-Salvietum* and the *Inuletum ensifoliae.*

Among them the most common association is the *Thalictro-Salvietum.* Stands of this association are found on a loess substratum on W, S, or SW exposures and have inclinations of 40-50° (70°) (Figs. 1, 2a). The *Thalictro-Salvietum* is characterized by considerable floristic richness; on average 30 species may be found here, including *Elymus hispidus* s.l., *Salvia pratensis, Campanula bononiensis, Thalictrum minus* and *Veronica austriaca,* and in some cases also *Salvia nemorosa* (Fig. 2b, Table 1).

On Cretaceous marls or limestone, on west- and southwest-facing slopes of 30-40° inclination, stands of *Inuletum ensifoliae* develop (Fig. 1, 2a). Among character species, besides *Inula ensifolia,* one can find here such rare plants as *Linum flavum, L. hirsutum, Reseda phyteuma, Senecio integrifolius* and *Aster amellus,* and also *Carex humilis* and *Avenula pratensis.* (Fig. 2b, Table 1). This association is also rich, having 40 species/stand on average. On rarely occurring gypsum *Sisymbrio-Stipetum* develops (Fig. 1, 2a). The stands of this association are connected with south-facing slopes of 40° inclination. Besides *Stipa capillata* other character species are: *Sisymbrium polymorphum, Festuca valesiaca, Oxytropis pilosa, Silene otites* and *Veronica praecox* (Fig. 2b, Table 1). Sometimes are intermediate stands of xerothermic grassland with the domination of *Brachypodium pinnatum,* related both to *Thalictro-Salvietum,* and to *Inuletum ensifoliae.* (Figs. 1, 2a). This community represents non-specific impoverished stands of xerothermic grassland with species such as *Ononis spinosa, Carlina acaulis, Melampyrum arvense, Falcaria vulgaris, Fragaria viridis* and *Phleum phleoides* (Fig. 2b, Table 1). Probably they are less frequently (or irregularly) burnt in comparison with other described associations.

Very rarely and only on steep escarpments in the Vistula valley bed, a successional plant community with *Cerasus fruticosa* develops, in which also *Rosa gallica* grows abundantly. The xerothermic grasslands cover less than 5% of the Proszowice Plateau. In its composition many xerothermic species (including protected ones) of relic geographical ranges (e.g. Pontic-Pannonian, Irano-Turanian, and Mediterranean) may be found (Table 1). As a rule they are rare, both on the scale of the region (Zając et al. 1998), as well as the country (Zając et al. 1997), and, unfortunately, under the threat of extinction.

Table 1. Phytocoenotical spectra and geographical elements (in part after Hultén & Fries 1986; Meusel et al. 1965; Walter & Straka 1970) of plant species occurring in habitat islands of xerothermic grassland on the Proszowice Plateau.

Species /Geographical element	S-St	Th-Sa	Br	In
Pontic-Pannonian				
Achillea pannonica	*x*	*x*	*x*	*xx*
Adonis vernalis	.	*x*	.	*xx*
Anthericum ramosum	.	.	.	*xx*
Asparagus officinalis	*x*	*x*	.	*x*
Aster amellus	.	.	.	*x*
Astragalus cicer	.	*x*	.	.
Campanula bononiensis	.	*x*	.	.
Campanula sibirica	*x*	*x*	*x*	*xx*
Falcaria vulgaris	*x*	*xx*	*xx*	.
Inula ensifolia	.	.	.	*xx*
Linum hirsutum	.	.	.	*x*
Linum flavum	.	.	.	*x*
Melampyrum arvense	.	*x*	*xx*	*xx*
Oxytropis pilosa	*x*	.	.	.
Phleum phleoides	.	*xx*	*xx*	*x*
Potentilla heptaphylla	.	.	.	*x*
Prunella grandiflora	.	*x*	.	*xx*
Rosa gallica	.	*x*	.	.
Tanacetum corymbosum	.	.	.	*x*
Veronica austriaca	.	*xx*	*x*	*x*
Veronica praecox	*x*	.	.	.
Irano-Turanian				
Hypochoeris maculata	.	.	.	*x*
Salvia nemorosa	*xx*	*x*	.	.
Sisymbrium polymorphum	*xx*	.	.	.
Mediterranean				
Elymus hispidus	*xx*	*xx*	*x*	*x*
Orthantha lutea	.	*x*	.	*x*
Reseda phyteuma	.	.	.	*x*
Silene otites	*x*	.	.	.
Central European				
Anthyllis vulneraria	.	*x*	*x*	*xx*
Brachypodium pinnatum	.	*x*	*xx*	*xx*
Carlina acaulis	.	*x*	*x*	*xx*
Gentianella ciliata	.	.	.	*x*
Potentilla alba	.	*x*	.	.
Eurosiberian				
Anemone sylvestris	.	*x*	.	*x*
Artemisia campestris	*xx*	*x*	.	.
Festuca valesiaca	*xx*	*x*	*x*	.
Fragaria viridis	.	*xx*	*xx*	*x*
Orchis militaris	.	.	.	*x*
Senecio integrifolius	.	.	.	*x*
Thalictrum minus	*x*	*xx*	.	.
Pontic-Pannonian-Central-Asiatic				
Carex humilis	.	.	.	*xx*
Stipa capillata	*xx*	*x*	.	.

Br = *Brachypodietum pinnati*; **In** = *Inuletum ensifoliae*; **St** = *Sisymbrio-Stipetum capillatae*; **Th-Sa** = *Thalictro-Salvietum pratensis* (*x* – occurrence, *xx* –optimum occurrence).

Ordination of the relevés (Fig. 2a,b) shows that the most important factor affecting the typological variability of the xerothermic grassland in the area studied is the kind of substratum. Axis I is correlated with the kind of substratum; the left part with gypsum, central with loess, and right with marl. Axis II displays a relation to soil humidity

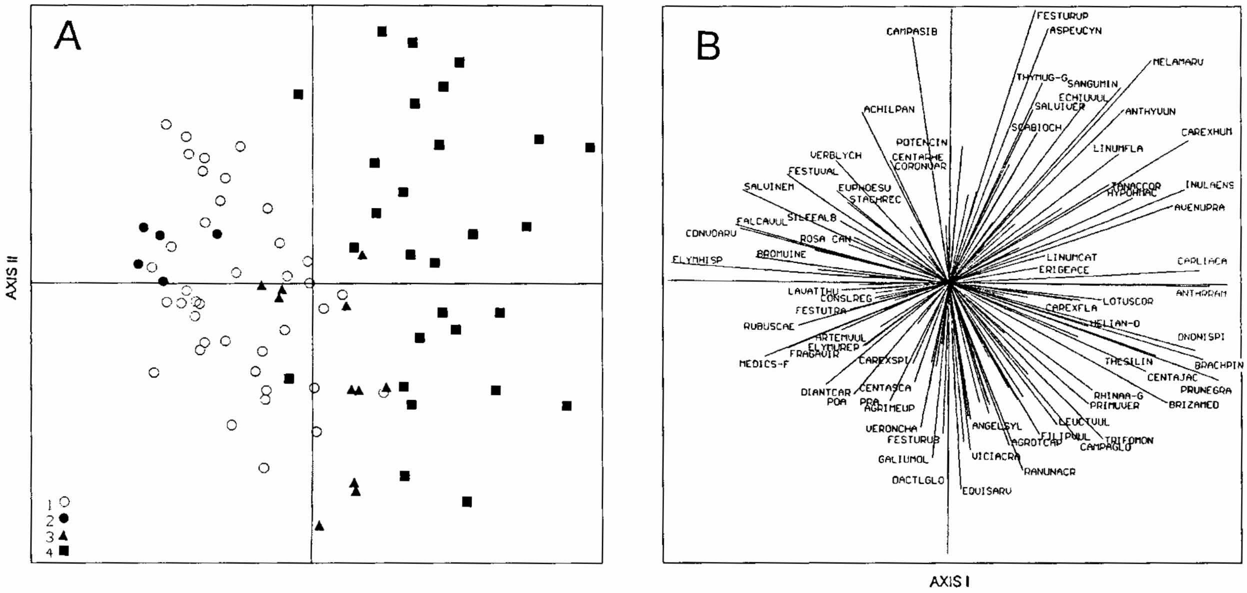

Fig. 2. Ordination of relevés (PCA) with imposed results of classification (minimum variance clustering and Euclidean distance): **A.** Ordination of relevés: 1 = *Thalictro-Salvietum pratensis*, 2 = *Sisymbrio-Stipetum capillatae*, 3 = *Brachypodietum pinnati*, 4 = *Inuletum ensifoliae*. **B.** Species loadings (eigenvectors); species abbreviations: achilpan = *Achillea pannonica*, agrimeup = *Agrimonia eupatoria*, agrotcap = *Agrostis capillaris*, angelsyl = *Angelica sylvestris*, anthram =*Anthericum ramosum*, anthyvun = *Anthyllis vulneraria*, artemvul = *Artemisia vulgaris*, aspeucyn =*Asperula cynanchica*, avenupra = *Avenula pratensis*, brachpin = *Brachypodium pinnatum*, brizamed = *Briza media*, bromuine = *Bromus inermis*, campaglo = *Campanula glomerata*, campasib = *Campanula sibirica*, cerexfla = *Carex flacca*, carexhum = *Carex humilis*, carexspi = *Carex spicata*, carliaca = *Carlina acaulis*, centajac = *Centaurea jacea*, centarhe = *Centaurea rhenana*, centasca = *Centaurea scabiosa*, conslreg = *Consolida regalis*, convoarv = *Convolvulus arvensis*, coronvar = *Coronilla varia*, dactglo = *Dactylis glomerata*, diantcar = *Dianthus carthusianorum*, echiuvul = *Echium vulgare*, elymhisp = *Elymus hispidus*, elymurep = *Elymus repens*, equisarv = *Equisetum arvense*, erigeace = *Erigeron acer*, euphoesu = *Euphorbia esula*, falcavul = *Falcaria vulgaris*, festurub = *Festuca rubra*, festurup = *Festuca rupicola*, festutra = *Festuca trachyphylla*, filipvul = *Filipendula vulgaris*, fragavir = *Fragaria viridis*, galiumol = *Galium mollugo*, helian-o = *Helianthemum ovatum*, hypohmac = *Hypochoeris maculata*, inulaens = *Inula ensifolia*, lavatthu = *Lavathera thuringiaca*, leuctvul = *Leucanthemum vulgare*, linumcat = *Linum catharticum*, linumfla = *Linum flavum*, lotuscor = *Lotus corniculatus*, medics-f = *Medicago falcata*, melamarv = *Melampyrum arvense*, ononispi = *Ononis spinosa*, poa pra = *Poa pratensis*, potencin = *Potentilla cinerea*, primuver = *Primula veris*, prunegra = *Prunella grandiflora*, ranunacr = *Ranunculus acris*, rhinaa-g = *Rhinanthus glaber*, rosa can - *Rosa canina*, rubuscae = *Rubus caesius*, salvinem = *Salvia nemorosa*, salviver = *Salvia verticillata*, sangumin = *Sanguisorba minor*, scabioch = *Scabiosa ochroleuca*, stachrec = *Stachys recta*, tanaccor = *Tanacetum corymbosum*, thesilin = *Thesium linophyllon*, thymug-g = *Thymus glabrescens*, trifomon = *Trifolium montanum*, verbalych = *Verbascum lychnitis*, veroncha = *Veronica chamaedrys*, viciacra = *Vicia cracca*.

(depending on soil thickness); the upper part of the diagram represents dry sites with e.g. *Campanula sibirica* and *Festuca rupicola*, and the lower part more mesophilous sites with e.g. *Dactylis glomerata*, *Angelica sylvestris* and *Ranunculus acris*.

The degree of xerothermic grassland preservation depends on factors impeding the succession, both natural and anthropogenic. The natural factors include steep slopes, shallow and eroded soil, while the anthropogenic factors include especially burning, and, to a lesser degree, grazing and mowing. The grasslands are burnt in the early spring and late autumn. Fire removes decayed plant remnants and eliminates the seedlings of trees, but does not destroy regenerative buds of perennials, which lie deeper.

The xerothermic plant communities in the Proszowice Plateau show, in spite of their relatively small total area and insular distribution, a large number of rare and endangered plant species of relic geographical ranges (e.g. Pontic-Pannonian, Irano-Turanian, and Mediterranean elements). Because the xerothermic grassland is a semi-natural plant community supported by (diminishing) extensive land use, there it is an urgent need for developing measures for active protection to maintain its biological diversity.

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Floristic variation and conservation of wet woodlands in Wales

Latham, J.[*]**, Stevens, D.P.**
& Blackstock, T.H.

Countryside Council for Wales, Plas Penrhos, Penrhos Road, Bangor, Gwynedd, LL57 2LQ, Wales, UK;
**Fax +441248385510; E-mail j.latham@ccw.gov.uk*

Abstract. The Countryside Council for Wales is undertaking survey, inventory and analytical work to develop conservation programmes for wet woodlands. This paper describes a multivariate analysis of 266 quadrat samples from 90 wet woodlands distributed throughout Wales. Detrended Correspondence Analysis (DCA) was used to determine the main axes of floristic variation, and correlations of species scores with Ellenberg numbers were used to give ecological interpretations to these axes. Communities and sub-communities characterised in the British National Vegetation Classification (NVC) grouped reasonably well in the ordination diagrams, suggesting that the classification system broadly accommodates much of the floristic variation of these woodlands in Wales. An extension of this analysis to include additional environmental factors, and the application of these results to conservation, are discussed.

Keywords: Detrended Correspondence Analysis; Ellenberg numbers; National Vegetation Classification; Plant community; Wetland.

Introduction

Wet woodlands occur widely on waterlogged or seasonally wet soils, and in Wales usually have *Alnus glutinosa*, *Salix cinerea* or *Betula pubescens* as the dominant species. Often they are successional habitats on bogs, fens, wet grasslands or lake margins. True floodplain forests have been lost, but fragmented remnants of woodland occur on riversides and as small inclusions on otherwise deforested floodplains. Wet woodlands also occur on flushed hillsides where they may form mosaics with dry woodland types.

The conservation value of wet woodlands has often been overlooked within the UK. Compared with dry woodland types there is relatively little known about their ecology, and the colonisation of woodland in open herbaceous wetland habitats has often been actively discouraged. Recently, awareness of wet woodlands and their biodiversity value has been raised. Residual alluvial forest is a priority habitat in the EU Habitat and Species Directive (Council Directive 92/43/EEC) and there is interest in re-creating floodplain forests at appropriate British localities (Peterken & Hughes 1995). The UK Government has published a Habitat Action Plan for Wet Woodlands (Anon. 1998), as part of its commitment to the Rio Convention (Anon. 1992). This Plan includes targets for wet woodland conservation, restoration and re-establishment across the UK.

In Wales, a programme of survey and inventory is in progress to produce better information on the status and floristic composition of wet woodlands. This paper describes a preliminary analysis of these data to explore the floristic variation within wet woodlands, and considers the effectiveness of the British National Vegetation Classification (NVC) (Rodwell 1991) in accommodating this variation. Potential applications of the results to conservation are outlined. Plant community codes and names follow Rodwell (1991).

Methods

Since 1991, the Countryside Council for Wales (CCW) has undertaken extensive surveys using the NVC. Their purpose has been to aid the development of conservation programmes by providing quantitative descriptions of the community composition of broadleaved woodlands and other semi-natural habitats in Wales. In addition, they provide data for analyses of relationships between vegetation and environment.

The data employed here derive from surveys covering a range of woodland types (Castle & Mileto 1994, 1995, 1998; Alexander 1996). Within each woodland, homogeneous stands of vegetation were identified and mapped. Stands were then placed within NVC communities (if possible) by use of keys provided in Rodwell (1991); British wet woodland communities are listed in Table 1. At least one relevé was recorded per stand, and at least five if community identification was in any way problematic. Each relevé consists of a 4 m × 4 m quadrat within which the abundance of all vascular plant and bryophyte species in the ground and field layer was recorded using the Domin scale; the canopy and shrub composition was recorded in an extended 50 m × 50 m quadrat. Species occurring in more than one vegetation layer (e.g. trees as seedlings, saplings and canopy components) were recorded separately.

Samples recorded from wet woodland communities were extracted for analyses from the NVC survey datasets, giving a total of 266 quadrat samples from 90 woodland sites throughout Wales. Detrended Correspondence Analysis (DCA) was used to identify the axes of greatest variation in the floristic data set, implemented with CANOCO version 3.12 (ter Braak 1988 and subsequent updates) with down-

Table 1. Wet woodland communities characterised in the National Vegetation Classification (Rodwell 1991).

Community code	Community name	Sub-communities
W1	*Salix cinerea - Galium palustre* woodland	-
W2	*Salix cinerea - Betula pubescens - Phragmites australis* woodland	2
W3	*Salix pentandra - Carex rostrata* woodland	-
W4	*Betula pubescens - Molinia caerulea* woodland	3
W5	*Alnus glutinosa - Carex paniculata* woodland	3
W6	*Alnus glutinosa - Urtica dioica* woodland	5
W7	*Alnus glutinosa - Fraxinus excelsior - Lysimachia nemorum* woodland	3

Table 2. Summary of Spearman rank correlation coefficients of DCA species axis scores with Ellenberg indicator numbers. The most significant values ($p < 0.01$) are shown in bold-face.

	Ellenberg indicator					
DCA axis	L	T	K	F	R	N
1	**0.38**	0.14	**0.25**	**0.33**	**-0.37**	**-0.44**
2	0.12	**0.28**	0.04	**0.45**	**0.33**	**0.24**
3	**-0.22**	**0.20**	-0.09	-0.14	**0.24**	**0.25**
4	**0.26**	0.09	0.01	0.12	0.16	0.17

L = Light; T = Temperature; K = Continentality; F = Soil moisture; R = pH; N = Nitrate/nutrient.

weighting of rare species. Ellenberg numbers (Ellenberg et al. 1991) have been shown to be reasonably successful as environmental predictors in studies of British vegetation (Thompson et al. 1993; Hawkes et al. 1997), and species scores for each DCA axis were correlated with their corresponding Ellenberg numbers (Spearman rank correlation) to give ecological interpretations to the DCA axes. Ordination diagrams for sites were plotted showing the NVC communities assigned to each quadrat recorded in the surveys.

Results

The first two DCA axes together explained 12.6% of the variation in the data-set; the third and fourth together explained only a further 6.1% and are not considered in detail here. Strong correlations were found between the species scores of all axes and Ellenberg numbers (Table 2). In the context of western Europe, Axis 1 may be interpreted as primarily a gradient from high to low pH and nutrient status, and increasing light; Axis 2 appears to represent a gradient of increasing soil wetness, pH, nutrient status and temperature. The first two DCA axes are plotted in Figs. 1 and 2. The wet woodland NVC communities (Table 1) overlap considerably but some occupy discrete areas within the ordination diagrams. The upper left of Fig. 1, representing conditions of high pH and nutrient status is occupied by samples of W6 *Alnus glutinosa-Urtica dioica* woodland. W4 *Betula pubescens-Molinia caerulea* woodland occupies a fairly discrete area at lower right, characterised by conditions of low pH and low nutrient status. The upper centre of Fig. 1 represents relatively light conditions and variable base status and pH, and there is considerable overlap among the W2 *Salix cinerea-Betula pubescens -Phragmites australis* woodland, W1 *Salix cinerea-Galium* woodland and W5 *Alnus glutinosa-Carex paniculata* communities. The single sample from *Salix pentandra-Carex rostrata* woodland W3 falls to the right of this cluster.

The most commonly recorded community was W7 *Alnus glutinosa-Fraxinus excelsior-Lysimachia nemorum* woodland. Samples from this community lie within the lower left of the ordination diagrams which may be interpreted as representing relatively dark and dry conditions. Fig. 2 shows the community split into its constituent sub-communities, which separate along Axis 2. The *Urtica dioica* sub-community (W7a) and the *Deschampsia cespitosa* sub-community (W7c) occupy the upper and lower halfs of this axis respectively, with the *Carex remota-Cirsium palustre* sub-community (W7b) overlapping both.

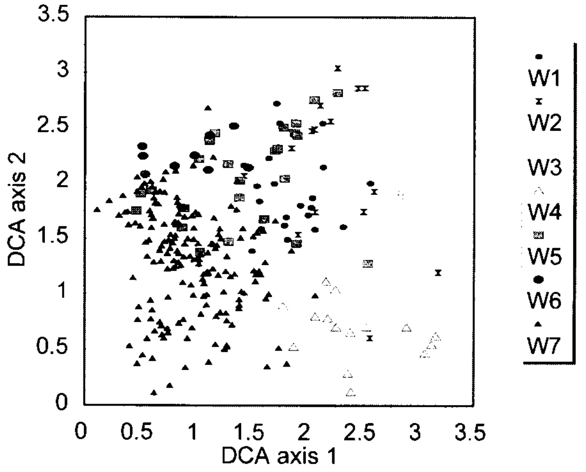

Fig. 1. DCA ordination diagram (Axes 1 and 2) for wet woodlands in Wales. Each point represents a quadrat sample; allocation of the samples to NVC communities is indicated.

Discussion

The positions of the NVC communities within the ordination diagrams largely corroborate what is known of their ecology, and suggest the classification system accommodates most floristic variations within wet woodlands in Wales. The overlap between the communities W2 *Salix cinerea-Betula pubescens-Phragmites australis* woodland, W1 *Salix cinerea-Galium palustre* woodland and W5 *Alnus*

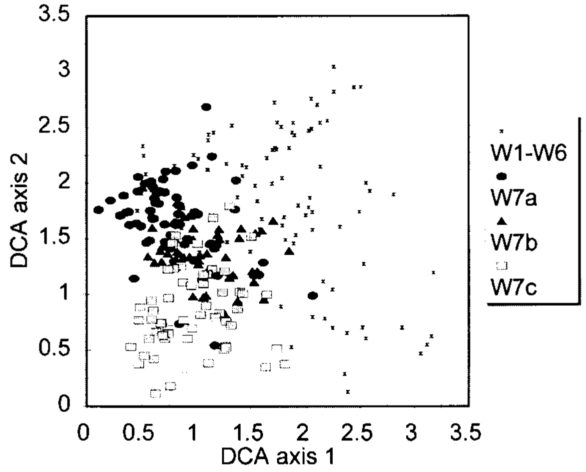

Fig. 2. DCA ordination diagram (Axes 1 and 2) for wet woodlands in Wales showing division of W7 *Alnus glutinosa-Fraxinus excelsior-Lysimachia nemorum* woodland into sub-communities. Each point represents a quadrat sample.

glutinosa-Carex paniculata woodland revealed by DCA suggests that further work may be required to fully characterise these communities in Wales. W5 *Alnus glutinosa-Carex paniculata* woodland is usually considered to be a very distinctive community, but is poorly defined in the ordination diagram The identification of this community rests heavily on the dominance of large *Carex* species. In Wales, *C. paniculata* is not common in woodlands, and other large *Carex* species are considered to replace it, notably *C. acutiformis*. The lack of coherence of these *Alnus-Carex* stands in the ordination diagrams indicates that they may have affinities to a variety of other communities, and that it is simplistic to consider 'W5' as it has been recorded for conservation assessments in Wales. In contrast, W1 *Salix cinerea-Galium palustre* woodland is often regarded as a loosely defined and species poor community, occurring as a widespread early successional phase on wet mineral soils in a range of situations. But the ordination clumps the W1 records fairly closely, suggesting more ecological coherence to this community than previously suspected and indicating a need to consider the community in more detail in conservation assessments. *Salix pentandra-Carex rostrata* woodland W3 has to date been recorded at only one locality in Wales (Hall 1997; Castle & Mileto 1998). It is notable that the single sample from this stand falls in a marginal part of the diagram, suggesting that this rare community may be ecologically distinct and a priority for conservation efforts in Wales.

The W7 *Alnus glutinosa-Fraxinus excelsior -Lysimachia nemorum* community is associated with relatively shaded and dry conditions. The community indeed has close affinities with drier woodland types, and may develop through succession to *Fraxinus* woodland (Latham & Blackstock 1998). The abundance of samples from this community reflects the frequency of long-established woodlands in the survey coverage, where it often occurs in mosaics with drier woodland vegetation. W7 sub-communities apparently separate according to nutrient status, and there is a suggestion of a continuum with the much rarer *Alnus glutinosa-Urtica dioica* woodland which replace W7 samples at high values on axis 2. If this is so, conservation assessements of W6 and W7 in Wales need to be carried out in a coordinated way.

The analyses summarized here could be extended by adding environmental, anthropogenic and other variables (including soil type and parent materials, climatic factors, woodland age, isolation, topographic situation and grazing management) to give a better indication of the prevailing influences on wet woodland floristics in Wales. Analysis of spatial relationships among communities and their landscape setting would provide a wider ecological perspective on this habitat.

The main mechanism for the statutory protection of sites for nature conservation in Wales is the series of Sites of Special Scientific Interest (SSSIs). Sites are selected so that the best examples of semi-natural vegetation types are represented within each of 12 'Areas of Search' in Wales (Blackstock et al. 1996). The majority of the wet woodland samples used in this analysis come from sites already notified as SSSIs. Future surveys will sample non-protected sites also, to ensure the full range of site conditions is accommodated. A better understanding of wet woodland floristics, and the relationships between communities will help to refine the series and improve the protection of wet woodlands. The UK Government's Biodiversity Action Plan has targets to expand wet woodland cover; knowledge of the relationships between wet woodlands and other semi-natural habitats will help to ensure that this will be undertaken in an ecologically informed way.

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pH and Ellenberg reaction values for Danish forest plants

Lawesson, Jonas E.[1*] **& Mark, Susanne**[2]

[1*]*Department of Systematic Botany, Århus University, Nordlandsvej 68, DK-8420 Risskov, Denmark; Fax: +45 89 42 47 47; E-mail: jonas.lawesson@biology.au.dk;*
[2]*National Environmental Research Institute, Department of Coastal Zone Ecology, Grenåvej 12, Kalø, DK-8410 Rønde, Denmark*

Abstract. Plant species and communities are often used as bio-indicators for pH, nitrogen, light or other factors. One bio-indicator system is the Ellenberg system of indicator values for Central Europe. The validity in other areas has been confirmed by several authors, but so far not in Denmark. In this study the correlation between Ellenberg reaction values and measured pH values is reviewed for 158 plant species occurring in Danish forests, and used for the calibration of the original indicator values.

In total 30 species differed with 2 units, and seven species with 3 units. In addition, 20 indifferent species were assigned averaged indicator values. New calibrations should regularly be carried out to improve the original indicator values. The use of indicator values seems a promising avenue for synthesis and integration of species response and community ecology, also in Denmark.

Keywords: Calibration; Indifferent species.

Introduction

One main topic in vegetation ecology is vegetation changes along environmental gradients. All species and plant communities respond to habitat factors in a specific way. When a few dominant environmental factors and long gradients are provided, the species response curves are likely to follow a unimodal form (Økland 1990). It is then possible to define ecological optima and amplitudes, and we can use the species as diagnostic taxa of certain plant communities and as indicators of environmental conditions. The ability of many plants to indicate the value of an environmental variable can be used to calculate average indicator values for sample plots. The species indicator system of Central European plants was developed by Heinz Ellenberg in the 1950's (see Ellenberg et al. 1992), for light, soil moisture, continentality, temperature, nitrogen and reaction. These indicator values express the relative response of plant species in their natural environment as compared to other species. Usually these average indicator values are assumed to represent good estimates of the values of the environmental variables studied, also outside Central Europe, and this has been observed in some studies (e.g. Vevle & Aase 1980; Mountford & Chapman 1993; Thompson et al. 1993; Diekmann 1994, 1995; Sastad & Moen 1995; Diekmann & Dupré 1997; Hawkes et al. 1997; Hill & Carey 1997; Hill et al. 1999).

The strong relation between indicator values and sociological-ecological species groups was reported by van der Maarel (1993). In this study we compare and calibrate Ellenberg reaction values with Danish quantitative data and discuss the applicability in Danish forest ecosystems.

Material and Methods

Study area

Data on forests were compiled from all Denmark, except Bornholm island, and grouped into (1) a prediction data set and (2) a test-data set. All available quantitative studies in beech, oak and coniferous forests, mainly from literature sources from before 1997 were compiled in the prediction data set. For all plots pH was provided, although the method of measurement was not always explicitly given. When several pH-values were available, pH(H_2O) was used. Plot size was usually larger than 10 m^2. The test data set contained data collected in 1997 throughout the country mainly in beech, oak and conifer forests, in 16-m^2 plots (Mark & Lawesson, this volume). In each plot, three soil samples were collected and mixed. pH was determined using 5 g of dried soil with 10 g of destilled water – pH(H_2O) –, and 10 g 1 M $CaCl_2$-solution – pH($CaCl_2$) –, respectively. Measurements were carried out with a pHM240pH/Ionmeter, Radiometer, Copenhagen.

Methods of data evaluation

The two data sets were edited with the software package TURBOVEG, vers. 1.06 (Hennekens 1996). The average indicator value for reaction (R) on the ordinal scale from 1-9, from strongly acidic (scale unit 1: pH < 3.4) to alkaline (9: pH > 7), were calculated based on the unweighted averages of the indicator values of all species present in each individual plot. The average indicator values for all plots from the prediction data set were regressed with the measured pH, in an ordinary linear regression model in the programme EXCEL, and the rounded predicted values R_{pre} at a confidence level of 95% were considered as the improved Danish indicator values. These new R_{pre} values were then compared with the species indications from each of the plots included. The original values (Ellenberg et al. 1992) however, were only replaced if two conditions were fulfilled: (1) The species in question should have its optimum in forest, and (2) R_{pre} should deviate with more than one unit on the indicator scale. In both cases were the new calibrated R_{pre} assigned to these species. The original, and the new set of improved Ellenberg values were then applied to the independent test data set. A linear regression model was applied to compare the application of the two sets of Ellenberg values.

Results

Prediction data set

In total 158 plant species from 897 plots complied with the requirements for inclusion in the analysis. The number of species per plot varied from 1 to 73 (mean 11 species). The correlation between calculated R for the samples and

Table 1. Species for which the improved indicator values deviated with (**a**) 3 units or (**b**) 2 units from the original Ellenberg values. Given are the average pH in plots, the original indicator values, and the new, improved values.

Species	Average pH	Ellenberg R	New R
a.			
Cirsium palustre	5,9	4	7
Galium verum	4,5	7	4
Holcus mollis	4,8	2	5
Polypodium vulgare	4,6	2	5
Pulmonaria obscura	4,6	8	5
Pyrola minor	5,3	3	6
Ribes alpinum	5,0	8	5
b.			
Actaea spicata	6,9	6	8
Agrostis canina	4,6	3	5
Agrostis gigantea	4,5	7	5
Allium oleraceum	5,0	7	5
Alnus incana	5,3	8	6
Anemone ranunculoides	5,3	8	6
Betula pubescens	4,9	3	5
Bromus ramosus	5,9	5	7
Calamagrostis arundinacea	4,3	6	4
Cardaminopsis arenosa	4,0	6	4
Carex elongata	5,8	7	5
Cirsium oleraceum	6,1	7	5
Corydalis cava	5,3	8	6
Crataegus monogyna	5,4	8	6
Crepis paludosa	5,6	8	6
Dentaria bulbifera	7,2	7	9
Festuca altissima	5,2	4	6
Gagea spathacea	4,5	7	5
Lamiastrum galeobdolon	5,0	7	5
Lathyrus linifolius	4,6	3	5
Lonicera periclymenum	4,6	3	5
Malus sylvestris	4,9	7	5
Mercurialis perennis	5,5	8	6
Platanthera bifolia	4,5	7	5
Prunus avium	4,9	7	5
Prunus padus	4,6	7	5
Sorbus torminalis	4,7	7	5
Trientalis europaea	4,5	3	5
Vaccinium myrtillus	4,3	2	4
Viola reichenbachiana	4,8	7	5

the pH values showed a significant correlation ($r = 0{,}610$, $p < 0.001$). For seven species, the difference between R and R_{pre} was 3 units (Table 1a), for 30 species it was 2 units (Table 1b). In addition, Danish R values were calculated for 20 indifferent species (Table 2).

Test data set

The independent data set used for test of the improved Ellenberg indicator values, as compared with the original ones, contained 176 plots, and 174 species. The number of species per plot varied between 2 and 31 (mean 10 species). All correlations between the measured pH and the calculated mean indicator values for the plots were highly significant (Table 3), yet the $pH(CaCl_3)$ produced a better correlation, and the improved indicator values based on R_{pre}, were better predictors of pH than the old R. The standard errors of prediction (SE) showed the same pattern (Table 3).

Table 2. Indifferent species according to the Ellenberg system, for which predicted values have been calculated. Given are the mean, maximum and minimum pH in plots, and new predicted indicator values; values for Sweden (Diekmann 1995) are also provided.

Species	Mean pH	Max pH	Min pH	New R	Sweden
Acer platanoides	5,1	5,8	3,9	5	7
Acer pseudoplatanus	5,4	7,0	2,7	5	
Cerastium fontanum	6,4	8,0	5,6	5	
Convallaria majalis	4,6	7,6	2,6	4	5
Corylus avellana	5,3	7,8	3,6	5	5
Dactylis glomerata	5,4	8,0	3,9	5	5
Festuca rubra	4,5	6,2	3,9	4	
Filipendula ulmaria	5,8	7,8	4,5	5	7
Fragaria vesca	5,3	7,2	4,0	5	5
Geum rivale	6,5	7,1	5,5	6	7
Geum urbanum	6,0	8,0	4,0	5	7
Juniperus communis	4,8	7,6	3,8	4	4
Melica nutans	5,7	7,5	4,6	5	5
Mycelis muralis	4,9	7,9	2,8	5	5
Poa pratensis	5,1	7,8	3,7	5	
Populus tremula	4,8	7,1	3,7	4	5
Quercus robur	5,2	7,9	2,6	5	5
Taraxacum officinale	5,9	8,0	3,5	5	
Veronica chamaedrys	5,5	8,0	4,0	5	5
Veronica hederifolia	6,4	8,0	5,2	5	

Discussion

The significant correlation between pH and the average unweighted values based on Ellenberg et al. (1992) shows the high quality of Ellenberg's system, even outside Central Europe, which was also confirmed in studies elsewhere. Among the 30 species in which R_{pre} deviated with 2 units (Table 2) species such *Actaea spicata*, *Bromus ramosus* and *Dentaria bulbifera* had higher improved indicator values (7 - 9), while a lower improved indicator value (5 - 6) was shown by several species (e.g. *Allium oleraceum*, *Corydalis cava*, *Crepis paludosa* and *Prunus padus*). For some species (e.g. *Lathyrus linifolius*, R = 5), the results are in accordance with Diekmann (1995), who also provided new indicator values for some species. Equal values were thus found for *Dactylis glomerata* (R = 5), and many indifferent species such as *Juniperus communis* (R = 4), *Corylus avellana*, *Fragaria vesca*, *Melica nutans*, *Mycelis muralis* and *Quercus robur* (R = 5), whereas differences of 2 units were found for *Acer platanoides*, *Filipendula ulmaria* and *Geum urbanum*. This is, however, not so surprising, as

Table 3. Correlations between actual soil reaction – $pH(H_2O)$ and $pH(CaCl_2)$ – and indicator figures for soil reaction fora test data set, with correlation coefficient (R), and standard errors of prediction (SE) for pH. Indicator values are based on Ellenberg's original indicator values (Ellenberg et al. 1992) and improved values from this study. All correlations are highly significant ($p < 0.001$).

Indicator values	Original		Improved	
	r	SE	r	SE
$pH(H_20)$	0,346	0,140	0,424	0,090
$pH(CaCl_3)$	0,380	0,120	0,477	0,081

the forest types studied in Sweden by Diekmann (1995) mainly belonged to the boreo-nemoral zone, while our study is confined to the nemoral zone. Some of the deviations between the original and improved values may be because Ellenberg did not explicitly include the species response to management, nor biotic effects such as competition with other plants and herbivory. Furthermore, although composed of many plots, the two Danish data sets may be biased as concerns representativeness of Danish forests and regions in Denmark. The majority of plots are from beech and oak forests and fewer from conifer plantations, while important forest types such as those with maple, lime, ash and hornbeam forests are largely ignored. This is the result of traditions in Danish vegetation science (Lawesson 1998). It should also be remembered that Ellenberg's system is supposed to be valid for the species in their whole ecological range, also outside forests, which is the vegetation type we studied. A more complete analysis with species in all Danish plant communities would thus be more comparable with the original Ellenberg system. Nevertheless, our study confirms that the Ellenberg system still is reliable and a useful concept and tool for vegetation studies in Denmark, but with space for improvements and additions, especially for the many species considered indifferent or without indicator values in Ellenberg et al. (1992). We suggest that the range and average indicator value for indifferent species, are further studied, as it may be suspected that many of the species assigned R values by Ellenberg may actually be more indifferent (having wider tolerances) than several so-called indifferent species.

Furthermore it is recommended that the many species without indicator values are examined and given an indicator value for the different factors in the Ellenberg system. It may here be relevant to conclude, that there is a considerable variation of measured pH. This is seen in other similar studies as well (e.g. Diekmann & Dupré 1997), and stresses the great ecological plasticity of many plant species and communities.

New and updated calibrations of ecological indicator values should be carried out regularly, both in Central Europe and elsewhere. As more and better data are collected, and with modern computer power, this is an easy task. In this connection, it is most relevant to investigate how the optima of species will change due to for instance acidification and eutrophication. The application of ecological indicator values in Denmark, instead of incidental measurements, thus represents a promising avenue of synthesis and integration, of both functional species response (Diekmann & Lawesson 1999) and community ecology.

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Vegetation of the lowlands of the Cape Region of Baja California Sur

León de la Luz, José L.

Centro de Investigaciones Biológicas del Noroeste, CIBNOR. Apdo postal 128, La Paz, Baja, California Sur, México 23000;
Fax +5211255343; E-mail jlleon@cibnor.mx

Abstract. A vegetation description of the southern part of the Baja California peninsula, NW Mexico, is presented. Three major vegetation types are distinguished, two of which occur in the Cape region of Baja California, the xerophilous Sonoran desert type and the dry tropical type. According to a PCA-ordination the plant communities of the Cape region can be arranged along both an altitudinal gradient. According to a cluster analysis six species groups are distinguished.

Keywords: Biogeographic transition; Clustering; Ecocline; Ordination; Sarcocaulescent shrubland; Sonoran Desert; Succulent vegetation.

Nomenclature: Shreve & Wiggins (1964); Wiggins (1980).

Introduction

The Cape Region forms the southern tip of the arid Baja California Peninsula, Mexico. The lowland environment has both tropical and xerophytic features. Tropical deciduous forest (TDF) occupies the foothills of the mountains, and Cape Sarcocaulescent Shrubland (CSCS) the alluvial plains. This region borders the southernmost sectors of the Sonoran Desert region of Baja California Peninsula.. Early descriptions of flora and vegetation of the Cape Region were given by Brandegee (1892) and Shreve (1937). The CSCS occupies an intermediate position along the geographic and environmental gradient between the TDF and the Sonoran Desert Sarcocaulescent Shrubland (SDSS). Our major objective was to analyse the floristic and physiognomic attributes of the CSCS to understand the nature of the vegetation transition between the xerophytic communities of central Baja California and the dry tropical environments of the Cape foothills.

We started from the hypothesis that, because of the presence of a large geologic discontinuity separating the granitic Cape Region from the northern volcanic ranges of the Sierra de la Giganta (Schmidt 1990), different environmental conditions prevail at either side of the transition, and the presence of different species pools (CSCS being more linked to the TDF, while SDSS being part of a large corridor of subtropical and temperate arid ecosystems), CSCS can be separated from SDSS vegetation types by different floristic composition and vegetation structure.

Material and Methods

We sampled 33 vegetation plots (1000 m^2 each): 15 in TDF, 12 in CSCS, and six in SDSS. Table 1 shows the general characteristics for each site. In each plot we recorded all perennial species and measured the height and canopy cover of each individual tree and shrub. For each species in each location, we calculated mean height, canopy cover, and density of individuals. Each species was classified as either of two life forms: trees (Tr) and shrubs (Sh). A general ranking table was made for each species in each community, considering frequency (the rate of presence in particular locations), mean height, mean individual density, and mean canopy coverage. A relative importance value (RIV) was calculated for each species as the average of the relative values of these four variables (Mueller-Dombois & Ellenberg 1974). Following Goldberg (1982), we arcsine-transformed each variable prior to analysis.

Using a presence-absence data matrix for 105 species and data from Table 1, we carried out a Principal Components Analysis (PCA) to detect floristic gradients that were related to environmental variation, and a numerical classification of species to detect guilds of plants with similar distribution types. For the PCA we used the cross-product matrix as our resemblance measurement, after having transformed our data by applying Gower's double-centering procedure. In order to identify non-trivial axes, we subsequently performed a broken-stick distribution test on the resulting component (Jackson 1993). The PCA-analysis was carried out with the public domain program ORDEN, developed by Exequiel Ezcurra. In the case of the numerical classification, we used the squared Euclidean distance calculated on the untransformed presence-absence data as the measure of similarity between species. The clustering procedure was done using the minimum variance procedure of the program MVS plus 2.1a (Kovach 1993)

Results

The PCA produced only two non-trivial axes: Axis 1 and Axis 2 accounted for 16.8% and 10.4% of the variation in the data set, respectively (Fig. 1a). Both axes produced a typical multivariate arch configuration, with the TDF sites in one extreme of the arch and the SDSS sites in the other. Most of the CSCS sites occupied an intermediate position, although some were located near the SDSS sites. The first axis was significantly related to altitude ($r^2 = 0.68$; $F_{1,31} = 66.3$; $P < 0.00001$), and rainfall ($r^2 = 0.50$; $F_{1,31} = 31.3$; $P < 0.00001$). The second axis, responsible for the curvature of the arch, was not related to any environmental factor, but it was negatively correlated with the site species richness ($r^2 = 0.24$; $F_{1,31} = 9.7$; $P = 0.004$). This correlation simply indicates that the sites at the extreme of the arch (all SDSS and some dry CSCS locations on one side, and a few TDF locations on the other) have lower species richness than the locations in the center of the gradient, where TDF and CSCS meet.

Table 1. Geographical and environmental characteristics of each of the sampling locations for the Cape Region (CSCS and TDF) and Sonoran Desert (SDSS). Rock = rockiness (scale 0 to 5); Dens. = no. of individuals; *S* = species richness.

	Lat.	Long. (m)	Alt. (mm)	Rain (°C)	T (°)	Slope 0 - 5	Rock	Dens.	*S*
CSCS									
1	24° 08'	110° 18'	20	245	23.9	3 - 5	0	297	25
2	24° 04'	110° 29'	150	230	23.8	5 - 8	2	395	36
3	23° 28'	110° 11'	100	160	21.9	4 - 6	1	361	24
4	23° 11'	110° 07'	30	260	22.0	5 - 6	0	557	28
5	23° 48'	110° 17'	80	160	21.9	2 - 4	0	304	15
6	23° 42'	109° 32'	30	210	23.1	6 - 9	2	270	40
7	23° 02'	110° 10'	70	205	24.0	6 - 8	2	348	33
8	23° 10'	110° 06'	60	255	22.0	7 - 10	1	510	32
9	24° 05'	110° 12'	50	270	23.8	15 - 18	4	614	25
10	23° 02'	109° 40'	20	280	23.7	5 - 8	1	276	32
11	23° 45'	109° 42'	40	255	23.7	12 - 16	3	299	24
12	23° 25'	110° 32'	120	260	23.6	6 - 9	0	302	21
13	23° 45'	110° 40'	70	150	21.9	4 to7	0	231	23
14	23° 42'	110° 20'	80	160	21.9	2 - 4	0	298	28
15	24° 15'	110° 18'	100	210	23.6	6 - 8	0	287	35
Mean			**64**	**221**	**23.0**	**7.2**	**1**	**357**	**28.1**
S.D.								**±114**	**6.6**
TDF									
16	23° 13'	109° 40'	220	410	22.6	12 - 16	1	658	45
17	23° 29'	109° 58'	580	300	23.5	18 - 22	3	341	24
18	23° 26'	109° 47'	370	295	23.5	8 - 10	1	509	32
19	23° 28'	109° 48'	450	305	23.5	9 - 13	3	225	28
20	23° 16'	109° 51'	230	390	22.3	17 - 22	3	217	23
21	23° 42'	110° 08'	450	370	21.4	20 - 23	3	476	28
22	23° 50'	110° 10'	670	400	21.5	25 - 28	4	303	27
23	23° 29'	109° 46'	450	305	23.5	7 - 10	1	385	24
24	23° 28'	110° 01'	450	500	22.7	8 - 9	1	235	18
25	24° 08'	110° 11'	500	395	21.5	26 - 29	3	354	28
26	23° 31'	109° 58'	550	510	22.7	21 - 24	4	178	18
27	23° 29'	110° 00'	450	510	22.7	27 - 30	4	487	35
Mean			**384**	**391**	**22.6**	**18.0**	**2.6**	**364.0**	**27.5**
S.D.								**±145**	**7.4**
SDSS									
28	24°13'	109°53'	105	210	22.6	32 - 34	4	281	14
29	24°28'	110°21'	90	170	22.4	29 - 35	5	155	23
30	24°47'	110°42'	170	110	22.4	17 - 22	3	187	23
31	24°12'	110°12'	60	125	22.7	21 - 25	3	226	21
32	24°15'	110°17'	45	135	22.6	7 - 9	4	255	15
33	27°32'	113°31'	70	100	20.9	4 - 5	0	200	12
Mean			**90**	**142**	**22.2**	**20.0**	**3.1**	**217.3**	**18.0**
S.D.								**±46**	**4.9**

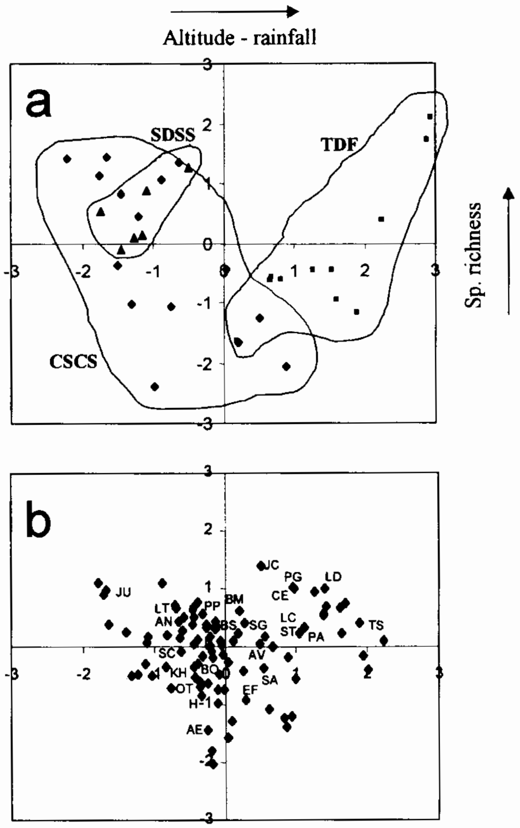

Fig. 1. Principal Component Analysis (PCA) biplot. **a**. Site ordination, locations for each community encircled. **b**. Species ordination:

Aeschynomene nivea (AN)
Atamisquea emarginata (AE)
Bursera microphylla (BM)
Cyrtocarpa edulis (CE)
Hyptis s.l. (H)
Jatropha cuneata (JU)
Larrea tridentata (LT)
Lysiloma divaricata (LD)
Pachycereus pecten-aboriginum (PG)
Plumeria acutifolia (PA)
Simmondsia chinensis (SC)
Stenocereus thurberi (ST)
Adelia virgata (AV)
Bourreria sonorae (BS)
Bursera odorata (BO)
Erythrina flabelliformis (EF)
Jatropha cinerea (JC)
Karwinskia humboldtiana (KH)
Lysiloma candida (LC)
Olneya teosota (OT)
Pachycereus pringlei (PP)
Senna atomaria (SA)
Stenocereus gummosus (SG)
Tecoma stans (TS).

Several species are strongly linked with a PCA-axis (Fig. 1b). Along Axis 1 *Jatropha cuneata* (JC), *Olneya tesota* (OT) and *Pachycereus pringlei* (PP) show strong links with the sites with negative scores (mostly SDSS and dry CSCS sites), whereas *Pachycereus pecten-aboriginum* (PG), *Karwinskia humboldtiana* (KH) and *Tecoma stans* (TS) show strong links with sites at the opposite end of Axis 1 (i.e. TDF). Along axis 2, a group of species strongly related to sites in the middle of the arch (CSCS and TDF) showed up, including *Bourreria sonorae* (BS), *Lysiloma candida* (LC) and *Adelia virgata* (AV). All these species are common in the CSCS type.

The cluster diagram of the numerical classification detected six distinct groups of species with clearly identifiable field distributions (diagram not shown). Table 2 shows seven species for each group, selected on the basis of their conspicuousness and ease of identification in the field, together with their RIV values within each vegetation type. Most of the clusters are made of sets of species that are present in more than one community.

Cluster III (20 species, mostly trees) is composed of species with a high importance value (RIV) in TDF, although the same species also may appear in CSCS and to a limited extent also in SDSS. *Lysiloma divaricata* (the most important tree species in TDF) and *Plumeria acutifolia* are disjunct species from the dry tropical areas of mainland Mexico, and their presence here is an indication of that kind of environment. Other species, although typical plants of TDF, also appear occasionally in CSCS, e.g. *Erythrina flabelliformis, Pachycereus pecten-aboriginum* and *Senna atomaria.* The TDF sites are located in the highest places, which receive high levels of rain (up to 500 mm/yr), and in

Table 2. Species composition of six clusters resulting from the cluster analysis (dendrogram not presented). Seven representative species of each group are shown with their relative importance value (RIV) and standard deviation. Frequency is the number of plots where a taxon was present out of the total number of plots (33). Tr = tree; Sh = shrub.

		TDF	CSCS	SDSS	Frequency
Group I (7 species)					
Tr	*Bursera microphylla*	7.1 ± 1.5	11.8 ± 3.9	10.9 ±1.8	23
Tr	*Cyrtocarpa edulis*	10.3 ± 3.5	11.1 ± 3.8	6.4 ± 3.4	20
Sh	*Jatropha cinerea*	14.5 ± 5.7	15.5 ± 7.1	8.1 ± 2.4	25
Sh	*Opuntia cholla*	7.2 ± 1.3	10.7 ± 4.5	12.7 ± 1.9	26
Tr	*Pachycereus pringlei*	4.7 ± 2.7	8.1 ± 1.5	9.8 ± 1.7	22
Sh	*Stenocereus gummosus*	6.9 ± 1.4	11.3 ± 3.9	10.4 ± 4.1	21
Tr	*Stenocereus thurberi*	9.6 ± 1.5	6.9 ± 1.8	6.3 ± 2.1	24
Group II (9 species)					
Sh	*Adelia virgata*	7.9 ± 1.1	7.1 ± 1.1	5.6 ± 1.9	15
Sh	*Bourreria sonorae*	5.1 ± 1.7	5.6 ± 1.5	7.6 ± 1.2	16
Tr	*Colubrina viridis*	10.3 ± 2.7	7.5 ± 1.1	6.7 ± 2.1	12
Sh	*Cordia brevispicata*	4.7 ± 2.1	4.9 ± 1.7		11
Sh	*Ferocactus s.l.*	4.4 ± 3.4	4.3 ± 2.9	4.1 ± 2.2	12
Tr	*Fouquieria diguetii*	9.2 ± 2.1	10.8 ± 3.3	10.5 ± 1.3	19
Tr	*Lysiloma candida*	10.2 ± 2.9	7.6 ± 0.8	8.4 ± 2.3	15
Group III (20 species)					
Tr	*Erythrina flabelliformis*	6.7 ± 1.6	2.7 ± 1.7		9
Tr	*Karwinskia humboldtiana*	7.4 ± 1.1	4.4 ± 1.9	5.9 ± 1.7	12
Tr	*Lysiloma divaricata*	12.4 ± 5.2			7
Tr	*Pachycereus pecten-aboriginum*	8.3 ± 2.5	3.4 ± 2.1	13	
Tr	*Plumeria acutifolia*	6.4 ± 1.6			5
Tr	*Senna atomaria*	8.6 ± 0.3	3.6 ± 2.1		8
Sh	*Tecoma stans*	9.5 ± 1.2	3.0 ± 2.7		13
Group IV (11 species)					
Sh	*Aeschynomene nivea*	5.1 ± 1.3	5.5 ± 2.4	11.7 ± 1.7	13
Tr	*Bursera odorata*	5.1 ± 2.1	7.1 ± 0.9	6.7 ± 0.9	15
Sh	*Castela peninsularis*	4.1 ± 1.6	5.8 ± 1.5		8
Sh	*Euphorbia californica*	6.2 ± 1.1	7.2 ± 1.5		13
Sh	*Jatropha cuneata*	7.5 ± 2.2	12.9 ± 6.9		10
Sh	*Krameria s. l.*	2.5 ± 1.1	4.9 ± 0.5	5.8 ± 1.2	6
Tr	*Olneya teosota*	5.6 ± 2.1	7.4 ± 2.5		9
Group V (18 species)					
Sh	*Coursetia glandulosa*	7.7 ± 1.4	3.6 ±1.2		7
Tr	*Esenbeckia flava*	7.6 ± 1.2	4.1 ± 1.6		9
Sh	*Haematoxylon brasiletto*	4.9 ± 2.3	7.1 ± 0.7		9
Sh	*Hyptis s. l.*	4.5 ± 1.2	6.8 ± 1.7	5.7 ± 1.6	9
Tr	*Lophocereus schottii*	2.2 ± 1.8	4.1 ± 1.6		5
Sh	*Mimosa brandegeei*	9.7 ± 3.1	6.4 ± 0.7	5.9 ± 1.8	12
Tr	*Pithecellobium confine*	7.6 ± 1.9	4.8 ± 1.2	6.6 ± 2.1	6
Group VI (40 species)					
Sh	*Acacia pacensis*		3.9 ± 1.2	4.3 ± 1.1	3
Sh	*Atamisquea emarginata*		4.0 ± 2.1	4.4 ± 1.1	5
Sh	*Fouquieria burragei*		3.9 ± 1.5	8.7 ± 2.1	4
Sh	*Haplopappus sonoriensis*	2.2 ± 1.4	2.2 ± 1.4	4.5 ± 1.7	3
Sh	*Larrea tridentata*		3.6 ± 1.5	9.6 ± 4.2	4
Tr	*Prosopis articulata*		6.3 ± 1.3		5
Sh	*Simmondsia chinensis*		2.8 ± 1.7	5.2 ± 3.1	4

moderately rocky environments (see Table 1).

Clusters I and II are formed by species with high RIV values that are widely and uniformly distributed in all the sampled locations. Group I is composed of widespread and dominant species including sarcocaulescent trees (*Bursera microphylla, Cyrtocarpa edulis* and *Jatropha cinerea*) and columnar cacti (*Pachycereus pringlei* and *Stenocereus thurberi*). Group II is formed by widespread but codominant species such as *Fouquieria diguetii* and *Lysiloma candida* with RIV values somewhat lower than those of Group I.

Cluster IV is heterogeneous. Most of the species (*i.a. Aeschynomene nivea, Olneya tesota* and *Bursera odorata*) have higher RIV values in SDSS than in CSCS, although in the desert communities the same species may appear with stunted growth and in dwarf form.

Cluster V is formed by plants that appear mostly in both CSCS and TDF and to some extent also in SDSS. This cluster appears to be nearly a replica of Cluster III but with lower RIV values.

Cluster VI is composed of species of low frequency of occurrence, mostly present in CSCS and SDSS. Of these species, most occur with higher RIV values in SDSS than in CSCS (*Larrea tridentata*, *Atamisquea emarginata* and *Simmondsia chinensis*); they are typical Sonoran Desert species.

Vegetation structure also differed significantly between TDF, CSCS and SDSS. Plants in TDF were higher, denser, and their canopy size was larger, while plants in SDSS were shorter, less dense, and had smaller canopies. The CSCS showed intermediate characteristics.

Conclusions

The Cape Sarcocaulescent Shrubland vegetation is different from sarcocaulescent shrublands of the more northern zones of the Baja Californica peninsula, where Sonoran Desert floristic affinities prevail. The floristic composition of CSCS is rich in species with dry-tropical affinities, its species richness is higher. The type is homogeneous in its species content and turnover, and it is denser and has a higher canopy than the northern desert shrublands. In conclusion, the boundary line separating the Cape sediments of granitic origin from the basalt-derived sediments of the Sierra de la Giganta to the north should be used as an easily identifiable landscape characteristic to delimitate this unique community.

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Plants as indicators of the conservation value of Danish beech forests

Mark, Susanne[1*] & Lawesson, Jonas E.[2]

[1*]*National Environmental Research Institute, Department of Coastal Zone Ecology, Grenåvej 12, DK-8410 Rønde, Denmark;* [2]*Department of Systematic Botany, Århus University, Nordlandsvej 68, DK-8420 Risskov, Denmark;* **Fax +4589201415; E-mail s.mark@wildmail.com*

Abstract. High nature values in forests are usually associated with low management impact and long forest continuity. Indicators of such past and present conditions are useful for monitoring purposes, and much needed. We therefore sampled vegetation, soil parameters, structural parameters and forest management factors, at the compartment level, in 31 representative locations in Denmark, including both managed and unmanaged forests. Indicator species were identified by comparing managed and untouched forest, by Canonical Correspondence Analysis, and tree-based modelling, each method relating nature values to species occurrences. Altogether, 22 indicators of high conservation value and 27 indicators of low value emerged from the analyses, partly in accordance with other studies of indicators of ancient forest or natural forest. The results support views that the suitability of an indicator species varies with respect to regions and methodology (type of forests compared, inventory scale, etc.). The indicators identified in this study can be used to assess nature quality at the compartment level in Danish beech forests. Evaluations of forests as a whole also need to consider wet areas and gaps, as well as the spatial arrangement of the forest.

Keywords: Canonical Correspondence Analysis; Continuity; *Fagus sylvatica*; Forest management; Tree-based models.

Nomenclature: Mossberg et al. (1994).

Introduction

The conservation value of forests is usually associated with the degree of management impact and forest continuity (e.g. Kirby 1986). Forest management has been shown to have an impact on the ground vegetation (Peterken 1993), e.g. in terms of species richness (Feilberg 1993) or the species composition (Aude & Lawesson 1998). Different species compositions in relation to management regimes have been documented (e.g. Ohlson et al. 1997).

Some vascular plants have been shown to be more or less restricted to ancient woodlands (Peterken & Game 1984), and are used as indicators of such woodlands. Several authors have identified indicators of ancient woodland in various parts of Europe (see Wulf 1997 and references therein), and also in Denmark some plants are designated as indicators of ancient forest (Løjtnant 1996). However, few studies in Denmark are based on quantitative data, with some exceptions concerning some parts of the country (Petersen 1994; Lawesson et al. 1998). In fact, identification of indicators has only rarely involved statistical tests (see Wulf 1997). In many cases, subjective field observations are the basis for selection of an indicator species, and the species selected in this way are often rare, and statistically inappropriate. Instead, indicators among more common species are necessary to achieve a useful evaluation method.

The nature quality concept combines management and continuity factors so that forests with low management impact and long continuity have a high nature quality. We aim to identify indicators to be used to assess nature quality of *Fagus* forests at the compartment level. Fores edges, clearings, and gaps were not included in the study.

Methods

Field survey

The study was performed in Denmark which is situated in the temperate-nemoral zone, i.e. the natural forests are composed of deciduous tree species. The geomorphology is dominated by moraine soils, clayey or sandy, out-wash plains and a raised sea floor (Jacobsen 1989).

31 locations were chosen to represent major geomorphology. In each location, managed and untouched (minimally 5 yr) *Fagus* forests were sampled in July 1997, all on relatively well-drained soils. Altogether, 43 managed and 56 untouched study sites were investigated. A 400-m^2 sample plot was subjectively placed within each study site in homogeneous vegetation, in which a subplot of 4 m ×4 m was placed at random. Each subplot was divided into 16 small plots of 1 m^2. The frequency of each species in a sample plot was determined by presence/absence in the 16 small plots. Structural characteristics such as the amount of dead wood and the age distribution of the trees were also noted. Forest and stand ages were compiled from documents and personal communication, as was the period the stand had been untouched. Among the soil variables determined were: soil type, thickness of humus layer and A1-layer, pH, and clay content.

Identification of indicator species

Three methods were used for identifying indicator species: (1) comparison between managed and untouched plots; (2) Canonical Correspondence Analysis (CCA) using soil variables as covariables; and (3) tree-based models. Species indicating forests of high conservation value (= HQ-indicators) and species indicating forests of low conservation value (= LQ-indicators) were identified.

Method 1. Species occurring much more often in managed or untouched plots were identified. Presence/absence data were used and species selected which occurred more than 5 ×, giving a pool of 63 species. Species occurring at least twice as often in untouched as in managed plots were chosen as HQ-indicators. Species for which the reverse was found were chosen as LQ-indicators. In addition, species were marked HQ or LQ if they, when present (at least 9 ×), occurred with a frequency at least twice as high in untouched and managed forests, respectively. This rendered a pool of 42 species.

Method 2: CCA was performed using CANOCO version 3.12 (ter Braak 1991) with the most important soil variables as covariables and with conservation value-related variables as constraining variables (Jongman et al. 1987). For this analysis, the explanatory variables were transformed, if needed, and standardized. Only species occurring more than 5 × were used, giving a pool of 63 species. The most important soil variables were determined by forward selection CCA (pH, soil type, humus and A1-layer and clay content). The conservation value-related variables (constraining variables) used in the analysis were forest continuity, stand age and untouchedness, age distribution and amount of dead wood. Default options in CANOCO were used, with the exception that sample scores were weighted mean species scores. A joint plot of species and environmental variables was constructed using CanoDraw 3.0 (Šmilauer 1992). Species with projection points at extreme locations in the diagram were appointed as indicator species (delineation arbitrarily drawn at axes units ± 1).

Method 3: Tree-based modelling was done using S-Plus version 4.0 (Anon. 1995). These models use binary recursive partitioning, whereby a data set is successively split into more and more homogeneous subsets (Chambers & Hastie 1993). A binary tree sequence is constructed using the splits. Deviance measures at each node report how heterogeneous the node is. A conservation value was assigned to each sample plot on the basis of management and continuity of the forest. This variable was used as response variable and the species data as predictor variables. Only species occurring more than 9 × were included, rendering a pool of 42 species, and presence/absence as well as abundance data were applied. The species used to split the data set were appointed as indicators.

Results

Method 1: On the basis of presence/absence data, four HQ- and 15 LQ-indicator species were found, on the basis of abundance data, seven HQ- and five LQ-indicators (Table 1). *Method 2*: In the CCA, the projection points of species onto environmental vectors suggested 15 HQ- and 14 LQ-indicators (Table 1). Total inertia of the data set was 9.53 and the variation explained by the CCA was 8%. *Method 3*: In the tree based modelling, the presence/absence data resulted in four HQ- and five LQ-indicators (Table 1). The abundance data resulted in four HQ- and six LQ-indicators (Table 1, see Fig. 1).

In total, 22 HQ-indicator species and 27 LQ-indicator species were detected by the analyses. Most of these species were detected by only one method (14 HQ- and 17 LQ-indicators), several by two methods (8 HQ- and 8 LQ-indicators), but only two (LQ-indicators) by all three methods. Of the 22 HQ-indicator species 10 were found as such in other studies, of the 27 LQ-indicators 12 were also in accordance with others.

Table 1. Conservation value indicators for Danish beech forests, obtained by three methods (1, 2 and 3; see Text); s = sapling. High value indicators are indicated with +, low with ÷; p = presence/absence data, a = abundance data. ? = methods gave conflicting results. ↑ = indicators supported by other studies; ↓ indicators in conflict with other studies; references are given at the bottom.

	Method					Other studies[÷]
	1		2	3		
Species*	p	a	a	p	a	
Actaea spicata	+		+			↑ Lø, H
Agrostis capillaris		+				
Bromus ramosus	+	+	+			↑ Lø, H
Calamagrostis arundinacea			+			↑ L(anc), Lø
Dryopteris dilatata	÷	+	+			
Dryopteris filix-mas				+	+	
Fraxinus excelsior (s)			+	+	+	↓ L(old)
Galium saxatile			+			
Hedera helix			+			↓ PG(rec)
Hordelymus europaeus					+	↑ Lø, Pe, R, H
Ilex aquifolium		+				↑ L(anc)
Lonicera periclymenum	+		+			↑ PG(und)
Lonicera xylosteum	+					
Maianthemum bifolium		+	+			↑ P, H
Prunus avium			+			
Quercus robur/Q. petraea (s)[1]		+	+			↑ P(anc)
Rubus idaeus					+	↓ PG(rec)
Sambucus nigra			+			↓ L(old)
Scrophularia nodosa			+			↑ PG(anc), W
Sorbus aucuparia		+	+			↓ L(old)
Stellaria holostea				+		↑ PG(anc)
Trientalis europaea			+	+		
Acer pseudoplatanus (s)				÷		
Athyrium filix-femina		÷				↑ L(old), ↓ H
Carex pilulifera	÷	÷		÷	÷	
Carex remota	÷		÷	÷	÷	↓ P, PG(anc), W, H
Dactylis glomerata ssp. *lobata*		÷	÷			↑ PG(rec)
Dactylis glomerata ssp. *glomerata*	÷		÷		÷	↑ PG(rec)
Deschampsia flexuosa	÷					↑ PG(rec)
Epilobium angustifolium	÷					
Fagus sylvatica (s)					÷	
Galeopsis bifida/G. tetrahit[2]	÷					↑ PG(rec)
Galium aparine		÷	÷			↑ PG(rec)
Geranium robertianum			÷			↑ PG(rec)
Gymnocarpium dryopteris	÷		÷			↓ L(anc)
Juncus effusus	÷		÷			↑ PG(dis)
Lapsana communis			÷	÷		
Luzula multiflora	÷					
Luzula sylvatica	÷					↓ L(anc), Lø, Pe, P, PG(anc), H
Melica uniflora					÷	↓ P, PG(anc), W, H
Milium effusum				÷	÷	↑ L(old), ↓ P, PG(anc), H
Moehringia trinervia			÷			↑ PG(rec), R(v)
Mycelis muralis			÷			
Picea abies (s)	÷					
Polygonatum multiflorum	÷					↑ L(old), ↓ Pe, H
Stellaria nemorum ssp. *nemorum*			÷			
Taraxacum spec.[3]			÷			
Urtica dioica	÷	÷	÷			↑ PG(rec)
Veronica officinalis	÷		÷			↓ PG(anc)

*: For two species not shown in the table, *Dentaria bulbifera* and *Rubus plicatus*, the methods gave opposing results.

[1] Saplings of either species, [2] Either species, [3] Specimens not identified at the species level.

[÷] Sources: H = Hermy (1994): ancient woodland species, Europe. L = Lawesson et al. (1998): anc = ancient forest species, old = old forest species (ca. 100-200 yr.), Denmark. Lø = Løjtnant (1996): indicators of old natural forest, Denmark. P = Peterken (1974): primary forest species, England. Pe = Petersen (1994): ancient woodland indicators, Denmark. PG = Peterken & Game (1984): anc: ancient woodland species; rec: recent woodland species; und: undisturbed woodland-species; dis: species found in areas of disturbance, England. R = Rackham (1980): s: strong association with ancient woodland; v: variable association, England. W = Wulf (1997): ancient woodland species, Germany.

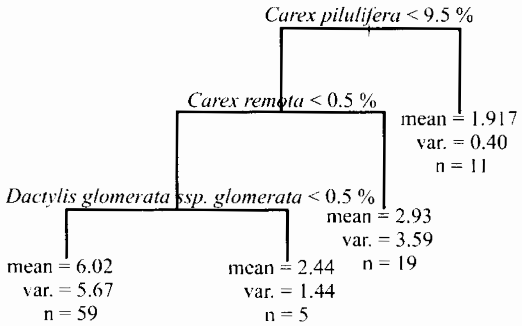

Fig. 1. Tree model showing the species (with abundance values) used to separate plots of different conservation value into more homogeneous groups. At each end node, the average conservation value is given (mean), along with the group variance (var.) and number of plots in the group (*n*). The tree should be read thus: If *Carex pilulifera* is found with abundance > 9.5%, we move to the right, into a group with a mean conservation value of 1.9. If not, we continue along the left side of the tree, and check for the abundance of *Carex remota*, etc. Initially, a 14-node tree was drawn, but after cross-validation (Chambers & Hastie 1993), a 4-node tree was suggested. A similar tree was drawn using presence/absence data.

Discussion

Many of the indicator species identified in this study are listed in the literature as such (Table 1), i.e. 22 out of 49, or 45%. Our study shows that indicator species detected in one country may not have been identified as such in other regions. Although there is a good agreement for many species between our findings and similar studies in the UK and Western Europe, the opposite is the case for other species. Still, in only 10 cases (20%) our detection is contradicted in any of the sources included. For 17 species (35%) there are no data available in the reference literature. This is remarkable since most of them are common forest species. On the other hand, 14 of them were detected by only one of our methods.

There are 10 HQ-indicator species which are previously mentioned as ancient forest indicators, indicators of old natural forest, or undisturbed forest (Table 1). Especially, *Actaea spicata*, *Bromus ramosus*, *Hordelymus europaeus*, *Ilex aquifolium*, *Maianthemum bifolium* and *Scrophularia nodosa* appear to have a wide applicability. Some of the LQ-indicator species are mentioned as 'old forest species' in Lawesson et al. (1998), i.e. forests aged 100-200 yr, but not 'ancient forests', and as 'recent forest species' in Peterken & Game (1984). These species may thus have a more general significance as LQ-indicator species. Six species, however, which we consider LQ-indicators in the present study, are found to be ancient woodland indicators in other countries, while two HQ-indicators are considered recent forest species by others (see Table 1).

Some species are known to have different ecological optima in different parts of their distribution area (see Diekmann & Lawesson 1999). There are clear phytosociological differences between beech forests in Europe, and some species with a northern distribution may be good indicators in Denmark, but do not occur in forests further south. This means that there are different interaction patterns between species, e.g. the competitive environment, which may lead to different indicator characteristics. Indicator species found in Denmark are therefore likely to be used best in this country only.

Two of the LQ-indicators in our study, *Gymnocarpium dryopteris* and *Luzula sylvatica*, were listed by Lawesson et al. (1998) as ancient forest species for Danish beech forests in eastern Jylland. Webster & Kirby (1988) noted that even within a country, species that are restricted to ancient forests in one region, are not necessarily so in other regions. Local differences in the interplay between management, soil and species colonization abilities could explain the observed results in that case. In the present case, however, the geographical areas covered in our study and in Lawesson et al. (1998) are overlapping, and further explanations are needed. Although regional and historical differences still may play a role, the differences observed may be related to the management regime, which is part of our conservation value concept; both species are found more often in managed forests.

An aspect not considered in this study, is the spatial arrangement of the forests. It is well known that for recent forests, the distance to ancient forests can be of major importance for species composition (e.g. Dzwonko & Loster 1992). Another aspect not included in this study is the effect of forest area. The positive correlation between forest area and species number has been reported in many studies (e.g. Zacharias & Brandes 1990 and references therein) although Lawesson et al. (1998) show that after the total species number is corrected for area, the smaller Danish forests tend to have higher diversity values. Fragmentation, rather than dispersibility could explain these latter results. Both aspects need also to be considered in evaluation of conservation values.

In conclusion, the use and comparison of indicators species for conservation value should be in close agreement with the way that they were identified. The indicators identified in the present study can be used to evaluate the nature quality across time or space in beech forest compartments in Denmark, but it is important to note that an evaluation of the entire forest also must include wet areas, gaps etc. Furthermore, a validation of the indicators is needed. With these indicators, however, any compartment could be evaluated, even if none of the rarer ancient woodland or forest indicator species are present. Another potential advantage lies in the use of LQ-indicators. With the registration of these species it should be possible to monitor unwanted disturbance effects more rapidly than if changes in the HQ-indicator species need to be awaited.

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Vegetation patterns on the stabilized sands of Doñana Biological Reserve

**Muñoz-Reinoso, José Carlos*
& García Novo, Francisco**

Dpto. de Biología Vegetal y Ecología, Universidad de Sevilla, Apdo. 1095, E-41080-Sevilla, Spain;
**Fax +3454626308; E-mail reinoso@cica.es*

Abstract. The spatial pattern of the vegetation of the Doñana Biological Reserve has been studied along a 10.5 km topographic gradient. Split Moving Window Boundary Analysis was used to identify boundaries between plant communities. The detection of these boundaries, together with the analysis of plant species composition, soil, water availability and topography allowed the identification of three different vegetation zones: (1) homogeneous zone, (2) ecocline and (3) ecotone. Based on the results of our analysis, a new model for shrub vegetation of the stabilized sands of Doñana Biological Reserve is proposed. The geomorphology exerts a multi-level control of vegetation patterns mediated through soil water supply. Water availability controls the vegetation (1) on a local scale, along the fixed dune slopes, opposing the dry dune ridges with xerophytic shrub to the slacks with hygrophytic shrub; (2) on a mesoscale, distinguishing two dune episodes (West and Central Sectors) with different altitudes, dominated by poikilohydric xerophytes and stenohydric xerophytes, respectively; and (3) on a regional scale, distinguishing the discharge zone of the regional aquifer, covered by shrubland with a low plant diversity.

Keywords: Diversity; Ecocline; Ecotone; Split moving window; Vegetation pattern.

Nomenclature: Valdés et al. (1987).

Introduction

The stabilized sands of Doñana Biological Reserve (DBR) represent a wide transition between the recharge and the discharge areas of the Almonte-Marismas aquifer. The Doñana ecosystems largely depend on the groundwater flows of this regional aquifer (Anon. 1983). The early studies of plant ecology in the stabilized sands of Doñana were carried out in the early 1970s by González Bernáldez and co-workers who developed the first vegetation model (González Bernáldez et al. 1971; Ramírez Díaz 1973). In this small scale model, the plant composition closely reflects local topography due to different soil water availability in summer, with xerophytic shrub on the (dry) old dune-ridges and heathlands on the (wet) slacks.

The extrapolation of this vegetation model to the whole DBR was published as the Ecological Map of DBR (Allier et al. 1974). In the map, three broad vegetation zones were distinguished in the stabilized sands: a western zone (*naves*) with a higher altitude and covered by xerophytic vegetation; an eastern zone dominated by hygrophytic vegetation; and easternmost, a transitional fringe (*vera*) between the sands and the marshes, covered by grassland. However, the vegetation patterns observed at DBR do not fit this coarse schematic division.

The aim of this contribution is to study the mesoscale spatial pattern of DBR vegetation and to discern whether the processes determining the vegetation patterns at different scales are similar or change with the scale of observation (Allen & Starr 1982; Wiens 1989; Reed et al. 1993).

Study area

In the Doñana National Park (SW Spain), four main landscape units were traditionally distinguished: inland marshes, mobile dunes, stabilized sands, and transition between the sands and the marshes (García Novo 1979). Within the limits of the Park , the DBR (6794 ha) is the core area; it includes the main representative ecosystems and enjoys the highest degree of protection. This work is focused on the stabilized sands.

Doñana has a Mediterranean type climate. The average annual temperature is 16.8 °C, the coldest months are December and January with mean temperatures just below 10 °C. Summer temperatures average 24 °C in July and August. Mean annual precipitation is 560 mm, but there are drier and wetter periods which may last several years. 80 % of the precipitation is concentrated from October to March with a maximum in November and December. In the summer (July, August), rains are scarce. Potential evapotranspiration is ca. 800 mm. The summer water shortage strongly affects the plant composition on the sandy soils.

The sandy soils are poorly developed due to the quarzitic nature of the substrate and correspond to the entisols and inceptisols types (Siljeström et al. 1994). The stabilized sands of Doñana exhibit a rolling topography due to the old dune morphology. Several episodes of dune movement can be distinguished (Rodríguez-Ramírez et al. 1996). The vegetation is largely dominated by Mediterranean shrubland with pine plantations, remnants of original forests and grasslands. The shrub composition follows the local topography, with species of *Cistaceae* and *Lamiaceae* such as *Cistus libanotis*, *Halimium commutatum*, *Rosmarinus officinalis* and *Lavandula stoechas* in the drier areas, and *Ericaceae* such as *Erica scoparia*, *E. ciliaris* and *Calluna vulgaris* in the wetter parts (García Novo 1979; Rivas Martínez et al. 1980).

Material and Methods

A 10.5 km long W-E transect was established in the DBR along a topographic gradient (from 40 to 4 m a.s.l.), crossing several ancient dune fields. 105 plots were located at 100-m intervals along the transect. At each plot, the cover of woody species was measured along a 30 m line perpendicular to the transect. A matrix of 105 plots × 32 woody species was analysed in order to detect boundaries between communities using the Split Moving Window Boundary Analysis

(Ludwig & Cornelius 1987; Cornelius & Reynolds 1991). This method allows identification of boundaries along transects and thereby different vegetation zones through the calculation of metric dissimilarities between adjacent groups of plots. Chord distance was used as the metric dissimilarity measure between adjacent groups of plots. The scale-dependency of the dissimilarity values was reduced by pooling the information from several scales (window sizes 4, 6, 8, 10 and 12), since the locations of peaks in a pooled dissimilarity profile are relatively scale-independent compared to the dissimilarity profiles at each window size. Previously the dissimilarity values from each window size were standardized using Monte Carlo simulation techniques according to Cornelius & Reynolds (1991). In the average Z-score (standardized variable) graph, the peaks extending above the mean plus 1 standard deviation were considered potential boundaries between plant communities, and further tested by Multi-response permutation procedures (Mielke 1991).

After vegetation boundaries have been located, plant diversity (expressed as species richness and Shannon diversity index) and the environmental variables were analysed within each zone. The screened environmental variables comprise: topography, water table depth, soil characteristics (pH, electric conductivity, soil texture and nutrient status).

Results

Dissimilarity profiles from small window sizes (4, 6) were more noisy than those from large ones, some peaks being prominent at all window sizes. The SMW analysis suggests the presence of seven significant boundaries separating eight vegetation zones (Fig. 1, panel A), whose species composition is shown in Table 1. Similar soil conductivity and pH values (Fig. 1, panel B), along with information about their common historical management (Granados Corona et al. 1988) and succession processes (Allier et al. 1974; Rivas Martínez et al. 1980), prompted to lump the first four vegetation zones (plots 1 - 48). The vegetation of this zone was dominated by *Rosmarinus officinalis* (19.6 %), with *Pinus pinea* (12.9 %), *Juniperus phoenicea* (12.6 %), *Halimium halimifolium* (10.9 %) and *H. commutatum* (9.7 %). This species composition is known to have resulted from repeated disturbances of the original juniper forest through logging, overgrazing, shifting cultivation, fires and, lately, pine plantation (Granados Corona et al. 1988).

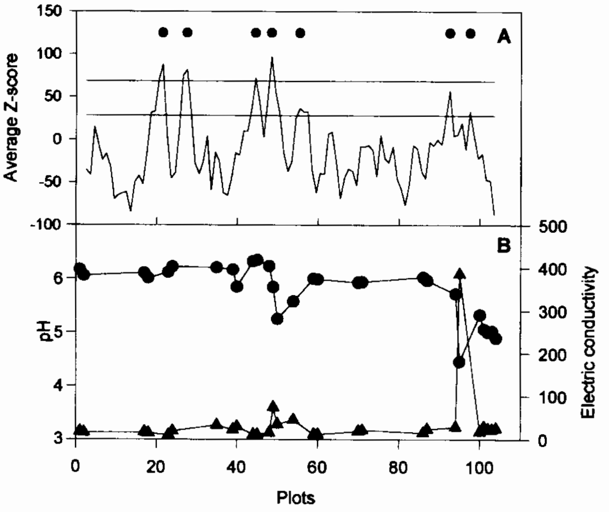

Fig. 1. Average Z-score (standardized variable) of window sizes 4 - 12, points show significant boundaries (**A**). Values of pH and electric conductivity (mS/cm) in several plots of the transect (**B**).

Table 1. Species composition (% cover of the main species) of the eight zones detected . Key to abbreviations:

Rof = *Rosmarinus officinalis*
Hha = *Halimium halimifolium*
Hco = *H. commutatum*
Jph = *Juniperus phoenicea*
Cli = *Cistus libanotis*
Ppi = *Pinus pinea*
Esc = *Erica scoparia*
Uau = *Ulex australis*
Phi = *Phillyrea angustifolia*.

Plots	*Rof*	*Hha*	*Hco*	*Jph*	*Cli*	*Ppi*	*Esc*	*Uau*	*Phi*
1 - 21	27.6	15.1	10.9	0.0	8.4	0.0	4.5	3.0	8.4
22 - 27	9.4	7.9	3.8	56.9	13.6	0.0	0.5	0.1	0.0
28 - 44	16.0	8.1	9.4	2.3	5.4	36.6	8.3	3.1	1.2
45 - 48	8.9	5.6	13.5	56.2	5.2	0.0	0.5	0.0	0.0
49 - 55	6.1	8.5	4.5	0.1	0.8	0.0	36.5	11.9	5.6
56 - 92	15.1	31.3	2.6	0.0	6.0	0.0	11.9	9.5	0.2
93 - 97	6.9	11.1	1.6	0.0	0.0	0.0	38.3	12.8	7.7
98 - 105	0.0	27.8	4.1	0.0	0.0	0.0	10.0	55.4	0.9

Species composition and environmental variables of the five resulting vegetation zones (Table 2) seem to show three large stretches of shrub (plots 1 - 48, 56 - 92 and 98 - 105), which will be addressed as West, Central and East Sectors, respectively, separated by heathlands (plots 49 - 55 and 93 - 97). In the heathlands more water and nutrients were available.

There was a noticeable drop in plant diversity among the detected sectors along the transect. The lowest diversity values were found in the East Sector, with 12 species and a value of 1.40 for the Shannon index.

Discussion

There is a W-E gradient of increasing soil water availability along the transect (Table 2). However, the heathlands do not cluster in the wetter part of the gradient as predicted by the topographic model of González Bernáldez. Rather, it is in those areas where groundwater discharges in which heathlands occur, regardless their absolute elevation. Furthermore, the strongest water-table fluctuations take place in the East Sector, close to the transition to the marshes. These fluctuations seem to be related to discharges of the regional aquifer (Muñoz Reinoso 1997). In this zone, due to the above-mentioned hydrological processes, pH values were lower and a soil iron accumulation developed (Siljeström et al. 1994).

Merino et al. (1976) identified three different types of ecophysiological responses to water stress in the shrub

Table 2. Environmental data and diversity values of the five final vegetation zones. EC = electric conductivity. N = nitrogen, P = phosphorous; K = potassium; Fe = iron; WTD = water table depth in July 1994; WTF = water table fluctuations between March and September 1994; *S* = species richness; *H'* = Shannon diversity index.

Plots	pH	EC (mS/cm)	N (%)	P (ppm)	K (ppm)	Fe (ppm)	C org. (%)	WTF (m)	WTD (m)	*S*	*H'*
1 - 48	6.15	18.3	0.039	3.52	6.4	12.4	0.44	0.36	4.52	24	2.47
49 - 55	5.56	53.0	0.113	3.08	13.3	338.3	1.83	0.40	2.35	25	2.28
56 - 92	5.98	17.4	0.041	2.08	6.3	16.0	0.45	0.46	2.18	22	2.19
93 - 97	5.09	207.4	0.110	5.63	12.0	317.5	2.13	0.37	1.69	18	2.13
98 - 105	5.06	22.3	0.045	2.88	6.8	36.9	0.48	0.56	1.41	12	1.40

vegetation of DBR: poikilohydric xerophytes, stenohydric xerophytes, and stenohydric hygrophytes. According to this classification, the shrubs of the West Sector (plots 1-48), such as *Rosmarinus officinalis* and *Cistus libanotis*, belong to poikilohydric xerophytes. The Central Sector (plots 56 - 92) is dominated by the stenohydric xerophytic shrub *Halimium halimifolium* and shows an increased occurrence of the stenohydric hygrophytic shrub *Erica scoparia*. The East Sector (plots 98 - 105), with the shallowest water-table and the wider water-table fluctuations is dominated by *Halimium halimifolium* and *Ulex australis*. The heavy browsing in the latter zone by game such as red deer (Braza et al. 1984; Braza & Alvarez 1987) may favour thorny *Ulex australis* and species with ability to response to predation such as *Halimium halimifolium* (Aguilar et al. 1996).

The geomorphology plays an important role in this vegetation pattern as is summarized in Fig. 2. Those three vegetation sectors seem to match different dune building episodes (Rodríguez-Ramírez et al. 1996) each resulting in a general, distinct elevation. In the transitions between those dune episodes, groundwater discharge takes place, and the sands become covered by heathland.

Three sectors may be classified as (1) homogeneous zone (West Sector, plots 1-48) with a deep water table, and where the observed differences in species composition in this zone are due to historical management, (2) ecocline (Central Sector, plots 56 - 92), with a gradual descent in elevation and increasing water availability, and (3) ecotone (East Sector, plots 98 - 105) influenced by important environmental (biotic and abiotic) stresses. The East Sector may be addressed as a *limes convergens* (van Leeuwen 1966), an ecotone *sensu stricto* (*sensu* van der Maarel 1976, 1990), and as an *asymmetric boundary* (Margalef 1982). This sector is a stress zone, controlled by strong water table fluctuations, iron accumulation, low pH, heavy browsing, and showing low plant diversity. It is between two plant communities at different stages of ecological succession.

Soil-water availability determines the vegetation patterns in the stabilized sands (Gonzalez Bernáldez et al. 1971; Allier et al. 1974; García Novo et al. 1996) and controls the patterns in different ways at different scales (Allen & Starr 1982; Wiens 1989; Reed et al. 1993). The water availability seems to control vegetation at three different scales (Fig. 2), namely (1) on a small scale (10 - 10^2 m), distinguishing dune ridges with xerophytic shrub from slacks with hygrophytic shrub; (2) on a mesoscale (10^2 - 10^3 m),

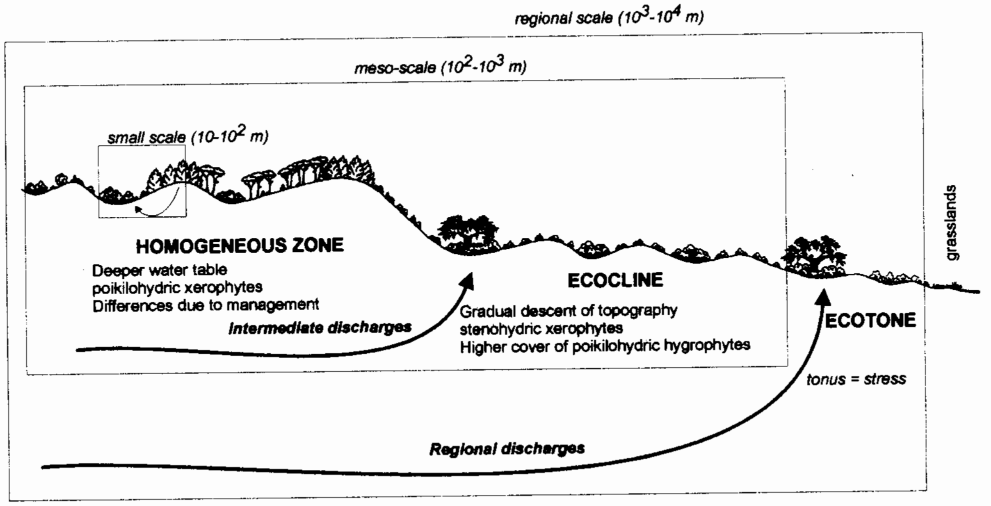

Fig. 2. Proposed vegetation model for the stabilized sands of the Doñana Biological Reserve. Water availability controls the vegetation at three different scales (local scale, mesoscale and regional scale) and allows the identification of three different zones: a homogeneous zone, an ecocline and an ecotone.

which tells apart the western and the eastern Sectors, the first dominated by poikilohydric xerophytes, and the second characterized by stenohydric xerophytes and a higher occurrence of stenohydric hygrophytes; and (3) on a regional scale (> 10^3 m), distinguishing the transitional shrubland on the discharge zone of the regional aquifer.

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Floristic composition of basiphilous scrub communities related to a rainfall gradient in Navarra

Olano, J.M.[1]*, Peralta, J.[2], Donézar, M.[3] & Osácar, C.[3]

[1]*Departamento de Ciencias Aroforestales, Escuela Universitaria de Ingenierías Agrarias, Los Pajaritos s/n, E-4200 Soria, Spain,* [2]*Departamento de Ciencias del Medio Natural, Universidad Publica de Navarra, E-31006 Pamplona, Spain;* [3]*Servicio de Estructuras Agrarias, Gobierno de Navarra, E-31011 Pamplona, Spain;*
**Fax +34975233160; E-mail jmolano@agro.uva.es*

Abstract. The relation between the species composition of scrub vegetation and a rainfall gradient was analysed by means of a Fuzzy Set Ordination (FSO). Apparent rainfall explained 68.9% of the actual rainfall. Thermicity and aspect were significantly correlated with the residuals of the regression between apparent and actual rainfall. Logistic models were used to estimate the response of a selected group of species to the apparent rainfall. The different resulting patterns and their relations with the distribution pattern of the species are discussed.

Keywords: Distribution pattern; Eurosiberian-Mediterranean boundary; Fuzzy Set Ordination (FSO); Logistic regression model; Spain.

Nomenclature: Tutin et al. (1964-1981) for plants; Loidi et al. (1997b) for syntaxonomical nomenclature.

Introduction

A rainfall gradient is claimed to be the main factor affecting vegetation variation in the Ebro Basin (Rivas-Martínez et al. 1991; Loidi et al. 1997b). Navarra (Northern Spain) is located in the western part of the Ebro Basin where there is a steep gradient from 1600 mm/yr in the Cantabrian Mountains and Pyrenees in the north to 400 mm/yr in the vicinity of the Ebro River, along a distance of 100 km. This rainfall gradient follows a NW- SE gradient related to the transition from temperate climate with weak summer drought to Mediterranean climate with heavy summer drought (Rivas-Martínez 1996a, b).

Different approaches have been accomplished to link the vegetation distribution with climatic factors. Some authors have related individual species to climatic parameters (e.g. Fernández-Palacios 1992), while others have worked at the community level (e.g. Moreno et al. 1990; Retuerto & Carballeira 1992; Escudero & Pajarón 1994; Gavilán & Fernández-González 1997). Recent contributions applying fuzzy set theory to vegetation science (Roberts 1986; Zhang 1994; Boyce 1998; Olano et al. 1998) provide a tool to relate vegetation to climatic factors. We decided to use Fuzzy Set Ordination (FSO; Roberts 1986) in order to determine the effect of rainfall on basiphilous scrub vegetation in Navarra. These communities are usually located on shallow soils, being very sensitive to changes of rainfall conditions.

The scrub vegetation is widespread throughout the study area, usually as substitution stage of the potential natural vegetation: deciduous broad-leaved forests (*Querco-Fagetea*) or evergreen broad-leaved sclerophyllous forests (*Quercetea ilicis*). Syntaxonomically, these scrub communities belong to three main types (Anon. 1991; Loidi et al. 1997a), such as the Pyreneo-Cantabrian cushion-heathland often dominated by *Genista hispanica* ssp. *occidentalis, Genistion occidentalis, Ononidetalia striatae*), Western Mesomediterranean calcicolous garrigues with *Rosmarinus officinalis* (*Sideritido-Salvion lavandulifoliae, Rosmarinetalia*), and Supra-mesomediterranean pre-Pyrenean garrigues with *Genista hispanica* ssp. *hispanica* (*Aphyllanthion, Rosmarinetalia*).

The aim of this work is studying the response of the main species of these communities to the rainfall gradient and to use FSO as a tool to assess the influence of topographic factors on this pattern.

Material and Methods

Floristic data were collected on 252 plots distributed over 3500 km^2 of Central Navarra during 1995-1997. Plot size was 9 m^2, species cover/abundance was estimated according to the Braun-Blanquet scale and data on slope, altitude, aspect and parent rock material were also collected. Local annual rainfall for every sample plot was estimated by overlay of plot locations on a precipitation map (Creus 1986).

Relevés were submitted to Fuzzy Set Ordination with total annual rainfall as environmental variable, following the technique described by Roberts (1996) and Boyce (1998). In this technique a similarity matrix is calculated for the data. Afterwards a series of algorithms are computed (see above references for full detail) to calculate the apparent rainfall of each relevé depending on its similarity to wetter and drier relevés. This value provides an estimate of the rainfall based on species composition. FSO was applied to two different matrices: in the first matrix data were transformed to presence-absence (P/A), while in the second matrix Braun-Blanquet cover/abundance values were transformed to a 1 -6 scale. In both cases data were normalized by relevé. As a result of this analysis values ranging from 0 to 1 were obtained indicating apparent rainfall. Both values for apparent rainfall were regressed on actual rainfall. As the P/A matrix showed a better fit with actual rainfall, this value was taken in the subsequent analysis. For each different class of actual rainfall, Spearman rank correlations between residuals of the regression and environmental data (slope, aspect, altitude and thermicity) were calculated. Thermicity is a variable resulting from the combination of aspect and slope:

$$\text{thermicity} = -\cos(\text{aspect}) \times \sin(\text{slope}). \qquad (1)$$

Probability of occurrence by means of logistic regression (ter Braak & Looman 1986) was calculated in order to analyse species preferences.

Results

Actual rainfall class *vs.* apparent rainfall regression showed very high coefficients of determination (R^2), 0.610 for the matrix with cover values and 0.689 for the P/A matrix (Fig. 1), $p < 0.0001$ for both regressions. As estimates for apparent rainfall were highly correlated ($r = 0.949$) only apparent rainfall for P/A matrix was used in further calculations.

Spearman rank correlation (Table 1) showed that aspect and thermicity explained most of the variation, but not at the extreme rainfall classes. Although for the wettest sites the probability was close to significance, for the driest sites p was > 0.6. Altitude is only significant for the rainfall class of 600 mm/yr, whereas slope is not significant for any rainfall class.

Fig. 2 shows the results of logistic regression models for 18 species selected according to their known phytosociological behaviour in the scrub communities considered. All of them are common in at least one of the three main types of scrub described above, and are not short-range endemics – they serve as characteristic species of alliances or higher syntaxonomical units as described by different authors (de Bolòs et al 1993; Loidi et al 1997a; Mucina 1997).

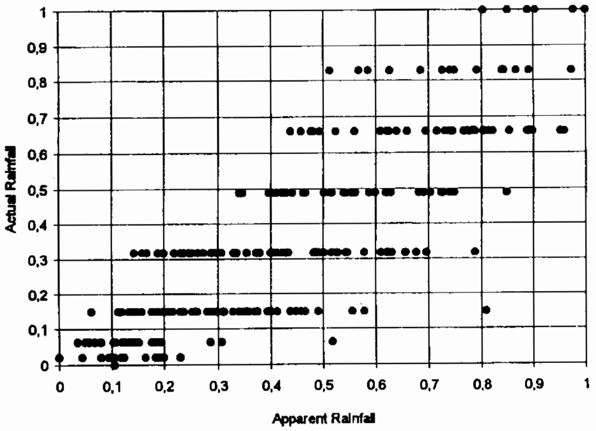

Fig. 1. Diagram showing the relation of apparent rainfall *vs.* actual rainfall. Note that actual rainfall values are given in classes.

Species response curves showed different patterns that can be grouped into four classes. The first (Fig. 2a) comprises species with an Atlantic or wide-European distribution common in temperate climate (chorological classification following de Bolós et al. 1993), these species, *Brachypodium pinnatum, Erica vagans* and *Genista hispanica* ssp. *occidentalis*), showed their optima in the upper apparent rainfall class or even outside the range considered. Where apparent rainfall decreased they were scarce. A second group (Fig 2b) is represented by those species which are absent or very rare at low rainfall classes but which are even rarer at higher precipitation levels. In this group two subpatterns could be noted, that of species which had optima in the middle of the gradient: *Avenula mirandana, Fumana procumbens* and *Linum appressum*, and that of taxa whose optima are displaced towards higher precipitation values: *Buxus sempervirens, Helictotrichon cantabricum* and *Potentilla neumanniana*. The first subgroup was formed by species of Mediterranean distribution (wide-Mediterranean, North-Mediterranean and also wide-European), while the second was related to plants with Submediterranean distribution. A third group (Fig. 2c) comprises species of wide-Mediterranean distribution: *Avenula bromoides, Brachypodium retusum, Genista scorpius* and *Thymus vulgaris*, very common in all types of Mediterranean scrub. They were rare or absent only where Mediterranean conditions disappear at the wettest sites of the gradient. The fourth group, with *Bupleurum frutescens, Fumana ericoides, F. thymifolia, Helianthemum rotundifolium* and *Rosmarinus officinalis*, includes taxa with optima at the driest sites, that are rarer with medium precipitation and are absent with higher amounts of rainfall (Fig. 2d). These are Mediterranean and Iberian and North African species that are restricted to the southern part of the studied area.

Discussion

According to the analysis, thermicity and aspect were the main factors explaining the difference between apparent and actual rainfall. On the other hand, altitude and slope did not seem to be very important to explain this difference. As may be expected, land form had a very important effect on

Table 1. Spearman rank correlation for each rainfall group between residuals of actual-apparent rainfall regression and slope, aspect, thermicity and altitude. *P* indicates significance probability and the numbers under each environmental variable indicates r_s.

Rainfall (mm)	*n*	Slope	*P*	Aspect	*P*	Thermicity	*P*	Altitude	*P*
450	15	0.071	0.080	−0.121	0.66	−0.130	0.645	−0.099	0.726
500	24	0.384	0.064	−0.632	0.001	−0.695	0.000	−0.400	0.053
600	62	−0.123	0.339	−0.540	0.000	−0.599	0.000	0.358	0.004
800	62	0.313	0.013	−0.542	0.000	−0.536	0.000	0.134	0.298
1000	31	0.093	0.617	−0.526	0.002	−0.536	0.002	0.156	0.403
1200	36	−0.013	0.938	−0.538	0.000	−0.579	0.000	0.280	0.098
1400	15	−0.035	0.911	−0.508	0.053	−0.471	0.077	−0.225	0.419

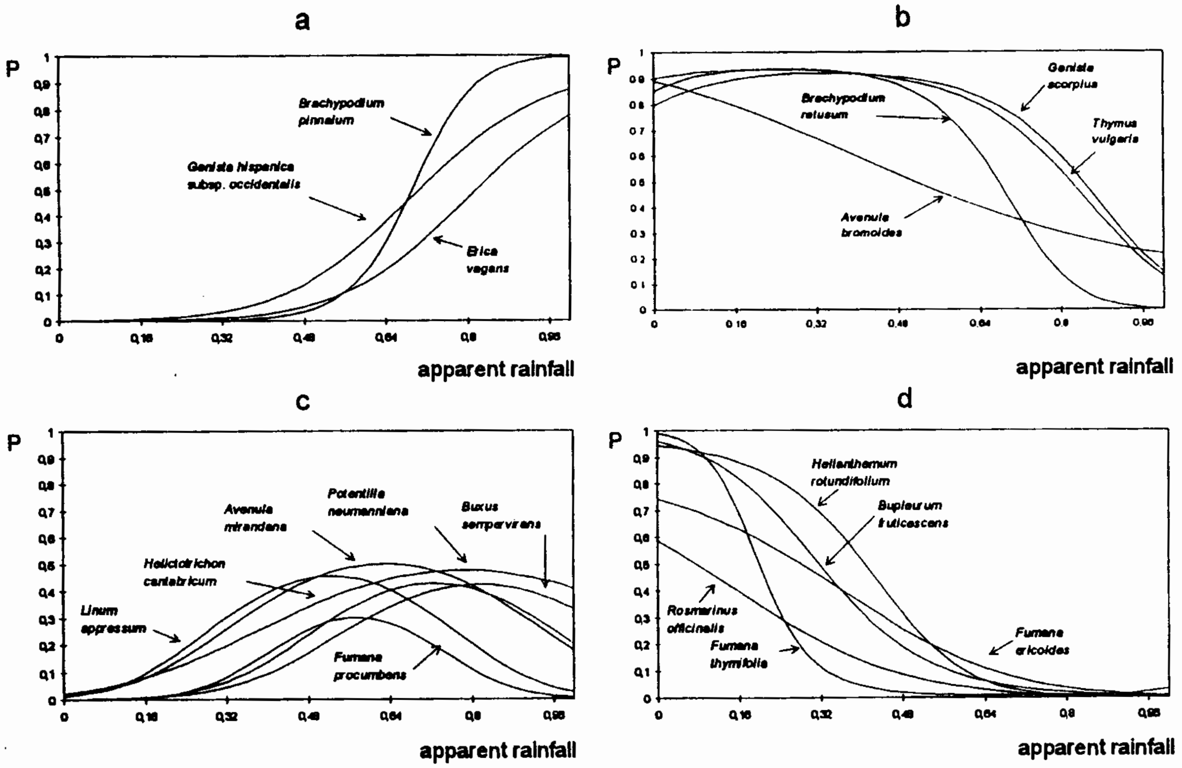

Fig. 2. Logistic models of 18 selected species; ordinate shows probability of occurrence and abscissa shows apparent rainfall (ranging from 0 to 1). **a.** Atlantic or wide-European species; ombroclimate subhumid or wetter. **b.** Wide-Mediterranean, North-Mediterranean, Submediterranean, wide-European species; ombroclimate upper-dry to subhumid. **c.** Wide-Mediterranean distribution species; ombroclimate dry to subhumid. **d.** Mediterranean and Ibero-Maghrebian species; ombroclimate dry.

ecosystem pattern (Swanson et al. 1988). This follows from the negative correlation of aspect and thermicity with the residuals of apparent/actual rainfall regression, with the southern and sunniest plots showing a lower apparent rainfall than the northern ones. Only for the extreme classes of actual rainfall this relation was not significant, especially for the lowest value (450 mm).

Fuzzy Set ordination appeared very sensitive to detect factors influencing water supplies for plants at two different scales. At a regional scale, rainfall amount determines water income rate, whereas at the local scale, land form (aspect and slope) modifies water availability by their influence on air and ground temperatures and evapo-transpiration rates. Taking into account edaphic parameters (soil depth, parent material) would be of interest in order to explain differences between actual and apparent rainfall.

The logistic models of species reflect the phytogeographical patterns recognized in regional surveys (Rivas-Martinez et al. 1991; Loidi et al. 1997a) although species in the rainfall gradient show a gradual replacement. The species replacement rates reflect the transition between two major European phytogeographical units – the Mediterranean and Eurosiberian Regions – in a geographically small area.

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Vegetation along the River Elegest in Tuva, Central Asia

Parschutina, Lyudmila P.

Komarov Botanical Institute, Russian Academy of Sciences, Popov St. 2, 197376 St. Petersburg, Russian Federation; Fax +78122344512; E-mail arid@TN4128.spb.edu

Abstract. Variation in vegetation types along the valley of the River Elegest from the source in the mountains to the river plain depends on such intrazonal factors as the valley fall (downward gradient of valley), pattern of sedimentation on the accumulation terrace, and water regime peculiarities. A description of the most typical communities of forests, meadows, swamps and steppes is presented. A fragment of a large-scale map of part of the valley of the River Elegest shows the vegetation pattern.

Keywords: Mapping; Mountain; Natural vegetation cover; River valley.

Nomenclature: Cerepanov (1995).

Introduction

Tuva is located in southern Siberia at the boundary of Russia and Mongolia in the geographical centre of Asia. The vegetation of the region is primarily determined by the vertical zonality due to the occurrence of several mountain ranges at altitudes from 520 to 3976 m. Studies of the vegetation of Tuva were undertaken by Krylov (1903), Shishkin (1914), Sobolevskaya (1950) and Kalinina (1957). However, these studies paid insufficient attention to the vegetation of the river valleys. From 1976 to 1982 the vegetation cover of Tuva was studied by researchers linked to the Central Siberian Botanical Garden, Novosibirsk (Koropachinskii 1985). I have participated in these studies, traversed the area and described and mapped the vegetation of the Elegest River valley. In 1997 the trip was repeated along the river valley; only insignificant changes in the vegetation were noticed. In this paper I want to present a brief account of vegetation the valley of the Elegest River.

Study area a field survey

The River Elegest is the largest left tributary of Ulug-Khem (Upper Enysei) with a length of ca. 180 km (Fig. 1). Its source is on the northern slope of the Tannu-Ola Range at an altitude of 2100 m and it flows into the Enysei 25 km west of Kyzil. The total altitudinal difference from source to estuary is 1540 m. The Elegest River is a typical mountain river for its upper and middle reaches, while in the lower part it flows through a 4-5 km wide valley. A flood plain terrace is virtually lacking (Klopova 1957). Floods are heavy but short. Soils are heavy with a gley horizon beneath, sometimes with seasonal permafrost resulting in the absence of drainage. The Elegest River valley bears many springs, brooks, and rivulets. All above-mentioned factors affect the composition and arrangement of vegetation consisting of a variety of natural ecosystems in Central Tuva and on the northern slope of Eastern Tannu-Ola. From the source to the confluence with the Ulug-Khem one can distinguish three parts in the Elegest valley differing in environmental conditions.

Vegetation description

The upper part from the source to the village of Ak-Tal (breadth 1-4 km) bears features of a trough. The fall of the riverbed reaches 10 m per km which has led to the prevalence of pebbles, gravel and coarse sands in the post-glacial river alluvium. These sediments are overlain by a 45-cm thick clay layer. The Elegest bed terrace is developed unevenly; comparatively well-developed segments alternate with patches without floodplain terrace or with narrow bands of course river alluvium (pebbles and cobbles). Such ecological diversity causes a variety of vegetation types.

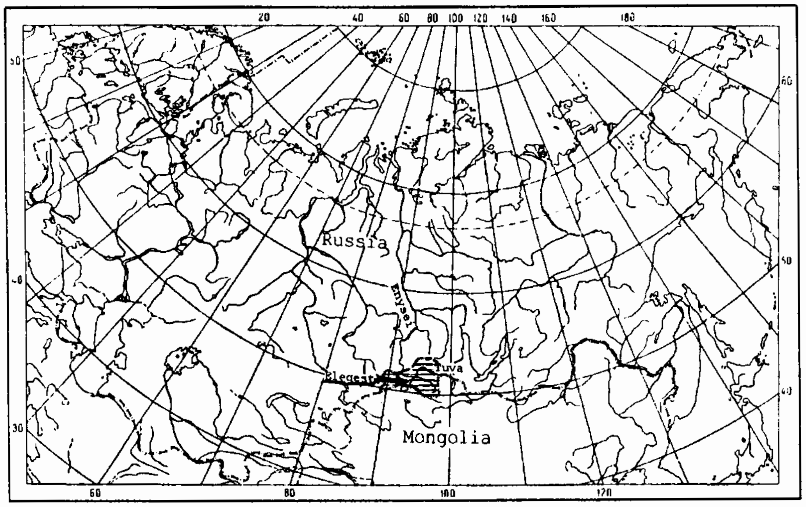
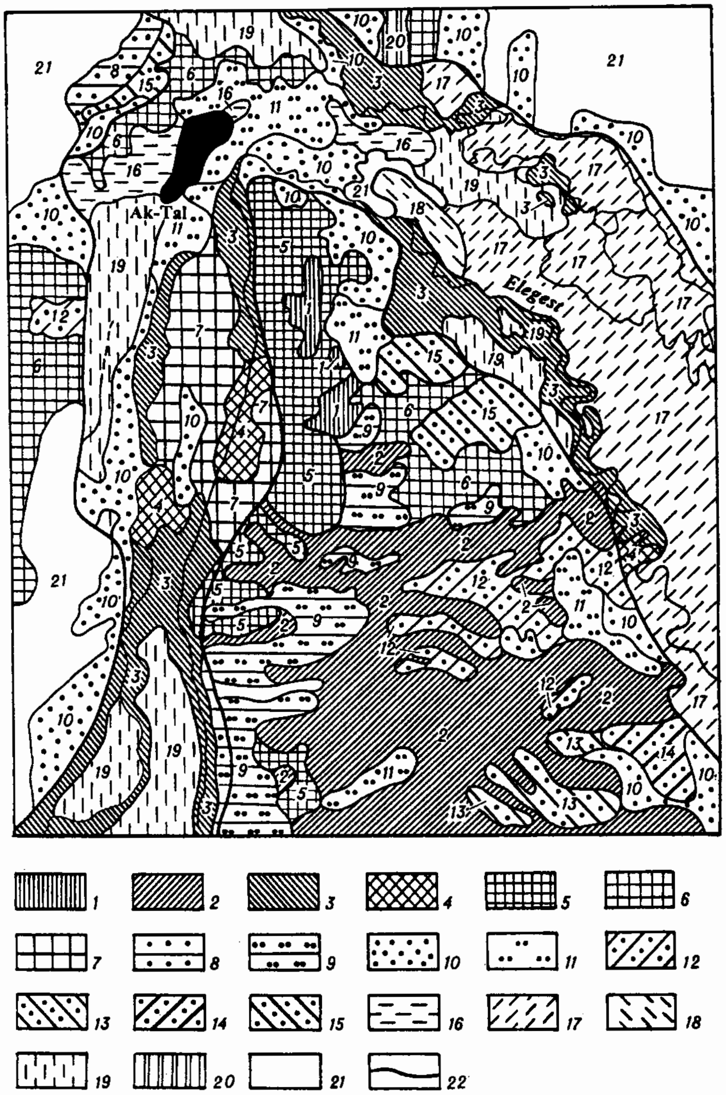


Fig. 1. The location of the investigated region.



1. Larch (*Larix sibirica*) forests with moss cover (*Pleurozium schreberi*)
2. Larch (*Larix sibirica*) forests with grass-forb cover (*Iris ruthenica, Aquilegia sibirica, Rubus saxatilis, Calamagrostis pavlovii*)
3. Larch (*Larix sibirica*) forests with *Populus laurifolia, Betula microphylla, Pentaphylloides fruticosa, Caragana spinosa* and with forb-grass-sedge cover (*Carex pediformis, Bromopsis pumpelliana, Poa sibirica, Elymus sibiricus, E. dahuricus, Iris ruthenica, Veronica longifolia*)
4. Fluvial willow scrub (*Salix viminalis S. rosmarinifolia*) with *Pentaphylloides fruticosa* and *Swida alba* and with herb cover (*Poa pratensis, Elymus sibiricus, Agrostis gigantea, Veronica longifolia, Senecio nemorensis*)
5. Pea-shrub vegetation (*Caragana pygmaea*) with grass steppe cover (*Koeleria cristata, Cleistogenes squarrosa, Stipa krylovii*)
6. Pea-shrub vegetation (*Caragana spinosa*) with *Pentaphylloides fruticosa* and with forb-sedge-fescue steppe cover (*Festuca valesiaca, Carex duriuscula, C. pediformis, C. obtusata, Galium verum, Veronica incana*)
7. Pea-shrub vegetation (*Caragana spinosa*) with *Pentaphylloides fruticosa* and with forb-species of *Kobresia*-sedge cover (*Carex enervis, Kobresia myosuroides, K. filifolia, Saussurea parviflora*)
8. Steppe communities of *Helictotrichon (H. hookeri, H. shellianum)*
9. Steppe communities of *Helictotrichon desertorum* with *Carex pediformis*
10. Typical bunch grass steppes (*Festuca valesiaca, Koeleria cristata, Helictotrichon desertorum, Cleistogenes squarrosa, Agropyron cristatum*)
11. Bunch grass-sedge steppes (*Carex duriuscula, Festuca valesiaca, Koeleria cristata*)
12. Steppe communities of couch grass (*Elytrigia geniculata, E. gmelinii*) with *Festuca valesiaca*
13. Steppe communities of *Arctogeron gramineum* with *Gypsophila patrinii* and *Ephedra distachya*
14. Steppe communities of *Carex rupestris*
15. Steppe communities of *Selaginella sanguinolenta*
16. Sedge-grass communities (*Agrostis gigantea, Hordeum brevisubulatum, Festuca rubra,Carex enervis*) and meadows with *Cirsium esculentum*
17. Grass-sedge communities (*Carex enervis, C. cespitosa, C. schmidtii, Hordeum brevisubulatun, Agrostis gigantea, Deschampsia cespitosa*) swampy meadows with *Equisetum arvense, Salix rosmarinifolia*
18. Grass-forb-sedge communities (*Carex enervis, Equisetum palustre, Poa pratensis, Festuca rubra, Trisetum sibiricum*) meadows with *Caragana spinosa, Betula humilis* and Salix rosmarinifolia
19. Grass-*Kobresia*-sedge communities (*Carex enervis, Kobresia filifolia, K. myosuroides, Hordeum brevisubulatum, Agrostis gigantea, Deschampsia cespitosa*) swampy meadows
20. Vegetation of rocky habitats
21. Ploughed fields
22. Boundaries of the valley

Fig. 2. Vegetation map of part of the Elegest valley near the village of Ak-Tal (1:50 000).

The largest area is covered by steppe communities which occupy positions on distant sites from the riverbed with insufficient water supply, or close to the river on light soils where in floods water penetrates deeply for roots horizons. The most typical are bunch grass steppes – type of steppe communities with dominance of xerophilous bunch grasses and small participation of xerophilous forbs and sedges. Bunch grasses and sedges form the turf. Phytocoenotic parameters are summarized in Table 1 and in the legend to Fig. 2 (no. 10).

Table 1. Parameters of some plant communities near the village Ak-Tal. The numbers correspond to those in Fig. 2. The horizontal structure of the vegetation was estimated visually.

Number	10	11	16	17	19
Parameters					
Cover %	60-65	50-60	90-95	95-100	90-100
Mean height cm	12-15	8-10	50-60	45-50	30-35
Horizontal structure		Pattern		No pattern	
Species richness (100 m^2)	22-25	16-18	29-31	27-30	30-33
Mean production (tons/ha)	0,3-0,6	0,2-0,3	2,0-2,2	1,0-1,2	1,2-1,4

At sites with more favourable water supply (shallow depressions up to 20 cm deep) *Carex pediformis* is abundant. The local co-dominants are *Festuca valesiaca* and *Koeleria cristata*. All steppes are used as spring and autumn pastures. After degradation due to the use as pasture *Carex duriuscula* becomes dominant (Table 1, no. 11). Sites of steppes with trees of *Larix sibirica* are found.

A typical feature of the upper part of the Elegest valley is the occurrence of *Caragana spinosa* occupying vast areas and participating in various plant communities. It grows on shallow soil in places where it can easily reach the ground water. The mean height of *Caragana* is 1.5 - 1.7 m. Among the shrubs, *Pentaphylloides fruticosa* is common. The herbaceous layer is 10 - 12 cm tall and covers 50 to 70%. Such shrub stands of *Caragena* sp. are sometimes used as pastures (no. 6). Large areas are covered by shrub stands of *Caragana spinosa* with swampy herbaceous cover (no. 7). Willow communities are typical of unstable ecological conditions at the Elegest river (no. 4). They occur as bands of usually 5-6 m up to 30 m and border meanders and tributaries. The mean height of the shrub layer is 4-6 m and the density of shrub stands is 0.4 - 0.5 (40-50% is covered by fluvial willow bush. The height of the herbaceous layer is 40 - 50 cm, its cover 60 - 70 % and mean production 2.5 tons/ha (dry weight).

Forests occur in the upper part of the valley and occupy small areas. Forests of *Larix sibirica* do not occur at altitudes below 1200 m. Larch forests with forb-grass-sedge cover prevail. The height of the trees is 20 - 25 m and the coverage percentage of leaf canopy attains values between 0.4 and 0.5. These forests represent a zonal vegetation in the middle belt of northern slope of the Tannu-Ola range (no. 3). Larch forests with grass cover containing *Poa sibirica, Elymus sibiricus, Festuca rubra* and *Elytrigia repens* occur along small riverbeds, brooks and the main riverbed of the Elegest River, particularly in places with auxiliary water supply (springs and soil water). Tree height attains 12 - 14 m and crown density values are between 0.2 and 0.4. In the undergrowth *Betula microphylla, Pentaphylloides fruticosa* and *Caragana spinosa* co-occur.

In the upper part vast sites of the *Kobresia* sedge swampy meadows with grass species occur (Table 1, no. 19). Near Ak-Tal sedge-grass meadows are found (Table 1, no. 16).

Close to the slope of the valley swampy communities on peat are frequent. Here, water supply is from runoff from the slope and from neighbouring drains. The peat layer is ca. 25 cm deep. The central parts of these communities are open water spaces bordered by bunch sedges – *Carex cespitosa* and *Carex schmidtii* forming hummocks of 30 cm in diameter and 20 cm tall. Hummocks usually include *Salix rosmarinifolia*. Towards the periphery the sedge cover is made up of *Carex enervis, C. microglochin, C. capillaris, C. coriophora, C. panicea, C. capitata* and *C. orbicularis*. The moss cover is dominated by *Amblystegiaceae*.

Near Ak-Tal village the Elegest changes its course (Fig. 2). The middle part of the river valley starts here. It shows trough characteristics as the upper part. The width of the valley varies here from 2.5 to 6 km. The fall of the riverbed is only ca. 1 m/km . This means a smaller water permeability of recent deposits on the accumulation terrace. The thickness of the loam layer increases from 45 to 120 cm. These features imply some drainage and the formation of a gley horizon. Almost the entire area in the middle part of the valley is covered by grass-sedge swampy pastures (Table 1, no. 17).

In shallow depressions of the valley under conditions of mineral richness and alternating humidity bunch sedge swamp is frequent. The dominating species are *Carex cespitosa* and *C. schmidtii*, both forming large hummocks, 30 - 40 cm tall. Between the hummocks *Carex dichroa, C. rostrata, C. enervis, Calamagrostis macilenta, Agrostis divaricatissima, Festuca rubra, Alopecurus arundinaceus, Equisetum fluviatile, Triglochin palustre* and *Comarum palustre* occur. The herbaceous layer is 25 - 30 cm tall, covers 85 - 95 % and has a production of 2.0 - 2.1 tons/ha. In the central part of these bunch sedge swamps small patches (10 - 15 m^2) with *Scirpus tabernaemontani* and *Typha latifolia* occur. These swampy areas are used as early summer pastures.

Besides grass-sedge swampy meadows and bunch sedge swamps in the middle part of the Elegest, larch forests (no. 3), fluvial willow scrub (no. 4), meadows (nos. 18 and 19) and patches of swamps on peat occur.

The lower part of the Elegest is characterized by a variety of plant communities. In the plain, the main riverbed becomes subdivided into temporary streams with ever-changing directions. On the river banks, forests of *Populus laurifolia* without a herbaceous layer may prevail. Close to the foothills, valley sediments are mainly cobble and gravel mixed with coarse sand. Here dwarf semi-shrub bunch grass desert steppes with *Artemisia frigida* and nearly vegetation-free habitats supporting only *Nanophyton erinaceum* and *Spiraea hypericifolia* are present.

Downward, channel banks are rich in fluvial willow and poplar forests (*Populus laurifolia*) with steppe herbaceous cover of *Poa attenuata, Polygonatum odoratum, Euphorbia discolor, Calamagrostis epigeios* and *Astragalus austrosibiricus* (cover 40 %). The height of the trees is 20 - 22 m and the crown density 0.2 - 0.4. In the undergrowth *Salix bebbiana, Rosa acicularis* and *Caragana spinosa* occur.

Slightly salt meadows are typical of this lower part of the Elegest valley. Dominating species are *Elymus dahuricus, Calamagrostis epigeios* and *Agrostis gigantea*. The height of the herb layer of these mown meadows is 60 - 80 cm, the cover 100 %, and the production is 2.2 - 2.3 tons/ha. On upper well-drained sites of the valley, steppe meadows with *Bromopsis inermis, Arctopoa tibetica, Elymus dahuricus, Medicago falcata* and *Potentilla bifurca* are found. These meadows are 40-50 cm tall, with a cover of 80-90%, and a production of 2.5-2.7 tons/ha. At the overlap of the valleys of the Elegest and Medjegai forb-sedge swampy meadows with *Carex enervis, C. cespitosa, C. schmidtii, C. capillaris, C. coriophora, C. songorica, Juncus filiformis, Bistorta vivipara* and *Equisetum palustre* prevail. These pastures are 30-40 cm tall, cover 100% and yield 2.0-2.1 tons/ha.

In the lower part of the valley large stands of typical bunch-grass steppes (no. 10), bunch-grass-sedge steppes (no. 11), and shrub stands of *Caragena* sp. (nos. 6 and 7) are found. Communities of *Achnatherum splendens*, utilized as winter pasture, occur on salty soils.

Forests occupy small areas only. Larch forests do not occur below altitudes of 1100-1200 m. Communities of *Larix sibirica* with a forb-grass-sedge understorey are considered as zonal vegetation of the middle belt of the northern slope of the Tannu-Ola Range. In the plains, the larch woodlands are substituted by poplar forests.

Shrubs are represented by willows and shrub stands of *Caragena* sp.

Steppes occupy vast areas in the valley especially in the upper part of the Elegest. Typical bunch grass steppes make up the zonal vegetation of Central Tuva. Dwarf semi-shrub bunch grass desert steppes with *Artemisia frigida* occur in the lower part of the valley.

Meadows are mainly distributed in the upper and middle parts of the Elegest. Swampy meadows are more frequent than typical meadows. Swampy communities mainly consist of bunch sedge swamps with *Carex cespitosa* and *C. schmidtii*. Small plots of swampy communities on peat are encountered. Nearly barren lands with *Nanophyton erinaceum* or *Spiraea hypericifolia* are met on gravel and pebble substrates in the lower part.

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Effect of landscape fragmentation on coniferous/broad-leaved forests

Rogova, Tat'yana V.[1*], Mukharamova, Svetlana S.[2] & Saveliev, Anatoly A.[2]

[1]*Department of Landscape Ecology, Kazan State University, 420008 Kazan, Tatarstan Republic, Russian Federation;* [2]*Department of Ecosystem Modelling, Kazan State University, 420008 Kazan, Tatarstan Republic, Russian Federation;*
**Fax +78432380412; E-mail tatiana.rogova@ksu.ru*

Abstract. In the study area of ca. 8530 km^2 located in the western part of the Tatarstan Republic in the Middle Volga Basin we investigated the effects of landscape fragmentation as a result of human-induced forest loss. The purpose of the investigation was to understand the dynamics of vegetation spatial structure and positions of woody dominants at the southern boundary of the mixed coniferous/broad-leaved forests of the Southern Taiga Subzone and at the northern boundary of the Northern Broad-Leaved Forest Subzone. This boundary coincides with the southern margin of *Picea abies, Picea obovata* and *Abies sibirica* distribution areas. The pre-agricultural landscape of mixed forests has been largely replaced by agricultural, urban and industrial sites.

A vegetation map (scale 1 : 100 000) for the whole region and a map (scale 1 : 10 000) for the protected area of 205 ha were used for the spatial analysis of landscape and vegetation structure. The current vegetation map was compared with the map of climax vegetation, which has been regenerated using information about ecotopes. Several indicators of vegetation pattern were computed, including the number of different types, number of patches, average patch area size and perimeter, index of landscape shape complexity, index of landscape heterogeneity, Shannon's diversity index, fractal dimension and others. The study showed that old-growth *Picea* and *Quercus* communities as well as secondary *Betula* and *Populus* forests are more fragmented and less stable, while *Tilia* and *Pinus* forests are more stable.

Keywords: Forest dynamics; Fractal dimension; Middle Volga; Spatial analysis; Vegetation pattern.

Nomenclature: Cherepanov (1995).

Introduction

The spatial vegetation pattern in modern anthropogenic landscapes is determined by ecotopological mosaics on one side and by forms and levels of human influence on the other. Knowing forest dynamics and patterns of forest loss and landscape fragmentation, especially for zonal ecosystems at the boundaries of their distribution is necessary for answering questions related to the long-term stability of ecosystems and biodiversity under the conditions of global climate changing (Baker 1995).

Dynamics of spatial heterogeneity of vegetation, characterized both by its composition and configuration, can be investigated by comparing inventory maps of current and climax vegetation maps, which are generated using the information about ecological heterogeneity of ecotopes. A large amount of statistical data, which is needed for such kind of analysis, demands the use of special methods of investigation. GIS-related techniques and environmental modeling provide capabilities for analysing the space/time distribution of vegetation, flora and other ecological phenomena. Vegetation pattern detected in ecological mosaics is a function of scale. This should be taken into account when comparing spatial vegetation structure of landscapes investigated at different scales (Viktorov 1986; Krummel et al. 1987; McGarigal & Marks 1994; Fox et al. 1995; Miller et al. 1995).

The aims of the present study were to examine the composition and configuration of mixed coniferous/broad-leaved forests at the southern boundary of its distribution under conditions of human-induced landscape fragmentation and dynamics from primary to secondary zonal forests. For the quantitative analysis of vegetation pattern one can use both of the following measures: (1) integral measures (*i.a.*, patch density, landscape heterogeneity index, Shannon's diversity index), which characterize the whole study area (region, landscape or some elements of it); (2) individual measures (patch area, perimeter, circular index, fractal dimension, etc.), which can be analysed statistically and spatially, and be used for producing maps. For example, the ratio of patch perimeter to area is a good indicator for assessment of the degree of anthropogenic influence on landscapes. Using spatial analysis models and applying GIS-techniques certain statements could be made about positions and stability of main woody species and their forest formations in recent landscapes of the Middle Volga.

Material and Methods

Study area

The study area of ca. 8530 km is located in the western part of the Tatarstan Republic in the Middle Volga Basin (55°48' N; 49°6' E). The Middle Volga Valley is located between two bedded banch uplands – the Volga Upland in the west and the High Transvolga in the east. The valley is bordered by the southern rim of the Viatka Ural Upland in the North. Kazan is the most ancient city of Middle Povolzhie. It was founded about 1000 yr ago on the left bank of the River Kazanka, a small tributary of the Volga. In this area the Volga is crossing the southern section of the Viatka Bar, cutting into limestones and dolomites of the Kazan stage of the Upper Permian (Dedkov 1990).

According to the current botanical-geographical division (Gribova et al. 1980) some northern parts of the study area are included in the subzone of coniferous/broad-leaved forests of the subtaiga (Fig. 1; Landscapes 31,32,33), while the southern and southeastern parts (Fig. 1; Landscapes 49, 56,57) are included in the subzone of northern broad-leaved forests – with a small amount of *Picea* × *fennica*. The boundary between these two subzones is determined by the isoline of the hydrothermic coefficient which is equal to

1 in this case. The diversity and distribution of the climax vegetation in this biogeographical transition zone are determined in the first place by relief and mechanical texture of soils and the hydrological regime of ecotopes. All landscape vegetation units are being brought together here – from formations of coniferous forests of south taiga and broad-leaved forests to formations with a contribution of typically steppe elements (Porfiriev 1967). The *Tilieto-Picietum* – with different variants with dominance in the ground layer of *Aegopodium podagraria, Mercurialis perennis* or *Carex pilosa*, prefers weakly podzolized loamy soils with a high level of fertility and sufficient humidity. The *Tilieto-Pinetum ruboso-aegopodietosum* is found on sandy-loam soils with medium level of fertility and humidity; it usually occurs in landscapes of river valleys. Formations of the *Querceto-Tilietum, Quercetum, Tilietum* and variants with the dominants *Aegopodium podagraria, Mercurialis perennis* and *Carex pilosa* are found on grey, clayey and weakly podzolized loamy soils of watersheds and their slopes. The *Piceeto-Pinetum hylocomietosum* occurs on sandy, loamy-sandy, middle- and high-podzol soils with a low level of fertility and high humidity on the terraces of rivers. The *Pinetum cladinoetosum* and *cladino-hylocomietosum* occupy dunes covered by latent-podzol soils with low fertility and humidity. Formations of *Alnetum* and *Pinetum sphagnoetosum* can be found in the low-lying elements in habitats with a high humidity level. The areas of these last types are small in the region. Mostly, the forest formations of the region are situated in the Volga-Kama Nature Reserve (VKNR).

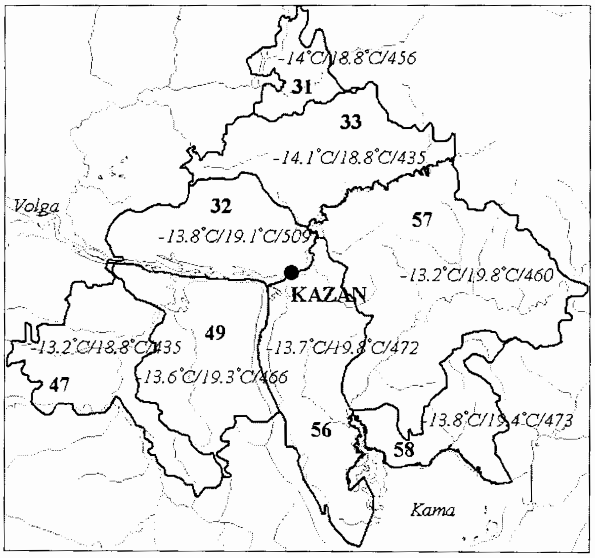

Fig. 1. Landscape typology of the of studied area: 31 - Eletskii High Flat Landscape (coniferous/broad-leaved forests of the South Taiga Subzone); 32 - West-KazanVolga Valley Terraces Landscape (pine forests); 33 - Kazan Erosive Flat Landscape (coniferous/broad-leaved forests); 47 - Civil-Kubninskii Erosive High Flat Landscape (steppe forests); 49 - Volga-Sviyagskii Ridge Dismembered Landscape (broad-leaved forests); 56 - Volga-Meshinskii Valley Terraces Landscape (pine forests); 57 - Lower- Meshinskii Flat Dismembered Landscape (broad-leaved forests); 58 - Kamskii Bank Ridges Landscape (broad-leaved forests). January and July temperature in C; precipitation in mm/year.

The change of one zonal climax formations for derivatives of certain compounds occurs accordingly to the form and degree of human influence and with the decrease in total forest areas in the background. The zonal coniferous/broad-leaved and broad-leaved forests have been replaced by *Tilietum, Betuletum, Populetum* and *Alnetum* of different types, depending on the ecotope. Different types of grassland communities, from floodplains to meadows and steppe-meadows depending on the soil humidity, take areas occupied by forests because of logging and further haymaking. Fire has produced a number of pyrogeneous variants of the *Pinetum*, such as *calamagrostietosum* and *convallarietosum*. Grazing and recreation on forest lands form ruderal variants of forest communities. Natural reproduction is actually minimized in such communities.

Floristic analysis revealed that the forests which had been formed in the area of the original mixed coniferous/broad-leaved forest landscapes, tend to diminish in the number of forest flora elements, both boreal and nemoral elements, while meadow and ruderal species increase, along with the growing landscape exploitation. There is also a clear increase in the amount of xerophytes and eurytopic species, therophytes, cosmopolites and naturalized species. The order of importance of plant families in the modern forest formations corresponds to that of the zonal flora, the most important families being *Compositae* and *Gramineae*.

Methods of data sampling

A vegetation map (scale 1:100 000) for the whole region and a vegetation map (scale 1:10000) for the protected area of 205 ha in the Volga-Kama Nature Preserve were used for the spatial analysis of landscape and vegetation structure. The current vegetation map was compared with the map of the climax vegetation, which has been generated using information about ecotopes.

The map of vegetation patches (scale 1:100 000) was divided into A4 sheets and scanned at 150 DPI. Files were recorded in PCX format. With the vectorizing package EasyTrace all scanned images were adjusted and merged into one geo-referenced project. Results of the vectorization were saved in DXF format and imported into the DIGITMAP vector map editor, where the topology was built and cleared. After editing of the object geometry, tabular information was added to each vegetation patch, and both geometry and tabular information were saved in internal DIGITMAP format SMD. That file was converted into the MapInfo exchange format MIF/MID and imported into MapInfo Professional v. 4.0.2. The MapInfo Professional was used to calculate data for each patch (area, perimeter, centre point) and for results mapping. Then statistical analysis of produced tabular data was performed, and indices were calculated.

Several indicators of vegetation pattern were computed, including the number of different patch types (m), number of patches (n), i-th patch area (A_i) and perimeter (P_i), total area (A), mean patch area (MPA), patch density (PD), landscape complexity index (LCI), landscape division index (LDI), landscape heterogeneity index (LHI), Shannon's diversity index (H), Landscape stability index (H_1) – see Table 1. The circular index (CI) and fractal dimension ($FRACT$) were calculated using the following formulas:

$$CI = 4pA_i / P_i^2 \qquad (1)$$

$$FRACT = 2\ln(P_i) / ln(A_i) \qquad (2)$$

Results and Discussion

The study showed 83 patches in the protected area in the reserve, represented by 41 plant community types defined by dominating species. The actual vegetation pattern has changed considerably: the number of patch type components had increased by a factor 8, the number of patches 9 ×, mean patch area and patch density decreased to 1/10, the landscape complexity index increased 100× and Shannon Diversity index with a factor 3 (Table 1).

The same approach has been used for the analysis of vegetation cover for the region as a whole. Patch picking here was conducted at the level of formations according to a dominating species. Increase in vegetation pattern complexity in the conditions of present anthropogenic landscape takes place as well. But there is a tendency for increased uniformity because of increased rural areas. The total number of indicated patches is 3702, 2537 of them being forest patches, including planted forests. When we compare the significance of the indicators describing the distribution of different formations within the boundaries of the studied area, we note the definite importance of the formations' spatial distribution and for the degree of stability of their spatial structure. For the climax formations these differences are determined first of all by ecological conditions of ecotopes. Within the boundaries of the study area *Piceetum* and *Quercetum* are characterized by higher fragmentation and lower stability. Formations of *Pinetum* and *Tilictum* are less fragmented and more stable. Derived *Betuletum* and *Populetum* formations have the highest fragmentation, *Populetum* formations have the least stable spatial structure.

Assuming that the fragmentation of the vegetation cover is a result of silviculture and agriculture (ploughing, forest clearing, stock grazing etc.) – which disturbs original boundaries of vegetation formations in the natural landscape – we attempted to evaluate the degree of anthropogenic pressure on the territory on the basis of the fractal dimension of the vegetation patches. A high value of FRACT indicates a more fragmented landscape, and the highest values are expected at the boundaries of neighbouring landscapes (Fig. 2a). As for different vegetation types the most complicated is the form of pasture grasslands (Fig. 2b).

According to the fractal dimension map (Fig. 3) low values of FRACT are rare in the region. A map of fractal dimension was made (scale 1:500 000, Fig. 3) to fulfil a task of assessment of the anthropogenic pressure.

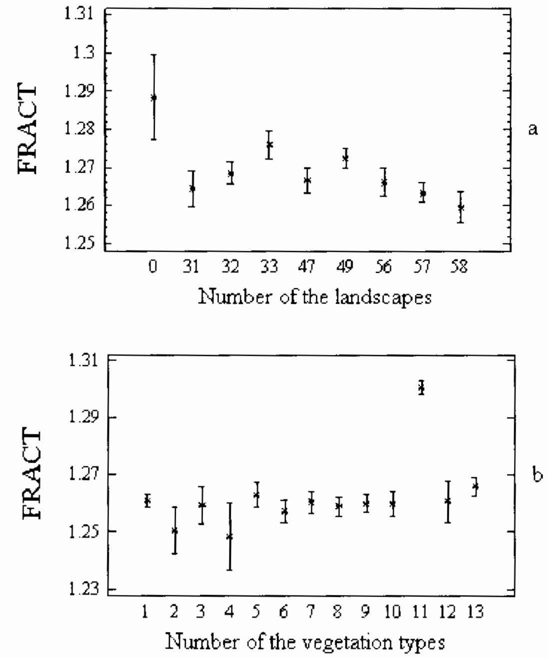

Fig. 2. a. Means and 95% confidence intervals of fractal dimension (FRACT) for the landscape types. Numbers of landscape types are given in Fig. 1; 0 - patches on the boundaries of the neighbouring landscapes. **b.** Means and 95% confidence intervals of fractal dimensions (FRACT) for the following vegetation types: 1 - Oak; 2 - Oak plantation; 3 - Spruce; 4 - Spruce plantation; 5 - Pine; 6 - Pine plantation; 7 - Lime; 8 - Birch; 9 - Aspen; 10 - Pastured forest; 11 - Pastured grassland; 12 - Meadows; 13 - Rural areas.

The circular index (CI) was clearly dependent on patch area (A_i). So this property is less appropriate as a form indicator. Fractal meanings in turn appeared to be relatively independent of patch area. We therefore recommend the use of fractal dimensions for further spatial form analysis of vegetation patterns.

Table 1. Vegetation pattern dynamics at the protected area of the Volga-Kama Nature Reserv.

Pattern criteria	Symbol	Climax vegetation map	Current vegetation map
Number of patch types	m	5	41
Number of patches	n	9	83
Mean patch area	$MPA = A / n$	22.7	2.4
Patch density	$PD = n / A$	0.04	0.40
Landscape complexity index	$LCI = n / MPA$	0.40	36.4
Landscape division index	$LDI = MPA/A$	0.114	0.012
Landscape heterogeneity index	$LHI = m(1-\Sigma(A_i/A)^2)/(m-1)$	0.41	0.88
Shannon diversity index	$H = -\Sigma(A_i/A)\log(A_i/A)$	1.26	3.92
Landscape stability index	$H_1 = (\log(m)-H)/\log(m)$	0.46	0.27

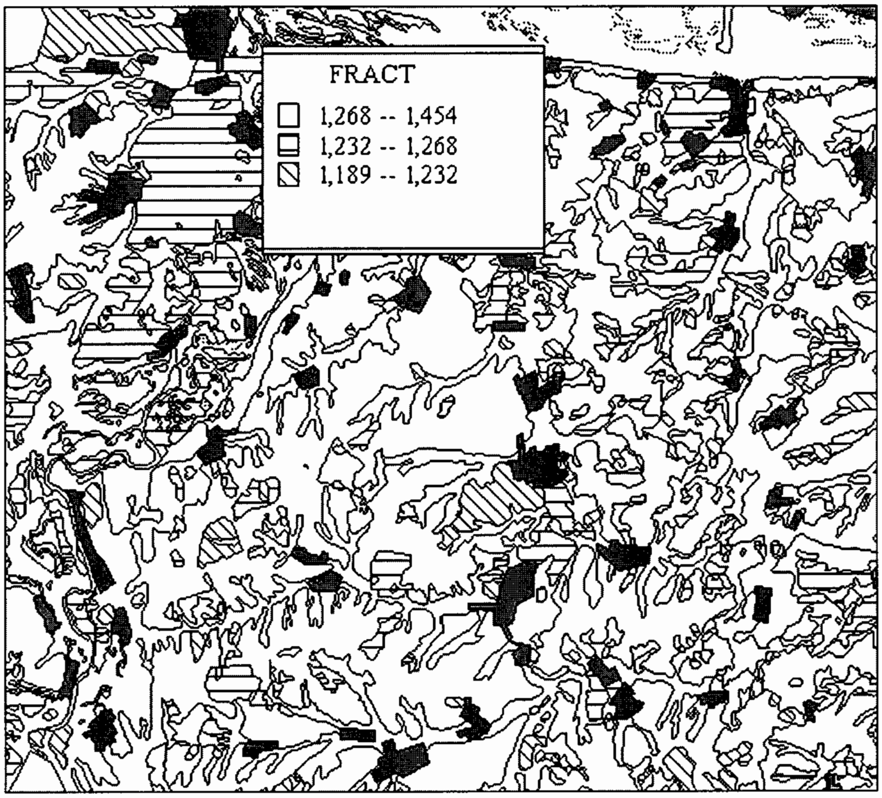

Fig. 3. Fragment of a fractal dimension (FRACT) map of the studied area.

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Vegetation at different levels of organization as an indicator of environmental conditions

Roo-Zielińska, Ewa

Institute of Geography and Spatial Organization, Polish Academy of Sciences, Twarda 51/55, P-00-818 Warsaw, Poland; Fax +48226978903; E-mail e.roo@twarda.pan.pl

Abstract. This paper presents an approach to assess selected features of the abiotic environment on the basis of the distribution of plant communities characterized by certain spectra of Elleberg indicator values. The study area is located in the vicinity of Pińczów, southern Poland. Phytosociological relevés were used (separately or grouped according to syntaxonomic unit) to determine the range of habitat requirements in relation to soil moisture (index F), acidity (reaction index R) and nitrogen content (index N). On the basis of indicator values for syntaxa and the map of the real vegetation of the study area three maps were derived showing habitat conditions as to moisture, acidity and nitrogen content. These served in the generation of a map depicting types of Ecological Regions; 14 such regions were distinguished which differed in the combinations of the three factors analysed.

Keywords: Acidity: Characteristic species; Ecological Region; Moisture; Nitrogen; Soil; Syntaxon.

Nomenclature: Matuszkiewicz (1981) for syntaxa.

Introduction

Methods using indicator schemes, including those involving Ellenberg indicator values have been used to assess selected components of the natural environment at a given site, on the basis of phytosociological relevés (Roo-Zielińska & Solon 1994). Ellenberg indicator values have been tested in several European countries, for instance by Degórski (1982), Koziowska (1991) and Roo-Zielińska (1996) in Poland, (Diekmann 1995) in Sweden, and van der Maarel (1993) in The Netherlands.

Although some authors rejected the approach because of problems with the calculation of averages, there is evidence that vegetation indicator values are correlated with field measurements of soil and climate parameters (e.g. Degórski 1982; Ellenberg et al. 1991; Diekmann & Falkengren-Grerup 1998).

The Ellenberg approach is used not only for site characteristics and arrangements of ecosystems but also for the cartographic presentation of the spatial distribution of ecological features. Advantages and disadvantages of the usefulness and reliability of such an approach has been widely discussed in literature (e.g. Zonneveld 1988). Roo-Zielińska & Solon (1988, 1990) investigated to what degree a phytosociological typology of plant communities conforms to the ecological arrangement of communities based upon indicator values of plant species.

The paper presents a regional differentiation of habitat conditions in a study area in southern Poland on the basis of an indicator analysis of syntaxa.

Material and Methods

Study area

Detailed studies on the structure, phytosociological typology and ecology of plant communities were conducted in the predominantly rural landscape surrounding the town of Pińczów in southern Poland (Kostrowicki & Solon 1994). The typological and spatial diversification of potential and actual vegetation were analysed in an area of 580 km^2. 87 basic typological units of vegetation were distinguished (Solon 1994).

Basic data

The indicator analysis was based on (1) a map at scale 1:25 000) of the real vegetation, and (2) on 371 relevés made over the years 1983-1989 representing the regional variation in vegetation.

Determination of indicator values for syntaxa

Edaphic requirements such as moisture index F, reaction index R, and nitrogen index N for various plant species were estimated according to Ellenberg (1974). On the basis of the cover-abundance values of the species a weighted average of Ellenberg indicator values for each relevé were calculated. For all vegetation types (syntaxa) represented on the map both amplitudes and mean values for the three indicator values were calculated.

Generation of the map of Ecological Regions

The main sources used to generate a map of Ecological Regions included: (1) the map of the real vegetation, and (2) the average indicator values F, R and N for all vegetation units represented on the map of real vegetation. Three maps showing the requirements of the vegetation in relation to the three ecological factors (F, R, N) were derived.

Then, areas with similar indicative characteristics corresponding to the class intervals of habitat requirements were aggregated on each of the three maps. This rendered three maps of regions that differed in terms of the requirements of the vegetation with regard to the considered ecological factors. The map of Ecological Regions is a result of overlay of the three maps produced for F, R, and N, respectively.

Results

Indicator values for syntaxa

Ecological amplitudes were presented for selected examples of plant communities, namely xerothermic (dry) grasslands and mesic meadows of syntaxa of various ranks of the *Festuco-Brometea* and *Molinio-Arrhenatheretea*.

In spite of the partial overlap of the ranges of minimum and maximum values on the scale of variability of the Ellenberg indicator values, it was still possible to determine ecological differences between the syntaxa (Fig. 1).

A fragment of a list of syntaxa showing the differences in the indicator values is presented in Table 1. The mean values for the syntaxa are clearly different, and lie within the intervals: F 3.3-9.0, R 2.3-8.1, N 1.6-7.0.

Table 1. Mean values of Ellenberg indicator values for moisture (F). reaction (R) and nitrogen (N) for 10 selected syntaxa. *n* = number of relevés.

	n	F	R	N
Caricetum gracilis typicum	8	8.6	6.1	4.3
Leucobryo-Pinetum	6	4.3	2.9	3.7
Circaeo-Alnetum	4	6.4	6.2	7.0
Phragmitetum australis	4	9.0	6.9	5.2
Tilio-Carpinetum	19	5.2	5.5	5.4
Inuletum ensifoliae	6	3.4	8.1	2.9
Calluno-Nardetum	3	3.3	2.3	1.6
Spergulo-Corynephoretum	5	3.5	4.3	2.6
Koelerio-Festucetum sulcatae	4	3.5	7.8	2.9
Thalictro-Salvietum pratensis	11	3.5	7.2	3.3

Ecological Regions

The identified Ecological Regions differ in the combination of habitat factors (Fig. 2). The final map of Ecological Regions, summarizing the spatial differentiation of the selected abiotic conditions, shows most of the study area to be occupied by soils that are dry (F 1-3), mostly neutral and alkaline (R 6-9), of moderate nitrogen status (N 4-6), covered mainly by corn and root-vegetable cultures. Regions with soils that are fresh (F 3-6), weakly-acid (R 3-5) and with moderate or of high nitrogen status (N 4-6, 6-8) are occupied by oak-hornbeam forest and fresh meadows and pastures, while those that are dry (F 1-3), very acid (R 1-3) and with a low nitrogen status (N 1-2) support pine forests. A large part of the study area has soils that are wet (F 9-10), neutral or alkaline (R 6-9), and of moderate (N 4-6) to high (N 6-8) nitrogen status. These mainly support moist meadows, rush and sedge communities, as well as alder and ash carrs (Fig. 2).

Conclusions

The indicator analysis describing particular patches of vegetation is suitable for the determination of habitat requirements for that vegetation and the presentation of spatial differences to abiotic conditions (Roo-Zielińska 1982; Küchler & Zonneveld 1988; Faliński 1991). However, it is difficult to produce such detailed documentation for large areas for which a vegetation map was derived by means of aerial survey or satellite imagery. In such situations, a quick and precise evaluation of the environment on the review scale is made possible by a method of determining habitat conditions based on mean values for a syntaxon calculated from selected test plots. The suitability of the method depends on the range of values for the Ellenberg indicator values the narrower this range is, the more precise and unambiguous is the conceptualization of abiotic conditions (Roo-Zielińska 1996).

Maps of Ecological Regions obtained by way of indication do find application in spatial planning (Roo-Zielińska 1982), and may also constitute one of the bases upon which to predict transformation in the natural environment under the influence of natural processes and anthropogenic impacts (Roo-Zielińska & Solon 1991).

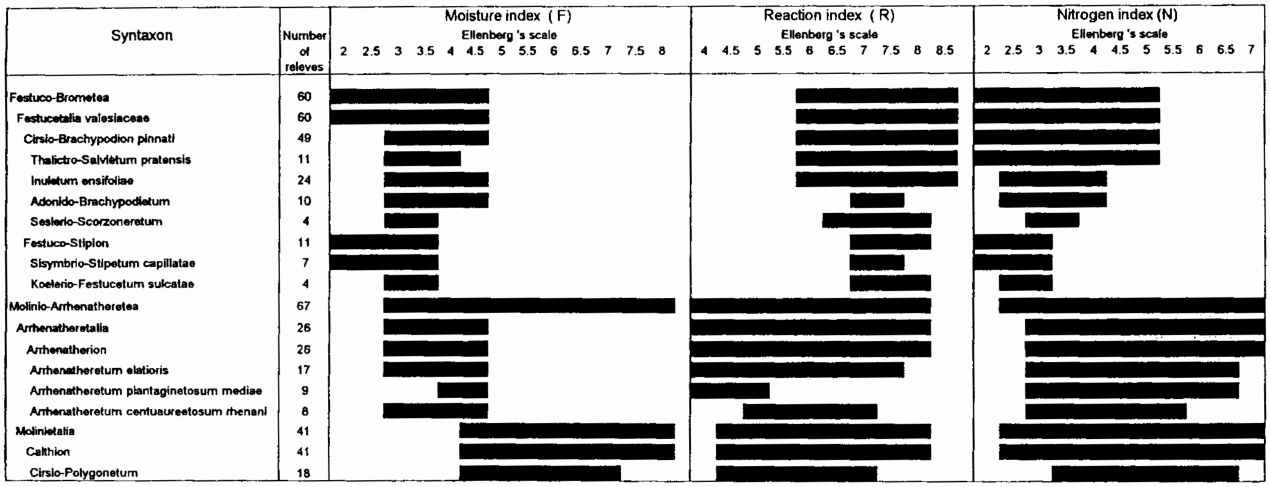

Fig. 1. Amplitude of Ellenberg indicator values in real plant communities: xerothermic grasslands (*Festuco-Brometea*), and mesic meadows (*Molinio-Arrhenatheretea*).

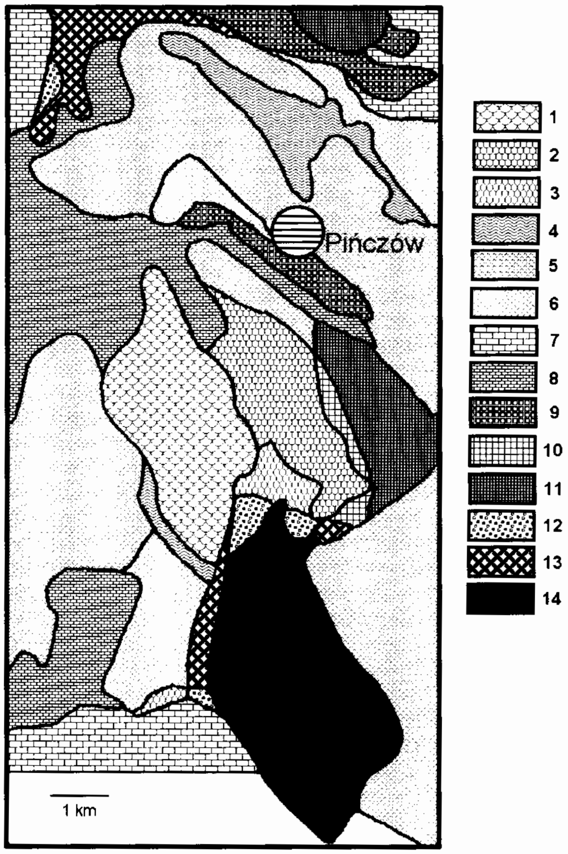

Fig. 2. Typology of Ecological Regions.

1. F - dry, R - very acid, N - low;
2. F dry, R - acid, N - moderate;
3. F - dry, R - acid, N - high;
4. F - dry, R - weakly acid to basic, N - low;
5. F - dry, R - weakly acid to basic, N - moderate;
6. F - dry, R - neutral, basic, N - high, very high;
7. F - fresh, R - acid, N - high, very high;
8. F - fresh, R - weakly acid, neutral, N - moderate, high;
9. F - fresh, R - weakly acid to basic, N very high;
10. F - moist, R - acid, N - moderate;
11. F - moist, R - weakly acid to basic, N - moderate, high;
12. F - wet, R - acid, N - high;
13. F - wet, R - weakly acid, neutral, N - moderate, high;
14. F - wet, R - neutral, basic, N - moderate, high.

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Northern taiga forests with *Pinus sylvestris* in West Siberia

Vasiliev, S.V.

Institute of Soil Science and Agrochemistry, Siberian Branch of the Russian Academy of Science, Sovetskaya St. 18, Novosibirsk, 660099, Russia;
Fax +73832227652; E-mail sv@mail.nsk.ru

Abstract: Five forest community types and two woodland community types were distinguished based on 218 stand tables of *Pinus sylvestris* forests from four regions in the north of West Siberia. Along of a 38 km long landscape transect across 60 forest sites in the valley of the Left Khetta River the ground water table and the composition of surface deposits were determined and 69 fire scars on tree trunks were collected. Variation in ground water level explains only part of the phytocoenotic structure of the forests communities, while the variation in surface deposits of the sites was more important factor. Under conditions of a high groundwater table *Sphagnum*-lichen woodlands are developed. Lichen-rich woodlands are formed partly through wind action. Tree structure in the stands is connected with the forest fire regime. The abundance of the feather mosses and lichens does not depend on dynamic phenomena, but seems to vary in relation to tree layer density.

Keywords: Forest; Fire; Groundwater; Lithology; Tree stands; Understorey vegetation.

Nomenclature: Cherepanov (1981); Abramova et al. (1961); Abramov (1971-1978).

Introduction

The aim of this work is to reveal the importance of soil factors (groundwater and the composition of deposits) and forest fires for the phytocoenotic structure of pine forest communities in the northern taiga of West Siberia. The main element in the identification of forest types in Russia is the dominance of species in the understorey vegetation. I want to evaluate whether the phytocoenotic structure of pine forests may be used for the site indication in forest typology.

Pine forests are widely spread in northern West Siberia up to the forest-tundra boundary zone (Iljina et al. 1985). They are mainly developed on sandy and sandy loam soils without permafrost. In the tree layer *Pinus sylvestris* is the common dominant, often accompanied by *Betula pubescens* and *Larix sibirica.* Prolonged fire-free periods may lead to formation of tree stands with *Pinus sibirica* and *Picea obovata. Pleurozium schreberi, Cladina stellaris, C. mitis, C. arbuscula* dominate in the forest floor. The floristic composition of pine forest communities on dry soils allows to assign their associations to the *Dicrano-Pinion.* Observations indicate that there is no clear relation between the phytocoenotic structure of the communities and soil conditions of sites.

Material and Methods

Vegetation relevés were made in different parts of northern West Siberia. They were united in several groups: (A) the Left Khetta River basin (the left tributary of the Nadym River), 65° N, 73° E; 1987; 150 relevés; (B) the Kazym River basin, Poluy eminence, 64°15' N, 70° E; 1988; 28 relevés; (C) Siberian Slopes near Noyabrsk, 62°45' N, 75°E, 1993; 17 relevés; (D) southern part of Surgut Polesje, 61°45' N, 74°E; 1994; 23 relevés.

The relevés from groups B and C were united in one BC group as they appeared to be similar in physical-geographical conditions and phytocoenotic structure. The D and BC groups are relatively southern, while the A group is northern. The BC group is found in areas with sandy loam and loamy surface deposits, A and D in areas with solely sandy soils.

Relevés from group A were collected from a 38 km long landscape transect crossing the second alluvial terrace of the Left Khetta River, areas with glaciofluvial sediments and isolated mounds of bedded sands and gravels. The composition of surface deposits and groundwater table were determined in 60 sites along the transect by boring to a depth of 5 m. For each community type the detection frequency of ground waters and loamy layers on different depths were calculated. It shows how many cases are in which the ground water (loamy layer) meets on the certain depth or above.

In the tree layer the age and height of trees, the diameter of trunks, wood stock, and basal area were determined. A distinction was made between syngenetic, epigenetic and residual tree stands and forest layers by the age and age structure, the presence of vestiges of a forest fire and by the tree species composition.

Syngenetic tree stands are tree stands of the first generation appearing and developing simultaneously with layers of moss and grass. Primary syngenetic tree stands appear in newly formed sites in floodplains and on aeolian dunes. Secondary stands occur on sites destroyed by fire, windfall, and cutting. As a rule they are formed by light-demanding and fast-growing tree species. The post-fire syngenetic stands and layers are even-aged and trees in them have no fire scars on the trunks.

Epigenetic tree stands are tree stands of second and subsequent generations which appear and develop under the control of a preceding generation of trees. They are formed by shade-tolerant and long-living tree species. The epigenetic tree stands are multi-aged.

Residual tree stands can be formed from syngenetic and epigenetic ones under the effect of some selective factor (fire, cutting, windfall, etc.), when only part of trees destroys. The remaining part of trees formed residual tree stands. The syngenetic generation which is formed as a result of such an effect may coexist with a residual one. In this article I describe residual generations which are formed after forest fire. Fire-resistant species with thick bark, such as *Larix*, dominate in these stands. Trees in the post-fire residual stands have fire scars on trunks or charcoal on barks. Along the transect I checked 69 fire scars to determine inter-fire periods. The period after fire on sites when all trees were killed was determined by tree age in the syngenetic stands.

Results and Discussion

Five forest and two woodland communities were distinguished: (Table 1):

P	*Pleurozio-Pinetum*;
PCs	*Pleurozio-Pinetum cladinetosum stellaris*;
PCm	*Pleurozio-Pinetum cladinetosum mitis*;
Cs	*Cladonio-Pinetum cladinetosum stellaris*;
Cm	*Cladonio-Pinetum cladinetosum mitis*;
Sf	*Sphaerophoro-Pinetum*;
Sn	*Sphagno nemorei-Pinetum*.

All community types show relatively distinct floristic differences which correlate with the abundance of *Pleurozium schreberi*. The projective cover of *Pleurozium* is not more than 10% in the lichen-pine communities (Cs, Cm, Sf, Sn). In the lichen-feathermoss communities (PCs, PCm) it varies from 5% to 70%, and in the feathermoss community (P) - from 60% to 100%. Lichen abundance changes accordingly. In types with *Cladina stellaris* (PCs, Cs) the cover of this species exceeds that of the other *Cladina* species, which do not reach more than 10-15%. *Cladina arbuscula* and *C. rangiferina* co-dominate with *C. mitis* in the *C. mitis* types (PCm, Cm), but *C. stellaris* does not reach more than 5-30 (maximally 50%).

The understorey vegetation of *Pinus sylvestris* forests is formed by species which are widespread in the Holarctic, or have ecologically vicariant species. The Siberian character of the forests is formed by *Ledum palustre* and the northern character by *Vaccinium uliginosum, Arctostaphylos uva-ursi, Empetrum nigrum* and *Calamagrostis lapponica*. Groundwater is not a decisive factor for the phytocoenotic variation of communities (Fig. 1). Although a higher groundwater level leads to the formation of *Sphagnum*-lichen woodland (Sn) with *Sphagnum nemoreum* (Vasiliev 1994), other communities do not differ as to their groundwater relations.

Forest community sites are clearly different in the composition of surface deposits (Fig. 1). The loamy layer at 2 m depth (or less) may be found in 80% of the *Pleurozio-Pinetum*, 45% of the *Pleurozio-Pinetum cladinetosum mitis* and 10% of the *Pleurozio-Pinetum cladinetosum stellaris* sites. Both the *Cladonio-Pinetum cladinetosum stellaris* and *Cladonio-Pinetum cladinetosum mitis* are developed on pure sands. It means, that the composition of the understorey vegetation of pine forests is determined by soil factors which are connected mainly with a lithology and soil fertility under similar regimes of soil moisture. Pine-lichen woodlands may appear under wind impact at the same sites as forests of similar topographic conditions. However, the strong correlation between forest community types and the presence or absence of loamy layers in sand deposits is not found. It is possibly the effect of external factors and the overstorey canopy closure.

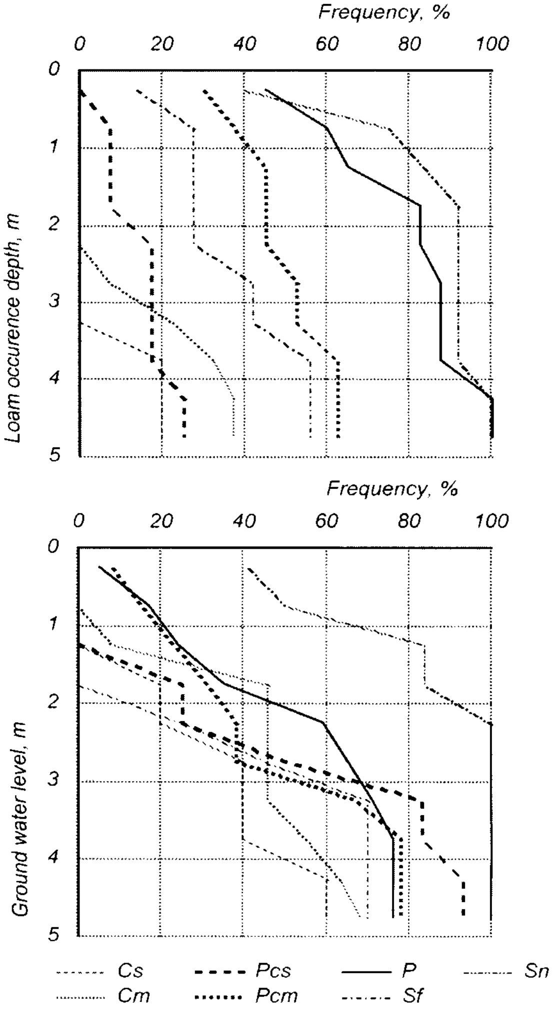

Fig. 1. Occurrence of groundwater (below) and loamy layers (above) at different depths. Frequency of occurrence indicates the probability (%) of finding the groundwater (loamy layer) up to a certain depth. For abbreviations of the community types, see Text.

Tree stand structure is largely determined by the impact of periodical forest fires. 53 (77%) fire scars on tree trunks collected at the Left Khetta River basin are from four periods: 1950 - 1957, 1910 - 1923, 1865 - 1873 and 1807 - 1809. The sum of these years with scars is 34. In intervals between these periods (in total 143 yr) only 16 fire scars were found. Besides, fire scars from 1740 and 1690 were observed. This all means an estimated periodicity of forest fires of 40 -70 yr.

The trees which have survived two, three or four forest fires dominate in communities with *Cladina mitis* (Cm). In such communities fires probably were of low intensity due to more frequent burning which prevented the formation of epigenetic tree stands. In forests with *Cladina stellaris* (Cs) the tree layers have a low density. In such communities crown fires do not develop, but surface fires may have a higher intensity due to a thicker and more continuous lichen floor.

The generation of trees of 60-70 yr dominate in 95% of

Table 1. Floristic composition of the pine forest communities. C = projective cover (%) for shrubs, herbs, mosses, lichens; tree stand density according to a 0 to 10-point scale for the main tree layer (a); share in tree species composition in points from 0 to 10 for tree regeneration layer (b). F = frequency in classes: I = < 20%, II = 20-40%, III = 40-60%, IV = 60-80%, V = 80 - 100%.

Community types	Sn		Sf		Cm		Cs						PCm		PCm		PCs		P		P	
Region groups	A		A		A		A		B,C		D		A		A		B,C		A		B,C	
Number of relevés	26		7		18		10		9		14		25		36		14		28		8	
	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F
Pinus sylvestris (a)	2	V	2	V	3	V	4	V					5	V	5	V			4	V		
Pinus sylvestris (b)	9	V	10	V	10	V	10	V					8	V	9	V			5	V		
Larix sibirica (a)		III		I		I		I						I		I			1	III		
Larix sibirica (b)		I		I		I		I					1	III		III			1	III		
Betula pubescens (a)		II		I		I		I						I		I			1	III		
Betula pubescens (b)	1	IV		I		I		I					1	IV	1	V			1	V		
Pinus sibirica (a)		I		I		I		I						-		I				I		
Pinus sibirica (b)		I		I		I		I						II		II			1	V		
Picea obovata (a)		-		-		-		I						-		-				I		
Picea obovata (b)		-		-		-		I						I		II			1	III		
Populus tremula (a)		-		-		-		-						I		-				I		
Populus tremula (b)		-		-		-		-						I		I				I		
Vaccinium vitis-idaea	10	V	10	V	10	V	5	V	5	V	5	V	10	V	10	V	5	V	10	V	15	V
Ledum palustre	10	V		IV		V		IV	5	V	5	IV	5	V	5	V	15	V	10	V	10	V
Cladina stellaris	40	V	30	V	30	V	80	V	80	V	70	V	30	V	70	V	60	V	5	V	15	V
Cladina rangiferina	10	IV	30	V	20	V		V	5	V	10	V	20	V	5	V	5	V	5	III		V
Cladina mitis + arbuscula	10	V	10	V	20	V		V		II		I	20	V	5	V		-	5	V		I
Pleurozium schreberi	20	V		I	5	V	5	II		V	5	IV	50	V	30	V	30	V	80	V	70	V
Vaccinium myrtillus	10	V		-	5	IV		II		IV		V	5	V	10	V	10	V	15	V	20	V
Dicranum polysetum + D. sp.		IV		I	5	V		II		III		III		IV		IV		IV		III		V
Empetrum nigrum s.l.		V		IV		V		III		V		V	5	V	5	V	5	V	5	V	5	V
Vaccinium uliginosum	10	V		IV		III		I	5	V	5	III	5	V	5	V	5	V	5	V		IV
Polytrichum juniperinum		-		III		V		III		IV		IV		V	5	V		I		III		III
Stereocaulon paschale		-		I		-		I		-		-		-		-		-		I		-
Betula nana		IV		II		-		II		III		-		-		I		II		I		I
Carex globularis		V		I		-		-		I		III		I		I		I		II		I
Andromeda polifolia		IV		-		-		-		-		-		-		-		-		-		-
Sphagnum compactum		V		-		-		-		-		-		-		-		-		-		-
Sphagnum nemoreum	10	V		-		-		-		-		-		-		-		-		-		-
Polytrichum strictum		I		-		-		-		-		-		-		-		-		-		-
Oxycoccus microcarpus		I		-		-		-		-		-		-		-		-		-		-
Sphagnum fuscum		I		-		-		-		-		-		-		-		-		-		-
Cetraria spp.		II		-		-		-		-		-		-		-		-		-		-
Festuca ovina s.l.		-		IV		II		III		-		-		III		IV		-		I		I
Sphaerophorus fragilis		-		V		II		I		-		-		-		-		-		I		-
Polytrichum piliferum		-		V		I		II		-		-		-		-		-		-		I
Cladonia spp.		II	10	V	5	V		II		I		III		II		I		I		I		I
Cetraria laevigata + islandica		III		III		V		IV		I		-		I		I		-		I		II
Cetraria nivalis[1]		-		IV		II		IV		I		-		-		I		-		-		-
Arctostaphylos uva-ursi		II		II		III		IV		I		II		-		II		I		-		-
Carex ericetorum		-		-		-		-		-		III		-		-		-		-		-
Calamagrostis lapponica		I		I		II		-		II		IV		III		IV		III		II		-
Solidago virgaurea		-		-		I		-		-		II		II		III		-		I		-
Antennaria dioica		I		-		I		-		-		II		I		III		-		-		I
Diphasiastrum complanatum		I		-		-		-		I		-		II		II		III		I		I
Juniperus communis		-		-		-		-		-		-		II		III		I		I		I
Peltigera aphtosa + canina		-		-		-		-		-		-		I		II		II		I		-
Salix bebbiana + phylicifolia		-		-		-		-		I		I		I		II		I		I		II
Polytrichum commune		V		-		I		I		I		I		I		I		I	5	III		II
Ptilium crista-castrensis		-		-		-		-		-		-		-		I		I		I		IV
Hylocomium splendens		-		-		I		-		-		I		I		I		I		II	10	V
Pedicularis labradorica		-		-		-		-		-		-		-		-		I		-		I

[1] *cucullata + ericetorum*

the *Pleurozio-Pinetum* communities; they often have a high density. This is also true for the feathermoss-lichen communities PCm and PCs, while in communities PCm and Cm a *Pinus* generation of 160-170 yr, often dominates. Feathermoss communities rarely burn, because the period of dry matter accumulation is longer, but crown fire intensity may be higher since the density of the tree stand is bigger. The high density of the tree canopy in such communities may determine the domination of feathermosses.

The described forest stands are mainly dominated by *Pinus sylvestris*, but *Betula pubescens*, *Larix sibirica*, *Picea obovata* or *Pinus sibirica* may take part or even co-dominate in them under various conditions (Fig. 2). Birch has a high abundance and frequently dominates in syngenetic

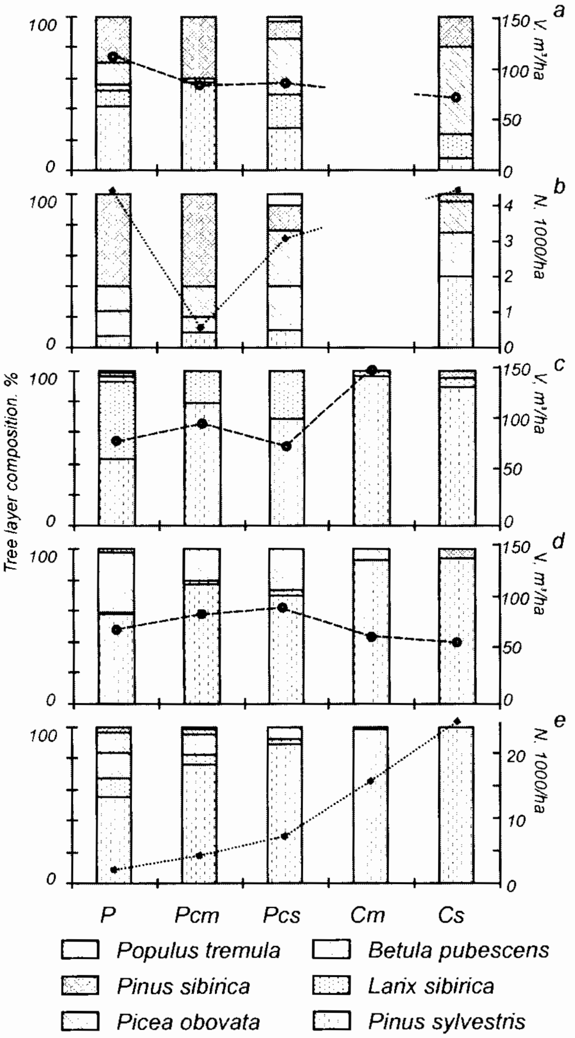

Fig. 2. Tree stands composition (columns), wood stock (V, stroked line) and stem number of tree regeneration (N, dotted line) in *Pinus sylvestris* forests of West Siberia: **a.** Main layer of epigenetic tree stands, 130-200 years old; **b.** Tree regeneration in epigenetic tree stands; **c.** Main layer of residual tree stands, 120-150 years old; **d.** Main layer of syngenetic tree stands, 40-80 years old; **e.** Tree regeneration in syngenetic and residual tree stands. For abbreviations of community types, see Text.

tree stands, larch in residual ones. The abundance of *Pinus sylvestris* in syngenetic and residual tree stands increases continuously from the feathermoss (P) to the lichen (Cs, Cm) community types. The shift from a *P. sylvestris* to a dark coniferous stand is more probable in communities with feathermoss (P), as the regeneration of *Picea abies* and *Pinus siberica* is abundant here. In epigenetic tree stands wood stock and basal area rise regularly from Cs to P, which is probably related to the soil conditions. However, the variation in the relative abundance of *P. abies* and *P. siberica* between types cannot be considered as diagnostic. So, in the Cs type communities pure *P. siberica* stands were revealed. In all cases these stands occurred in sites either directly adjoining the floodplain or situated in the vicinity. This is probably related to the availability of *P. siberica* seeds to these sites, transported by animals from floodplain forests.

The fact that epigenetic tree stands are described practically in all community types shows that the variation in phytocoenotic structure of the understorey vegetation is not connected with dynamic phenomena. Feathermoss (P) and feathermoss-lichen (PCm, PCs) forests are different mainly because of the differences in deposit composition. They have a similar tree stand structure and their understorey vegetation may be used as a key to the differentiation of site types by the presence or absence a loam in the soil. *Sphagno nemorei-Pinetum* woodlands are characterized by a high groundwater table. *Sphaerophoro-Pinetum* communities are formed under distinctive topographic conditions, where the wind activity is high. Lichen forest communities (Cm and Cs) are formed on pure sands, which are hardly different from sites with feathermoss-lichen (PCm, PCs) forests. In this case the fire regime is different and the lichen dominance in Cm and Cs is related to the low density of the forest layers.

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The gradient structure of Swiss forest vegetation: Evaluation of the traditional Swiss forest classification

Wohlgemuth, Thomas, Wildi, Otto, Schütz, Martin & Keller, Walter

Swiss Federal Institute for Forest, Snow and Landscape Research, CH-8903 Birmensdorf, Switzerland;
Fax +4117392215; E-mail thomas.wohlgemuth@wsl.ch

Abstract. Abrupt spatial changes in species composition of Swiss forests reflect small-scale patterns in topographical and geological site factors as well as management influences. Therefore, it has always seemed appropriate to define discrete forest units, i.e. plant associations or vegetation units generated by clustering, rather than by the arrangement of plots along underlying environmental gradients. Well-defined forest units are essential for mapping projects aimed at management applications. After having revised the old classification system of Ellenberg & Klötzli (1972) on the basis of new data, we faced a lively resistance to the new classes, primarily by people who had classified forests in specific regions. In search of a solution to the problem, we tested the old classification system by using direct and indirect gradient analyses on more than 6000 relevés. We found that these forest relevés are arranged continuously. We compared the resulting gradients with secondary site factors. Previously described vegetation units were reviewed by displaying them in ordination space.

Keywords: Complementary Analysis; Correspondence Analysis; Forest gradient; Revision.

Introduction

In Switzerland, a multitude of geological formations as well as different climates meet on a small area of only 40000 km^2. Consequently, the resulting vegetation varies considerably. The real vegetation was classified into numerous types and there was also good reason to distinguish between many different species assemblages.

It is widely believed that large areas of the forests are in a rather natural state and it is a declared objective of forestry departments to maintain or to re-establish this state. Also in the federal forest law, site or vegetation classification is declared mandatory as a basis for all forest projects.

A cornerstone in forest vegetation classification was set by Ellenberg & Klötzli (1972). The authors divided the total forest vegetation of Switzerland into 71 units by applying the so-called relevé punch card method on 5000 relevés (Ellenberg & Christofolini 1964; Mueller-Dombois & Ellenberg 1974). This procedure corresponded to some extent to a modern computer classification. Since this publication appeared, the new system has been applied to numerous regional forest vegetation surveys (e.g. Schmider et al. 1993; Frey 1995; Ott et al. 1997). The old classification is in fact still used today, even though the data base has increased meanwhile to as many as 15000 relevés.

We established a data base consisting of 15000 available relevés in order to revise the old classification system (Wohlgemuth 1992; Wildi et al. 1996). The most obvious weakness of the data collection is that there has never existed an underlying statistical sampling design. This led to various problems such as over- and under-representation of types, limited reliability in the determination of species, different homogeneity of the different relevé plots. Data from ca. 300 different sources of publications were compiled in the data base. Many of these studies were based on preferential sampling, which generally reinforces the discrete view of vegetation. On the other hand, we hoped that the large number of relevés would compensate for some of the weaknesses.

We faced a lively resistance to our new classification system, primarily by people who had classified forests in specific regions of Switzerland earlier. In particular, they did not agree with the proposed new units. In search of a solution to the problem, we tested the old classification system by using direct and indirect gradient analyses. Evaluating a classification system is a delicate task because classification is often considered an art rather than a scientific method and hence influenced by personal preferences. In this paper we address the following questions:

1. Are Swiss forest communities discrete units?
2. Which are the predominant gradients in Swiss forests?
3. Does the traditional classification system of Swiss forests need a revision?

Material and Methods

In order to test the traditional alliances and associations, we created an ordination space using as many relevés as possible (CANOCO, version 4; ter Braak & Šmilauer 1998). Two data sets served as test data: 'Switzerland' with nationwide data (6525 relevés) and 'N Switzerland' (6266 relevés) consisting of relevés from Swiss areas north of the Alps (Table 1). A majority of the relevés of the data base describe natural forest stands, i.e. the vegetation is considered close to the potential natural vegetation (PNV; Tüxen 1956; Westhoff & van der Maarel 1978). The data sets include a considerable number of core relevés which were originally used by Ellenberg & Klötzli (1972) to define the 71 old units. In order to test the quality of the old classification we visualized the core relevés in ordination space built by the large data sets. This procedure is also known as complementary analysis (Kent & Ballard 1988).

Apart from the species information, we also included secondary environmental variables. According to Walter (1960), we defined the following easily measurable variables as secondary factors: climate (radiation, rainfall, temperature), relief (slope, aspect), soil (type, structure, chemical properties, water storage), biotic factors (man, animals, plants). Ecologically relevant factors with a direct effect on plants are considered primary: warmth, light,

Table 1. Data sets used in the analyses.

Data set	Switzerland	N Switzerland
Data constraints	- tree cover > 50 % - coordinates available - plot size 50 to 300 m^2 - date > 1950	- tree cover > 50 % - coordinates available - located in Jura Mts, Central Plateau or Northern Prealps (Wohlgemuth 1996)
No. of relevés	6525	6266
No. of species in layers	1820	1563

water, chemical factors (nutrients) and mechanical factors (wind, snow, disturbance).

In order to detect discrete relevé groups as well as primary site factors which often are revealed by species positions along the axes, we conducted Correspondence Analysis (CA) on both data sets (percent coverage of species, downweighting of rare species). In an additional analysis – not presented here – we ran Canonical Correspondence Analysis (CCA) including environmental variables.

Results

In the CA-ordination diagrams of the relevés, no discrete groups are detectable (Fig. 1). The relevés are arranged along gradients. Distinct arcs are visible in the ordinations of both data sets. In addition, the ordination displays reflect unbalanced distribution of relevés.

According to the positions of the species along the axes, we interpreted the first two axes in ecological terms i.e. with primary factors. CA-axis 1 corresponds best with the mean availability of nutrients and, partly, with warmth and soil acidity (geological substrate). CA-axis 2 corresponds best with drought stress or water demand, or more commonly, moisture.

Core relevés are displayed in the CA-ordination space based on the data set N Switzerland. Their assignment to different traditional units is indicated with different symbols, following the classification hierarchy in Ellenberg & Klötzli (1972), i.e. alliances, associations and subassociations. With respect to the system of alliances, ordination results correspond with the traditional classification, i.e. groups of core relevés overlap only partly in ordination space. With respect to the system of associations and subassociations, the units overlap considerably (Fig. 2).

Discussion

Discreteness and continuum

Our CA-ordination results revealed a continuous gradient system of Swiss forest vegetation. This, on the one hand, is not very astonishing because the large number of relevés involved presumably could blur discrete patterns. On the other hand, even in the highly structured landscape of Switzerland, the expected discreteness of at least few

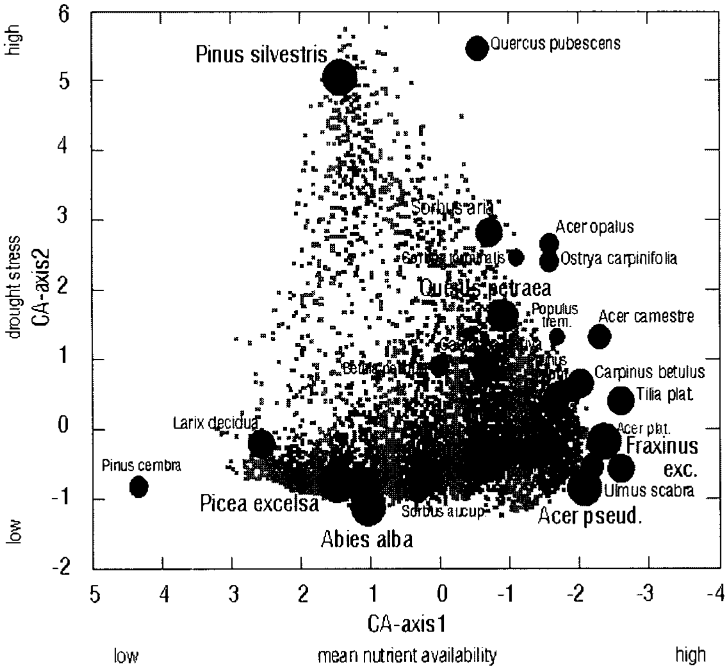

Fig. 1. CA-ordination of 6525 relevés and 28 tree species of data set 'Switzerland'. Species symbols reflect the log transformed weights resulted from CA. Axes are labeled according to the interpretation that is based on the relative positions of the tree species. In order to compare the CA-ordination with the ecogram for Central Europe (Ellenberg 1963, 1988), the first CA-axis is reversely displayed.

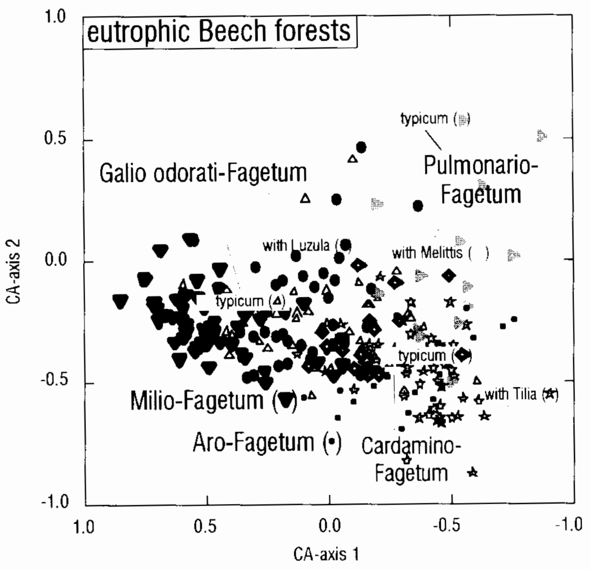

Fig. 2. CA-ordination of core relevés which were used by Ellenberg & Klötzli (1972) to define forest associations and sub-associations (data set). Ordination space was built using the data set 'N Switzerland'. The display shows core relevés of the alliance *Eu-Fagion* (eutrophic beech forests).

associations is not visible. This in turn raises the question about the delimitation of vegetation types. While in early 1970, the data available (ca. 5000 relevés) did not cover the entire ecological variation and therefore reflected more discreteness, today we face three times more data resulting in more difficulties for classification because the patterns are more continuous now. Future classifications need to emphasize gradients and reference relevés within the vegetation continuum rather than preferentially sampled data which until recently served as core units.

Gradients

The CA-ordination of the data set Switzerland revealed the primary factors: mean nutrient availability (CA-axis 1) and drought stress – moisture (CA-axis 2). Nutrient availability is strongly dependent both on water availability and warmth, though. A proper distinction between the factors, nutrient availability and moisture, is almost impossible. This effect is expressed exactly by the tree species in ordination space. We compared the CA gradient system with the ecogram of Ellenberg (1963, 1988). The ecogram is considered a direct ordination (Wildi 1986) using the two axes of acidity and moisture. In contrast to our results, the ecogram was designed with expert knowledge of the region. The species positions along the axes of the CA-ordination correspond fairly well with the ones in Ellenberg's ecogram, although the first axis of the ecogram is originally defined as acidity. Ellenberg & Klötzli (1972) adopted the ecogram concept but replaced 'acidity' as the denomination of the first axis with 'nutrient richness', which in turn corresponds to our first CA-axis. This implies that the meaning of the well-accepted and widely applied ecogram is ambivalent with respect to the first axis. In a different study we paid special attention to this problem (Wohlgemuth et al. 1999).

The predominant gradients in Swiss forest vegetation are nutrient availability and moisture in terms of primary factors. In terms of secondary factors, the forest vegetation is best explained by the factors degree days, annual rainfall and soil skeleton. Soil acidity i.e. the geological substrate, is masked by the availability of nutrients (Fig. 1, CA-axis 1). Low availability of nutrients corresponds to sites at higher altitudes where the substrate is not of primary importance. In contrast, floristic differences of sites at low altitudes can be well explained by the geological substrate. However, these differences again are strongly related to nutrient availability.

Evaluation of the traditional classification system

Results of complementary analyses confirm the problems that emerge in all the new regional classification projects concerning forest vegetation in Switzerland. These problems include the fact that many of the defined vegetation units overlap, and hence, there are considerable difficulties of distinction, not only between, but also among regional associations. Generally, associations are well defined within the alliances at the end of the vegetation gradients (low availability of nutrients, high drought stress; e.g. mixed oak forests). In beech forests, in contrast, only about 50% of the associations are well-defined. In the centre of the CA-ordination, distribution patterns of many associations overlap considerably. We consider mainly two reasons for that. 1. For methodological reasons, CA-ordinations result in a dense centre with many relevés and a scattered periphery consisting of few relevés with different species composition. 2. Mesic sites in lowlands are suitable for almost all trees in Switzerland, resulting in an increased competition pressure. Small ecological differences in these sites result in considerable differences of tree, shrub and herb species composition. Ecological differences may be, in addition, caused by large plot size or differences in forest management. Taking into account additional random variation, the ecological interpretation of the units in terms of species is difficult. We conclude that it is not a coincidence that exactly the mesic forest units are the ones leading to the most distinct contradictions in actual mapping projects. Our results show that some parts of the traditional system need to be revised. To generalize rather than divide vegetation units would often be justified.

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Vegetation of Seili and adjacent islands, SW Finland

Wojterska, Maria*[1], Balcerkiewicz, Stanisław[1], Brzeg, Andrzej[1], Bujakiewicz, Anna[1], Kasprowicz, Marek[1], Łuszczyński, Janusz[4], Rusińska, Anna[2], Szwed, Wojciech[3], †Tobolewski, Zygmunt, Wojterska, Halina & †Wojterski, Teofil

[1]*Department of Plant Ecology and Environment Protection;* [2]*Department of Geobotany, Adam Mickiewicz University, Al. Niepodległości 14, 61-713 Poznań, Poland;* [3]*Department of Botany, Higher Pedagogical School, Konopnickiej 15, 25-406 Kielce;* [4]*Chair of Forest Botany, Agricultural Academy, Wojska Polskiego 71 D, 60-625 Poznań; † Deceased*
**Fax+48618523615;E-mail mwzerios@main.amu.edu.pl*

Abstract. Geobotanical studies were conducted on Seili and 12 adjacent smaller islands in the Turku Archipelago in Finland and aimed at comprehensive analysis of vegetation structure on different islands of the archipelago in correlation with habitat differentiation, human impact and island size.

The flora consists of 1288 species (625 taxa of vascular plants, among them 18 new to the Turku region and 663 taxa of cryptogamic plants as well as lichens and macromycetes). The share of species with different historic-geographical status, of socio-ecological groups and of geographic elements was analysed and compared to the flora of the region and country.

Vegetation studies comprised differentiation and description of plant communities, their structure and relation to habitat conditions. The distribution of syntaxa was shown in the vegetation map on the scale 1: 4000. Seven new associations have been described, mainly from the group of meadow-, sward- and forest-edge communities.

Keywords: Braun-Blanquet approach; Bryophyte community; Flora; Hemiboreal zone; Lichen community; Macromycete; Vegetation complex; Vegetation mapping.

Nomenclature: Mirek et al. (1996); Hamet-Ahti et al. (1986); Faltynowicz (1993); Söderström (1995); Ochyra et al. (1992).

Introduction

The main aim of these studies was to analyse the vegetation structure on the islands of the archipelago in relation to habitat differentiation, human impact and island size. The present paper presents the scope of the investigations and shows only some of the results of an elaboration, which comprises the following items: flora, plant communities, complexes of plant communities and the map of the actual vegetation.

Material and Methods

Study area

The geobotanical studies comprised Seili and 12 smaller islands (Table 2) and skerries, situated ca. 30 km SW of Turku at the northern boundary of the Hemiboreal zone (Ahti et al. 1968). The investigated part of this archipelago has a humid climate. It has a lower annual precipitation – 600 (612) mm/yr, a higher annual temperature – 5.0 (4.5)°C and more sunny days compared to Turku, situated on the mainland (Turku data in brackets) (Petäjä & Juusti 1979). The dominant geological formations are paleoproterozoic granite and gneiss rocks with a small share of tills, as well as coarse sand and gravel of different origin. The valleys are filled with marine deposits (Anon. 1997). The maximum altitude is 55 m. The total land upheaval is 5 mm/yr (Petäjä & Juusti 1979).

In 1962 a 17th century hospital was closed and in 1977 its buildings were converted to the Archipelago Research Institute of the University of Turku. This brought about the cessation of land use, mainly in the valleys and resulted in major changes in vegetation. Plantations of trees of different geographic origin were introduced on the abandoned fields.

Geobotanical studies were designed and first conducted by the late Prof. Teofil Wojterski, during seven vegetation seasons during the period 1978-1997. Preliminary results on the investigations were published by Wojterska (1989) and Wojterski et al. (1993).

Collection and evaluation of data

Floristic data were collected separately for each island and the flora of mosses, liverworts and vascular plants additionally in squares 500 m × 500 m each. Phytosociological studies including 1100 relevés according to the Braun-Blanquet approach, in which 89 communities were documented, preceded the designation of cartographic units.

Results

The flora of the Seili Archipelago, which has an area of approximately 10 km^2, counts totally 1288 taxa. On the investigated islands 220 taxa of lichens were found, 71 of which are considered very rare. These are mainly epilithic species from the genus *Lecanora* (*L. achariana, L. cenisia, L. frustulosa* and *L. grumosa*) and several species growing on the bark of trees. Boreal and subboreal species (Duell 1984, 1985) make up 21.3% of the total moss flora (183 taxa), a further 38% are related to two zones: boreal and temperate. Worth mentioning are subarctic-alpine species such as: *Kiaeria blyttii, Oncophorus wahlenbergii, Plagiothecium piliferum* and *Polytrichastrum alpinum*. Two northern-oceanic species: *Amblystegium serpens* var. *litorale* and *Bryum salinum* quite often occur in halophytic vegetation. The suboceanic *Andreaea rothii* is endangered in Finland (Rassi & Väisänen 1987). There are 45 taxa of liverworts, which makes up 30 % out of the flora (147 taxa) of the Turku region (Söderström 1995). Boreal species are dominant and prevail in the moss communities on the rocks. The epiphytic species *Metzgeria furcata* and *Radula complanata*, mainly belonging to the temperate zone (Duell 1983), occur on Seili in the *Alnus* forests. Some oceanic species: *Calypogeia sphagnicola, Nowellia curvifolia* and the endangered *Cephalozia lacinulata* (Rassi & Väisänen 1987) were found on Seili in only one locality. *Lophozia atlantica* is a North-suboceanic-alpine element and the epilithic *Scapania scandica* is the only subarctic-montane species.

215 species of fungi, mainly *Agaricales* and *Aphyllophorales*, were recorded. Almost half of them were found in the *Lysimachio-Alnetum*, since investigations were focused on this habitat. The most interesting are: *Tubaria confragosa*, a northern species; a fairly large group of *Conocybe* species, occurring on fertile soils, rich in nitrogen (*C. dentatomarginata*). Relatively rare are saprotrophic species growing on wood: *Ganoderma lucidum* and *Phellinus laevigatus*. In the ecological group of epigeic species the most important species are the mycorrhiza-forming species, such as *Lactarius obscuratus* and *Naucoria scolecina*.

In the group of 625 taxa of vascular plants there are 526 spontaneously growing and 99 cultivated species. The number of archeophytes is high (132), whereas established (37) and casual (14) aliens are less numerous. The index of anthropophytization (ratio of all anthropophyta to the total number of spontaneous species multiplied by 100; Jackowiak 1990) equals 35, which is a high value for a region with apparently low human impact. Comparison of the spontaneous flora of the studied area, with the flora of the Turku region (11 500 km^2 - 1215 species; Lahti et al. 1988) (Table 1) shows, that 43 % of all species found in the region occur there. Anthropophyta are present on all islands, independent of the existence of permanent settlements or land use. In the socio-ecological groups (Table 2) the most important are: forest-, littoral-, meadow- and xerothermophilous species. The share of forest species (especially coniferous forests) and of littoral species is proportionally larger in the flora of the smaller islands.

The vegetation was characterized on different levels of organisation – from microphytocoenoses (epilithic lichen and moss communities) to complexes of plant communities.

On steep coasts the *Umbilicarietum deustae* (Hilitzer 1925) Frey 1933 is found, one of the most important cryptogamic communities in the landscape. Epilithic moss communities of the *Andreaeion rupestris* Hadač & Klika 1944 and *Rhacomitrion lanuginosi* Krusenstjerna 1945 occur here as well, while on the rocks with salt spray communities with *Caloplaca marina* and *Verrucaria maura* are found. Deforested rocks in the interior of the island form suitable habitats for the *Candelarielletum corallizae* (Almborn 1955) Massé 1964 and the *Parmelietum centrifugae* Fries 1913 as well as for communities of the *Hedwigion ciliatae* Philippi 1956 and the *Ceratodonto-Polytrichetea* von Hübschman 1967. On hill tops and in pine forest gaps the *Cladina rangiferina-Cladina mitis* community occurs. On boulders in open pine forests, patches of the *Parmelietum omphalodis* Du Rietz 1921, *Parmelietum saxatilis* auct. and the *Parmelia incurva-Parmelia sorediata* community are found and on shaded, humid rocks in the forests patches of the *Cystocoleo-Rhacodietum* Schade (1924) 1932 and communities of the *Grimmion hartmanii* Philippi 1956.

Table 1. Share of groups (in %) of different historic-geographical status in the flora. F = Finland, RA = Regio Aboensis, S = Seili archipelago.

	F	RA	S
Native species*	59	51	65
Archeophytes	13	16	25
Established aliens	12	11	7
Casual aliens	16	22	3

*Categories after Hämet Ahti et al. 1986.

The *Juncetum gerardii* Nordh. 1923 is the most important type of littoral vegetation. It occurs both on primary and on secondary sites, where it is promoted by grazing. Since the salinity level is low (6‰ acc. to Petäjä & Juusti 1979), in sheltered bays vast areas are covered by reeds of the *Phragmitetum communis* (Gams 1927) Schmale 1939 and, on rocky beaches, by narrow bands of the *Phalaridetum arundinaceae* (Koch 1926) Libbert 1931.

Natural mesophilous deciduous forests are limited to the belts between cultivated land and rock outcrops in the southern part of Seili. Habitats of the *Ulmo-Tilietum* Kielland-Lund in Seibert 1969 are predominant there. Tree stands are partially replaced by hazel thickets assigned to the *Melico-Coryletum* Fremstad 1979. In the sheltered bays there are habitats of *Lysimachio-Alnetum* Kielland-Lund 1971,

Table 2. Share (in %) of socio-ecological groups in the flora of investigated islands, ordered according to their decreasing size. Se = Seili; Hö = Högholmen; La = Lammasluoto; Pä = Päiväluoto; Jä = Jäämäluoto; Kn = Kolkan; Kt = Katavaluoto; Sn = Saunasaari; Bj = Björkholmen; Al = Ålderman; Si = Siikakari; Kv = Kalvgrundet; Mt = Matinkari.

	Se	Hö	La	Pä	Jä	Kn	Kt	Sn	Bj	Al	Si	Kv	Mt
Forests	19	33	20	29	23	26	18	28	27	27	18	21	20
Littoral	11	21	14	24	30	28	25	24	45	28	39	35	46
Meadows and pastures	17	15	22	24	13	21	23	21	14	20	19	17	15
Xerothermophilous swards and forest edges	12	10	17	8	14	8	14	11	2	8	13	8	12
Nitrophilous tall herbs	6	9	8	7	9	10	10	6	9	10	4	13	5
Peats and mires	3	4	4	4	3	2	2	4	0	1	5	3	0
Crevices	1	3	3	3	4	1	1						

which on deeper soil are bordered by juvenile stands of the *Ulmo-Fraxinetum* Sjögren 1971. There was only one locality where *Sphagno squarrosi-Alnetum* Lemee 1937 was found.

Coniferous forests dominate on all the islands. Five communities of the *Dicrano-Pinion* Libb. 1933: *Cladonio-Pinetum* Juraszek 1927, *Arctostaphylos-Pinus* comm., *Vaccinio uliginosi-Pinetum* Kleist 1929, *Vaccinio vitis-idaeae-Pinetum* (Cajander 1921) Kielland-Lund 1981, *Melico-Pinetum* Marker 1969) and three communities of the *Vaccinio-Piceion* Br.-Bl. 1939: *Sphagno-Piceetum* Polakowski 1962, *Linnaeo-Piceetum* (Cajander 1921) Kielland-Lund 1962 and *Melico-Piceetum* (Cajander 1921) Kielland-Lund 1962 were observed. In the mixed spruce-pine forest *Linnaeo-Piceetum* there is a distinct progression of spruce. The data from Seili were compared to those from other parts of Scandinavia (Kielland-Lund 1981; Dierßen 1996) and NE Poland. The differences between the *Dicrano-Pinion* and *Vaccinio-Piceion* become obscure there, since the number of *Dicrano-Pinion* species diminishes towards the north and they are not yet replaced by the *Phyllodoco-Vaccinion* species.

Grassland communities of the *Molinio-Arrhenatheretea* Tx. 1937 em. 1970 class: *Lysimachio-Filipenduletum* Bal.-Tul. 1978, *Achillea ptarmica-Deschampsia caespitosa* comm., *Alopecurus pratensis* comm., *Galio veri-Avenuletum pubescentis* Brzeg (ined), which previously were an important element of the landscape are now undergoing quick successional transformations as a result of the cessation of cultivation. Contemporary limitation of grazing brings about the reduction of the area covered by xerothermophilous swards: *Potentillo argenteae-Viscarietum* Balcerk. et Brzeg (ined.) and *Trifolium arvense-Filago arvensis* comm. (with the only exception of the *Sedum acre-Allium schoenoprasum* comm. which is expanding). On the other hand it promotes the development of thermophilous forest edge communities such as the *Trifolio-Agrimonietum* Th. Müller 1961, *Melampyretum pratensis* Pass. 1967 and *Cynancho-Origanetum vulgaris* Balcerk. et Brzeg (ined). They now seem to reach the optimum of their expansion in the deforested areas but in some places they have already been replaced with thickets.

Strictly synanthropic vegetation (Faliński 1969) has also diminished in the last three decades. The *Veronico-Lamietum hybridi* Krusem. et Vlieg. 1939 is the only segetal community. There are cosmopolitan ruderal communities, in particular the *Polygono arenastri-Matricarietum discoideae* (Siss. 1969) Th. Müller in Oberd. 1971 and *Sagino procumbentis-Bryetum argentei* Diem., Siss. et Westh. 1940, and the newly described syntaxa: *Rumici longifolii-Urticetum dioicae* Balcerk. et Brzeg and *Cuscuto europeae-Urticetum dioicae* Balcerk. et Brzeg. In many places synanthropic communities are being replaced by semi-natural ones.

Geobotanical landscape studies, based on the sigma-association concept (Tüxen 1973, 1979) rendered 11 types of vegetation complexes on Seili. Table 3 provides a survey of differentiation of an anthropogenic landscape: *Potentillo-Viscarietum/Galio-Avenuletum* complex on inland rock outcrops in the neighbourhood of settlements, *Carum carvi-Alchemilla gracilis* comm./*Veronico-Lamietum* strictly related to hamlets and *Alopecurus* comm./*Rubetum idaei* Pfeiff. 1936 em. Oberd. 1973 which forms a regeneration complex in the areas where cultivation ceased 30 yr ago.

The distribution of 55 syntaxa is shown on the map at the scale 1: 4000 as well as the zonation and sequence of vegetation units in the vegetation profiles, which could not be included in this paper.

Conclusions

1. In the last 20 yr there is a tendency towards a reduction of the number of synanthropic species, which is caused by changes in land use.
2. Boreal moss species are a conspicuous element in the flora.
3. Many forest associations on Seili occur at their distribution limit, which is reflected in their impoverished floristic composition.
4. Some communities of the *Molinio-Arrhenetheretea* Tx. 1937 em. 1970 were assessed as synanthropic (and not semi-natural as they usually are in middle Europe); this is related to the fact that many meadow species here are archeophytes.
5. Seven associations were newly described, mainly sward-, forest-edge- and synanthropic communities.

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Table 3. Vegetation complexes in the area of settlements in the Seili Archipelago, SW Finland.

Succesive number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Traces of human activities																				
Traditional red houses	.	.	.	+.	+.	2a	10	.	+.	.	10	20	30	.	.	.	.	.	.	.
Wooden houses	.	.	.	.	+0	.	20	.	.	1.	10	.	.	+0	.	.	+.	.	.	.
Brick houses	.	.	.	.	.	20	.	.	+0	.	.	.	.	.	.	.	.	.	.	.
Ditches	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2/	.	1/	1/	.	1/
Ornamental plants in containers	.	.	.	.	.	+.	.	.	1.	r.	.	.	.	.	.	.	.	.	.	.
Ornamental perennials	.	.	.	.	1/	.	+.	.	1/	+/	10	.	+.	+.	.	.	.	.	.	.
Ornamental shrubs	.	.	.	.	1.	+.	+.	.	1/	+.	+.	.	.	+.	.	.	.	.	.	.
Orchards	.	.	.	.	40	+.	10	.	40	20*	40	.	20	30	.	.	.	.	.	.
Vegetables	.	.	.	.	+/	+/	+0	10	1/	10	.	.	.	.	.	.	.	.	.	.
Potatoes	.	.	.	.	+/	10	+0	.	20/	20	.	.	.	.	.	.	.	.	.	.
Lawns	.	.	.	+0	20	40	40	10	10	10	30	30	10/	30	.	.	1/	.	.	.
Singular trees	.	1.	1/	.	r.	1.	10	.	.	+:	+.	+.	+.	1.	.	.	r.	.	.	.
Deciduous trees - plantations	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	40	40	40	30	.
Coniferous trees - plantations	1/	.	.	.	.	.	.	.	.	.	.	.	.	.	40	.	.	.	.	50
Plant communities																				
Carum carvi-Alchemilla gracilis comm.	.	.	.	+0	20	40	30	10	30/	10	30	30	10/	30	.	.	.	.	.	.
Polygono-Matricarietum	.	+/		1/	.	+/:	1/	+/	+/	+/	.	.	.	.	.	.	.	.	.	.
Veronico-Lamietum hybridi	.	.	.	.	.	10	+0	10	20/	10	.	.	.	.	.	.	.	.	.	.
Stellarietea fragm.	.	.	.	.	+/	+0	.	.	.	20	.	.	.	r.	.	.	.	.	.	.
Cuscuto-Urticetum	.	.	.	.	.	.	10	.	.	+.	.	1/	.	.	.	.	.	.	.	.
Rumici longifoliae-Urticetum dioicae	.	.	.	.	.	.	+.	.	.	.	.	.	.	+.	.	.	.	.	.	.
Sagino-Bryetum fragm.	.	.	.	.	.	.	r	.	.	.	.	.	.	r/	.	.	.	.	.	.
Agropyron repens agg.	.	.	.	10	.	+/	.	.	.	.	.	1/	.	.	.	.	.	.	.	.
Cladonio-Pinetum	1/.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Vaccinio vitis-idaeae-Pinetum typicum	2/	10	10	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Juniperus communis agg.	1.	1.	1;	1.	.	.	.	.	.	.	.	.	+.	.			r.	.	.	.
Potentillo-Viscarietum	+.	20	30	20	+.	1.	.	.	.	r	.	.	.	.	.	.	.	.	.	.
Galio-Avenuletum	10	30	2/	30	10/	20	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Poo irrigatae-Plantaginetum	.	1/		10		1/	+/	+/	2/	+:	1/	.	.	.	.	.	10/	.	.	.
Trifolio-Agrimonietum	1/	.	1/	30	+/	1/	.	10/	+0	.	20	.	30	+.	.	.	1	2/	.	+0
Alopecurus pratensis comm.	.	+0	.	.	.	+.	.	40	20	30	30	10	10	30	30	30	30	20	30	.
Rubetum idaei	.	.	.	.	.	+.	+.	.	.	10:	.	10	.	+.	20	10	+.	+0	+.	10
Lysimachio-Filipenduletum	.	.	.	.	.	.	.	.	.	.	.	1:	30	1/	20/	20	30	.	+:	.
Geranio sylvatici-Epilobietum angustifolii	.	.	.	.	.	.	.	.	.	r:	.	1/	.	.	10/	.	+.	10	.	.
Querco-Fagetea fragm.	+.	.	.	.	.	+.	.	.	.	.	.	.	.	10	r.	10*	20	+.		r.
Alopecurus-Betula, Pinus, Populus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	20	40	30	40	30	.
Lysimachio-Filipenduletum-Betula, Pinus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	10/	20/	20/	.	.	.
Rubetum idaei-Betula, Pinus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	20	10	.	.	.	.
Agrostis capillaris-Betula	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	20	.	.	.	.
Anthriscetum sylvestris-Pinus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	20	.	.	.	.	.
Equisetum sylvaticum-Pinus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	20	.	.	.	.	.
Molinio-Arrhenatheretea fragm.	.	.	.	.	40	.	30	.	.	20	.	.	.	.	.	.	.	.	.	.
Achillea ptarmica-Deschampsia caespitosa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+0.	.	+.	.
Lythrum salicaria comm.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+/	+/	.
Potentilletum anserinae	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1/	.
Abies spp. div. – *nudum* type	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	50
Complex of epilithic lichen comm.	30	2.	30	1.	.	2a0	+.	10	r.	.	.	10	.	.	.	.	.	.	.	.
Epiphytic lichen communities	.	.	.	1.	.	1.	.	.	.	.	2.	.	2.	.	2.	.	.	.	.	.
Melico-Pinetum	1/	.	.	.	10	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Populus tremula comm.	10	.	.	.	.	+.	.	.	.	1/0	.	.	.	.	.	.	.	40	.	.
Ribes-Sorbus comm.	2/	1.	1/	1.	.	.	.	+.	.	+:	.	+.	1/0	.		r.			+.	
Rosa dumalis-Rosa caesia comm.	.	1.	.	1/	.	.	.	.	.	.	.	.	.	.	.	r.	.	.	.	+0
Calamagrostietum epigei	+.	10	.	.	.	.	.	.	.	+.	10	20	+0	.	.	10	.	.	.	.

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Local species turnover on Mount St. Helens, Washington

del Moral, R.

Department of Botany, University of Washington, Box 355325, Seattle, WA 98195-532, USA;
Fax +12066851728; E-mail moral@u.washington.edu

Abstract. The 1980 eruption of Mount St. Helens provided a chance to study species turnover during succession. I used permanent plots to monitor species presence in 0.25-m^2 quadrats. Colonization and extinction were estimated for three several-year increments in 10 habitats starting seven seasons after the eruption by two methods. Extinction rates, measured by the proportions of initially filled quadrats that lost a species, varied little across sites. Extinction percentages, the proportion of all quadrats losing a species, declined from recovered to secondary to primary sites. Extinction percentages increased through time on successional sites. Colonization rates and percentages were similar on all sites. The proportion of extinction percentage to colonization percentage declined from recovered sites, where these processes were of similar magnitude, to primary sites, where the ratio was about 1 to 4. These results suggest that the carousel model is operative even during community assembly.

Keywords: Carousel model; Local colonization; Local extinction; Primary succession; Secondary succession; Volcano.

Nomenclature: Hitchcock & Cronquist (1973).

Introduction

The lateral eruption of Mount St. Helens on 18 May 1980 removed the north half of its cone. The blast seared ridges. Subsequent pyroclastic flows, pumice deposits and lahars created a new landscape. The south slope was impacted by tephra. Starting in 1980, I established permanent plots to monitor vegetation establishment and recovery. This paper describes species turnover (colonization and extinction) in permanent quadrats on new surfaces (primary succession), intensely impacted sites (secondary succession) and recovered sites (tephra).

Study area

Mount St. Helens is centered at 46° 20' N, 122° 18' W, with an elevation of 2549 m. This study used 10 sets of permanent plots that represent unique combinations of impact intensity. Del Moral & Bliss (1993) provided a map and detailed descriptions of these sites.

Recovered sites were impacted by air-fall deposits of coarse pumice (tephra) that buried vegetation on the southern slopes of the cone up to 20 cm. The coarse texture, shallow depth and subsequent erosion permitted significant survival and rapid recovery (del Moral 1983).

Secondary succession sites received a variety of impacts. Blast A is on the west side of the cone, at the edge of the directed blast. The blast killed woody plants, but some dormant herbaceous vegetation survived. Rapid snow-melt formed lahars (mud-flows) that scoured canyons and ridges before forming deposits at lower elevations. Two ridges were scoured on the east side of the volcano. Scour A is within 100 m of surviving herbaceous vegetation, while Scour B is more isolated. Scour C is on the south side of the volcano.

Three primary succession habitats were sampled. Lahars formed on meadows on the south side of the cone (del Moral 1998). Proximity to intact vegetation permitted rapid establishment. Blast B, on the northwest cone, was destroyed by the lateral blast (del Moral 1993). The Pumice site on the north side was seared by the lateral blast and covered by pumice (del Moral et al. 1995; del Moral & Wood 1993).

Methods

Each plot is permanently marked to permit accurate repeated sampling. Species presence and cover were recorded at 1-m intervals on four radii ($n = 24$). From 1986 to the present, 0.25-m^2 quadrats have been used.

Colonization and extinction were calculated from 0.25-m^2 quadrats during three intervals. In most cases, comparisons were from 1986 to 1991, 1989 to 1994 and 1991 to 1997. Blast A sites were not sampled from 1988 to 1993, so comparisons were from 1986 to 1994, 1987 to 1995 and 1994 to 1997. Pumice sampling started in 1989, so comparisons were from 1989 to 1992, 1991 to 1995, and 1992 to 1997.

The extinction rate of a species is the fraction of quadrats occupied at T_0 that are empty at T_1. The colonization rate is the fraction of initially empty quadrats that are occupied at T_1 (Fröborg & Eriksson 1997). Empty quadrats usually greatly outnumbered filled ones, so the same number of events produces a higher extinction rate than a colonization rate. Therefore, the extinction and colonization rates were also calculated as a percentage of the total number of quadrats.

Trends were summarized in recovered, secondary and primary sites. At each site, for each yearly comparison, the percent colonization and extinction were compared. If one was at least twice the other, it was so scored and the total score converted to an index from –1 to +1. For example, there are six possible comparisons on recovered sites. If a species had predominant extinction on 1, no difference on 2, and predominant colonization on 3 of the comparisons, the index would be equal to 3 colonizations less the 1 extinction/6 comparisons, or +0.33.

Results

Extinction and colonization rates

Extinction and colonization rates were calculated for species with at least four occurrences (Table 1) and the means determined for each habitat. Extinction rates during the three intervals showed no strong pattern on recovered sites. On secondary sites, they increased slightly. On primary sites, they generally increased, as cover developed. These values are unstable because several species were infrequent and short lived (e.g. *Epilobium angustifolium*, *Lupinus lepidus* and *Hypochaeris radicata*).

Colonization rates were usually lower than the comparable extinction rates because there were more quadrats to be colonized for most species in any year. There were no trends on either recovered or secondary sites. On primary sites colonization rates may be increasing.

Extinction and colonization percentages

Extinction and colonization rates cannot be compared directly among sites or intervals because they are affected by sample sizes. Though imperfect, a better view of between- and within-site trends is provided by the percentage of all quadrats that changed during an interval (Table 2).

There were always more colonizations than extinctions at successional sites, while no pattern emerged on recovered sites. Extinction percentages were high on tephra (4.6 to 12.3% of total quadrats), moderate on secondary sites (1.2 to 4.9% of quadrats) and low on primary sites (0.6 to 5.2%). Colonization rates were relatively high in all cases and demonstrated no pattern between sites. Tephra sites varied from 3.9 to 17.0% of the quadrats, secondary sites varied from 5.8 to 15.3% of the quadrats, and primary sites varied from 3.9 to 15.9% of the quadrats. The disparity between these two processes is reflected by the ratio of extinctions to colonizations. These ratios approach 0.9 on recovered sites, vary from 0.26 to 0.45 on secondary sites and from 0.19 to 0.26 on primary sites.

Individual species patterns support the statistical summaries (Table 3). Species on recovered sites showed low index scores, indicating no trend of either colonization or extinction. Secondary and primary site scores were all positive, some strongly so. Most individual species colonized more often than they became locally extinct.

Discussion

The concept of local species turnover is embedded in recent studies of vegetation dynamics (Hanski 1982; Lavorel & Lebreton 1992; Collins et al. 1993; Hoagland & Collins 1997). The rate of turnover at small scales in stable meadows is high (van der Maarel & Sykes 1993; Herben et al. 1997). Fröborg & Eriksson (1997) showed that local colonization and extinction rates in a stable forest understory at a scale of 100 m^2 over a 20-yr interval were relatively high. Van der Maarel et al. (1995) suggested that there was little evidence for niche structure on a small scale, indirectly supporting a carousel model. Van der Maarel & Sykes (1997) quantified the rate of local mobility among species and found it much larger than generally recognized.

The present study shows that species are locally mobile. It differs from previous studies of local turnover in that it explores an intermediate scale and it investigates the process against a successional background. Species present in 1986 may have survived the 1980 impacts, arrived by long-distance dispersal or grown into the quadrat. Once present, a plant may be lost by senescence (e.g. *Lupinus lepidus*, *Hypochaeris radicata* and *Hieracium gracile*), grazing (e.g. *Aster ledophyllus* and *Castilleja miniata*), die-back (e.g. *Penstemon cardwellii* and *Polygonum newberryi*), or competitive displacement from species such as *Agrostis diegoensis*.

Extinction rates in recovered, secondary and primary sites were similar and generally high. The highest rates

Table 1. Mean extinction and colonization rates on Mount St. Helens. The extinction rate is the fraction of quadrats that contained the species in the first year but lost that species by the next comparison year. The colonization rate is that fraction of empty quadrats in the base year that acquired that species by the next comparison.

	Recovered sites			Secondary sites				Primary sites		
	Tephra A	Tephra B	Tephra C	Scour A	Blast A	Scour B	Scour C	Lahar	Blast B	Pumice
Extinction Rate I	.36	.36	.20	.11	.24	.26	.24	.32	.03	.44
Extinction Rate II	.52	.34	.25	.16	.30	.26	.18	.08	.30	.35
Extinction Rate III	.37	.33	.29	.17	.29	.28	.33	.66	.39	.71
Colonization Rate I	.32	.10	.09	.06	.26	.16	.07	.08	.07	.04
Colonization Rate II	.20	.07	.11	.16	.23	.13	.07	.14	.16	.07
Colonization Rate III	.14	.12	.15	.09	.17	.14	.12	.11	.18	.11

Table 2. Mean extinction and colonization percentages on Mount St. Helens, calculated as the fraction of the total number of quadrats that were affected. The extinction to percent ratio was calculated from the mean rates.

	Recovered sites			Secondary sites				Primary sites		
	Tephra A	Tephra B	Tephra C	Scour A	Blast A	Scour B	Scour C	Lahar	Blast B	Pumice
Extinction % I	5.3	4.7	4.6	2.6	1.8	2.5	2.0	0.9	1.8	0.7
Extinction & II	12.3	6.3	4.8	2.8	4.9	3.3	1.2	0.9	0.6	1.5
Extinction % III	9.1	6.8	6.5	3.7	4.7	4.7	2.5	5.2	4.7	1.8
Mean Extinction Percent	**8.9**	**5.9**	**5.3**	**3.0**	**3.8**	**3.5**	**1.9**	**2.3**	**2.3**	**1.3**
Colonization % I	17.0	6.5	6.2	5.8	13.2	12.0	5.8	6.2	13.2	3.9
Colonization % II	6.1	3.9	7.1	7.6	15.3	8.3	6.8	12.4	15.9	6.1
Colonization % III	6.2	10.3	9.3	6.8	6.5	8.7	9.5	7.9	6.5	6.7
Mean Colonization Percent	**9.8**	**6.9**	**7.5**	**6.7**	**11.7**	**9.7**	**7.4**	**8.8**	**11.9**	**5.6**
Extinction/Colonization ratio	**0.91**	**0.86**	**0.71**	**0.45**	**0.32**	**0.36**	**0.26**	**0.26**	**0.19**	**0.23**

Table 3. Net extinction and colonization of representative species in each successional category. Values range from – 1.0 to +1.0 (see Text). Blanks indicate species absent or rare.

Species	Recovered	Secondary	Primary
Abies lasiocarpa			0.33
Agrostis diegoensis	0.5	0.88	0.67
Anaphalis margaritacea			0.5
Aster diegoensis	–0.33	0.12	
Carex mertensii		0.38	0.33
C. rossii	0.16		
Eriogonum pyrolifolium	–0.33	0.75	0.16
Hieracium albiflorum		0.25	0.33
H. gracile		0.25	
Hypochaeris radicata			0.67
Juncus parryi	0.16	0.75	0.33
Lomatium martindalei	0.0	0.25	0.16
Luetkea pectinata	0.0	0.5	0.33
Lupinus lepidus	0.0	0.25	0.67
Penstemon cardwellii		0.63	0.83
Pinus contorta			0.33
Polygonum newberryi	0.33	0.25	0.16
Spraguea umbellata		0.5	0.33
Stipa occidentalis		0.63	0.16

occurred on primary surfaces during the last increment. The development of these primary successional sites masks these high extinction rates. The extinction percentage declined from recovered to primary sites because there were far fewer quadrats with species at risk in primary sites than in stable ones. However, as successional sites developed, the extinction percent increased substantially.

The colonization rate was high, even on recovered sites. Empty plots are colonized at similar rates on all sites, provided neighbors are present. Colonization percentages, expressed as a percentage of all quadrats, are similar on all surfaces. This implies that population dynamics are similar on all sites. The ratio of extinction to colonization percentages provides a good basis for comparison. In recovered sites, extinction events are nearly as frequent as colonization events, varying largely with summer moisture conditions. In secondary sites, extinction events are one third as common as colonization events. On primary sites colonization events are more than four times more common than extinction events.

Small-scale extinctions and colonizations are based on individual life histories, dispersal ability and proximity to seed sources. Some deterministic extinction may have occurred in well-vegetated plots, but rates were also high in open plots. Colonization rates were no lower in recovered sites than the others, suggesting that the presence of moderately dense vegetation does not inhibit invasion. Stochastic extinction and colonization appear to dominate local population dynamics of successional sites. While successional status affected these rates, each habitat is dynamic. Species appear and disappear in ways consistent with the carousel model. The species in these habitats do not have narrow, discrete niches. Therefore, they may coexist in small samples or they may replace one another in a non-deterministic way.

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The northern slope of Mount Prado: a diversity hot spot within northern Apennine summit vegetation

Ferrari, C.*, Pezzi, G. & Portanova, A.

University of Bologna, Department of Evolutionary Biology, via Irnerio 42, I-40126 Bologna, Italy;
**Fax +39051242576; E-mail ferrari@alma.unibo.it*

Abstract. Mount Prado (2054 m a.s.l.) lies along the main ridge of the Northern Apennines at 44°14' N and 10°23' E. It is one of the highest peaks of this chain, whose areas above the timberline can be regarded as an 'archipelago' of alpine islands on the boundary between the Central European and Mediterranean regions in Italy. Timberline is at ca. 1800 m a.s.l. and corresponds to the local altitudinal limit of *Fagus* woods. The lithological substrate is a turbiditic compact sandstone (Upper Oligocene-Lower Miocene). Its northern slope is characterized by one of the widest and most typical Würm glacial cirques of the Northern Apennines. Its flora contains 208 taxa (including mosses and lichens) of the 391 taxa now known for the Northern Apennine summit flora. They form 22 plant communities (i.e. 73% of the plant communities described for the whole Northern Apennine summit vegetation). The vegetation mosaic is dominated by two *Vaccinium*-communities and the remaining communities cover small or very small areas. 41 rare taxa occur. Their types of rarity mainly relate to peripheral geographic distribution and, to a lesser extent, to habitat specificity, narrow geographic range and small population size. Plant community spatial data and distribution of rare species were compared. The highest frequency of rare species is found mainly in species-rich communities settled on small areas, at higher altitudes on NW-facing sites. These communities are some acidophytic and mesophytic grasslands, a snow-bed community (*Salicetum herbaceae*) and the rock-face community *Drabo aizoidis-Primuletum apenninae*. As a whole, such communities may be considered a 'focal point' within the vegetation considered.

Keywords: Italy; Phytogeography; Plant diversity.

Nomenclature: Pignatti (1982) for vascular plants except for the genus *Festuca* (Foggi & Rossi 1996; Foggi et al. 1999); Ellenberg (1988) & Grabherr (1993) for higher syntaxa; see Table 1 for other syntaxa.

Introduction

In the Northern Apennines, whose ridge is to be considered as the boundary between the Central European and Mediterranean phytogeographic regions in Italy (Pignatti 1979), the areas above the timberline are small and scattered. The summit flora contains 391 species. Phytogeographic analyses (Foggi 1990; Tomaselli & Agostini 1994) showed that its taxa are strictly connected with those of the Alps and, through these, with the alpine flora of other Central Europe mountains. The few endemics are closely related either to European orophytes or Alpine taxa. Ecological 'insularity' of the alpine vegetation belt and peripheral occurrence in the distribution area of most taxa, make the summit flora of these mountains a vulnerable natural wealth. Up to now, 30 plant communities have been described. *Vaccinium*-heaths are the climatic climax (Pignatti 1994; Ferrari & Piccoli 1997). Within the alpine islands of the northern Apennines the northern slope of Mt. Prado is outstanding for its vegetation diversity. It contains 22 plant communities, some of them being restricted to this mountain, such as the snow-bed associations *Salicetum herbaceae* and *Oligotricho-Gnaphalietum supini* (Tomaselli 1991). All communities have a high degree of naturalness (according to Westhoff 1983). Such mountain may be considered a diversity 'hot spot' (Wilson 1992) for the alpine vegetation of this chain, as well as a reliable study area for investigating its vegetation ecology and for monitoring the vegetation changes as bioindicators of climatic changes.

Material and Methods

Study area

Mt. Prado, or Prato (2054 m a.s.l.), is located on the main ridge of the northern Apennines at 44°14' N and 10°23' E. Its northern slope is characterized by one of the widest and most typical Würm glacial cirques of the northern Apennines (Losacco 1982). The timberline occurs at about 1750 m and the glacial cirque is above the timberline. The cirque has steep and rocky walls, with prevailing N and NW exposures. Its base is level and crossed by three orders of morainal deposits which probably correspond to different stages of glacial retreat and which enclose small wet areas. Periglacial morphogenesis is still active, mainly in spring and autumn, when the soil may be free from snow (Carton & Panizza 1988). The lithological substrate is a turbiditic compact sandstone (Upper Oligocene-Lower Miocene), locally named 'Macigno'. Annual precipitation ranges from 1000 to 3500 mm, with an average of 2000 mm (Rossetti 1988). From November to April, precipitation mostly occurs as snow and snow melts from May to the beginning of July, according to differences in topography and exposure.

Data handling

Species sampling was carried out from 1992 to 1994. For each taxon its local rarity was evaluated by calculating its Rarity Index (Géhu & Géhu 1980), as follows:

$$RI = 1 - (n/N) \qquad (1)$$

where N is the number of quadrants of the grid of the Atlas of the Central European Flora (Ehrendorfer & Hamann 1965; Ferrari et al. 1993) which include the northern Apennine areas above the timberline (N=28), and n is the number of quadrants where the taxon is found. Only the taxa with $RI > 0.20$ were considered as rare taxa.

Data on vegetation pattern are reported from Ferrari & Pezzi (1999). Their computerised vegetation map was used for describing the spatial distribution of the communities with the highest frequencies of rare species.

Table 1. List of plant communities.

Plant community		References
***Vaccinium* - heaths (*Rhododendro-Vaccinietalia* Br.-Bl. in Br.-Bl. et Jenny 1926)**		
Ve	*Empetro-Vaccinietum gaultherioidis* Br.-Bl.in Br.-Bl. et Jenny 1926 corr. Grabherr 1993 *juncetosum trifidi* Ferrari et Piccoli 1997.	Ferrari & Piccoli (1997)
Vh	*Hyperico richeri-Vaccinietum gaultherioidis* Pirola et Corbetta 1971 nom. inv.	Ferrari & Piccoli (1997)
Vb	*Vaccinium myrtillus - Brachypodium genuense* community	Ferrari & Piccoli (1997)
***Nardus* - grasslands (*Nardetalia* Oberd. 1949 em. Prsg 1949)**		
Gn	*Geo montani-Nardetum* Lüdi 1948	Tomaselli (1994)
Vn	*Violo cavillieri - Nardetum* Credaro et Pirola 1975 corr. Tomaselli 1994	Tomaselli (1994)
Ln	*Luzula alpino-pilosa - Nardus stricta* community	Tomaselli (1994)
Acidophytic grasslands (*Caricetalia curvulae* Br.Bl. in Br.-Bl. et Jenny 1926)		
St	*Sileno exscapae - Trifolietum alpini* Tomaselli et Rossi 1994	Tomaselli & Rossi (1994)
Ci	*Sileno exscapae - Trifolietum alpini, Cetraria islandica* variant Tomaselli et Rossi 1994	Tomaselli & Rossi (1994)
Ls	*Sileno exscapae - Trifolietum alpini luzuletosum spicatae* Tomaselli et Rossi 1994	Tomaselli & Rossi (1994)
Gs	*Sileno exscapae - Trifolietum alpini luzuletosum spicatae. Gnaphalium supinum* variant Tomaselli et Rossi 1994	Tomaselli & Rossi (1994)
Mesophytic grasslands (Syntaxonomy not yet defined)		
Fe	*Festuca* spec. community	Ferrari (unpubl.)
Tf	*Trifolio- Festucetum puccinellii* ass. nova prov. Rossi 1994	Rossi (1994)
Dc	*Deschampsia caespitosa* community	Ferrari (unpubl.)
Aa	*Aquilegio – Anemonetum narcissiflorae* Tomaselli 1994	Tomaselli (1994)
Bg	*Brachypodium genuense* community	Barbero & Bonin (1980)
La	*Trifolio- Festucetum puccinellii* ass. nova prov, *Luzula alpino-pilosa* variant Rossi 1994	Rossi (1994)
Snow - beds (*Salicetalia herbaceae* Br.Bl. in Br.-Bl. et Jenny 1926)		
Sh	*Salicetum herbaceae* Rübel 1912	Tomaselli (1991)
Og	*Oligotricho - Gnaphalietum supini* Tomaselli 1991	Tomaselli (1991)
Large-stoned scree vegetation (*Androsacetalia alpinae* Br.Bl. in Br.-Bl. et Jenny 1926)		
Cd	*Cryptogrammo - Dryopteridetum oreadis* Rivas - Martinez in Rivas - Martinez et Costa 1970	Tomaselli (1994)
Rock face vegetation (*Androsacetalia vandellii* Br.-Bl in Meier er Br.Bl. 1934)		
Dp	*Drabo aizoidis - Primuletum apenninae* Tomaselli 1994	Tomaselli (1994)
Acid fen vegetation (*Caricetalia nigrae* (W. Koch 1926) Nordh. 1936)		
Cn	*Caricetum nigrae* Br.-Bl. 1915, *Sphagnum subsecundum* variant	Ferrari (unpubl.)
Brooklet vegetation (*Montio-Cardaminetalia* Br. – Bl. et Tx. ex Klika et Hadač 1944)		
Cc	*Chaerophyllo – Cardaminetum asarifoliae* Gerdol et Tomaselli 1988	Gerdol & Tomaselli (1988)

Results

The 22 plant communities which are established on the northern slope of Mt. Prado are listed in Table 1. The whole local flora includes 208 taxa (species and subspecies; a checklist is available from the authors upon request).

Table 2 shows the 41 taxa with a rarity index (*RI*) > 0.20 and their occurrence in the plant communities. The degree of rarity varies from very high values ($RI = 0.97$) to medium-low values ($RI = 0.23$). The types of rarity mainly relate to peripheral geographic distribution and, to a lesser extent, to the other types of rarity (habitat specificity, narrow geographic range and small population size). However, high *RI*-values are prevailing: 20 species have *RI* 3 0.80. These species rarities are mostly due to peripheral distributions, seldom coupled with small population sizes and habitat specificity. One species (*Primula apennina*) is endemic and one (*Senecio incanus*) is a subendemic. 19 rare species are found in just one community.

Table 3 shows that communities with the highest frequency of rare species (R/N) are species-rich communities which cover small or very small areas, mainly with high patchiness. They are the acidophytic grasslands St, La, Ls, Gs, some mesophytic grasslands (Fe, Tf), the rock face community Dp and the snowbed community Sh.

The spatial distribution of the communities with the highest frequency of rare species is shown by Fig. 1.

Table 3. Data on vegetation pattern and rare species distribution. The vegetation map is shown in Fig. 1. *N* = number of species; *R* = number of rare species; *RI*: rarity index. For abbreviations of plant community names, see Table 1.

Plant community	Area (m^2)	Patches	*N*	*R*	*R/N*
Ve	176469	32	58	8	0.13
Vh	96722	15	60	11	0.19
Vb	21747	7	48	4	0.08
St	19819	8	53	17	0.32
Ci	447	1	37	3	0.08
Ls	15197	14	61	16	0.26
Gs	14666	14	45	10	0.22
Sh	6601	5	47	12	0.26
Og	4226	10	44	5	0.11
Cd	15774	23	31	3	0.09
La	3695	7	49	15	0.31
Tf	6406	4	23	6	0.26
Bg	251	2	26	3	0.12
Gn	8018	2	29	4	0.14
Vn	12892	8	28	5	0.18
Ln	10340	20	20	4	0.20
Dp	6059	18	22	6	0.26
Cn	5408	3	24	4	0.17
Fe	2832	3	22	6	0.27
Dc	160	1	9	1	0.11
Aa	.	.	30	5	0.17
Cc	.	.	22	1	0.05

Table 2. Rare species and their distribution in Mt. Prado plant communities. Chorotypes and types of rarity are indicated. Chorotypes: AA = arctic-alpine; CS = cosmopolitan; EN =endemic; EU = Eurasian; OR = orophyte; SC = subcosmopolitan; SN = subendemic. Abbreviations of rarity types are: Gr =narrow geographic range; Hs = habitat specificity; Pd = Peripheral distribution; Sp = small population size. Other explanations in the text. For abbreviations of plant community names, see Table 1.

RI	Taxon	Plant communities	Chorotype	Type of rarity
0.97	*Hieracium glanduliferum*	St	OR	Pd/Sp
0.97	*Leucanthemopsis alpina*	St, Ls, Sh, Fe	OR	Pd
0.97	*Pedicularis rostratospicata*	Ls	OR	Pd/Sp
0.97	*Salix breviserrata*	Ve	AA	Pd/Sp
0.97	*Salix herbacea*	St, Sh, La	AA	Pd/Hs/Sp
0.97	*Senecio incanus*	St, Ls, Gs, Sh, La	SN	Pd
0.97	*Soldanella pusilla*	Og	OR	Pd/Hs
0.90	*Carex foetida*	Ln	OR	Hs/Sp
0.90	*Gnaphalium supinum*	St, Ls, Gs, Sh, Og, La,Vn, Ln	AA	Pd
0.90	*Luzula lutea*	Ve	OR	Pd
0.90	*Lychnis alpina*	Gs, Sh, La	AA	Pd/Sp
0.87	*Luzula alpino-pilosa*	St, Ls, Gs, Sh, Og, Cd, La, Gn, Vn, Aa	AA	Pd
0.87	*Polygonum viviparum*	Tf	AA	Hs/Sp
0.83	*Carex ornithopoda*	Tf, Aa	EU	Pd
0.83	*Gentiana nivalis*	Ls	AA	Pd/Sp
0.83	*Soldanella alpina*	Vh, Ve, La	OR	Sp
0.83	*Viola palustris*	Cn	CB	Hs/Sp
0.80	*Carex canescens*	Cn	CS	Hs
0.80	*Primula apennina*	Dp	EN	Gr
0.80	*Silene acaulis* ssp. *bryoides*	St, Ls, Gs, Sh, La, Dp	AA	Pd
0.77	*Rhododendron ferrugineum*	Vn	OR	Pd/Sp
0.73	*Erigeron uniflorus*	Ls	AA	Pd/Sp
0.73	*Euphrasia alpina*	St, Ci, Ls, Gs, Sh, Og, Tf, Gn, Vn	OR	Pd
0.73	*Euphrasia minima*	Vh, Ve, Vb, St, Ci, Ls, Gs, Sh, Og, La, Gn, Vn, Ln, Fe	OR	Pd
0.70	*Lycopodium annotinum*	Vh,Vb	CB	Pd/Sp
0.63	*Armeria marginata*	La	SN	Gr
0.60	*Saxifraga latina*	Dp	EN	Gr/Sp
0.57	*Huperzia selago*	Vh, Ve, Vb, La	SC	Sp
0.57	*Sempervivum montanum*	Vh, Ve, Ls, Dp	OR	Pd
0.50	*Gentiana purpurea*	Ve, Gs, La, Fe	OR	Pd
0.43	*Leuchorchis albida*	Gn	AA	Sp
0.43	*Pinguicula vulgaris*	Cn, Cc	EU	Hs/Pd
0.40	*Botrychium lunaria*	Ls, Gn	SC	Sp
0.40	*Festuca violacea* ssp. *puccinellii*	Cd, Tf, Dp, Cn, Dc	EN	Pd
0.40	*Sempervivum arachnoideum*	St	OR	Sp
0.40	*Viola calcarata* ssp. *cavillierii*	Vh, Ve, St, Ls, Gs, Sh, La, Bg	EN	Gr
0.37	*Saxifraga moschata*	Dp	OR	Sp
0.27	*Aster bellidiastrum*	Ve, St, Ci, Gs, Cd, La, Tf, Dp, Fe, Aa	OR	Sp
0.27	*Astrantia minor*	Vh, Ve, St, La, Fe, Aa	OR	Pd
0.27	*Festuca riccerii*	St	EN	Gr
0.23	*Aster alpinus*	St, Ls	CB	Sp

Discussion

The northern slope of Mt. Prado is characterised by a rich natural vegetation mosaic dominated by *Vaccinium gaultherioides* and *Vaccinium myrtillus* heaths. There are many plant communities with high patchiness. Their patches mostly cover small or very small areas as spatial patterns are strongly affected by the glacial cirque landform discontinuities which cause steep ecological gradients. All the communities contain species that are rare for the northern Apennines, even if their type and degree of rarity are different. The very rare species are prevailing. Rarity is mainly due to geographic peripheral distribution, but small population size, habitat specificity and narrow geographic range are (in descending frequency) the other types of rarity.

The highest numbers of rare species can be found in some species-rich communities which cover small areas, i.e. in communities with the highest species density. Such communities are the *Sileno exscapae-Trifolietum alpini* (Ls, St), the *Trifolio-Festucetum puccinellii, Luzula alpino-pilosa* variant (La), the snowbed communities, *Salicetum herbaceae* (Sh). They are linked to sites with a long duration of snow cover (Ferrari & Rossi 1995). As far as we know their northern Apennine distribution is restricted to Mt. Prado. To these communities we have to add the mesophytic *Festuca*-grassland and *Trifolio-Festucetum puccinellii*, as well as the rock-face association *Drabo aizoidis-Primuletum apenninae*, which have a high frequency of rare species.

All communities are situated mostly in the highest part of the glacial cirque, on sites with mainly NW exposures (Ferrari & Pezzi 1999). The highest parts of the Mt. Prado glacial cirque show an unusual concentration of environmental resources for both the rare communities and species within the alpine vegetation of the northern Apennines. According to Walker (1995), the summit sites of Mt. Prado – altogether – may be considered a 'focal point' within a diversity hot spot! The Mt. Prado glacial cirque contains a natural wealth due to its unique high plant diversity within the northern Apennines.

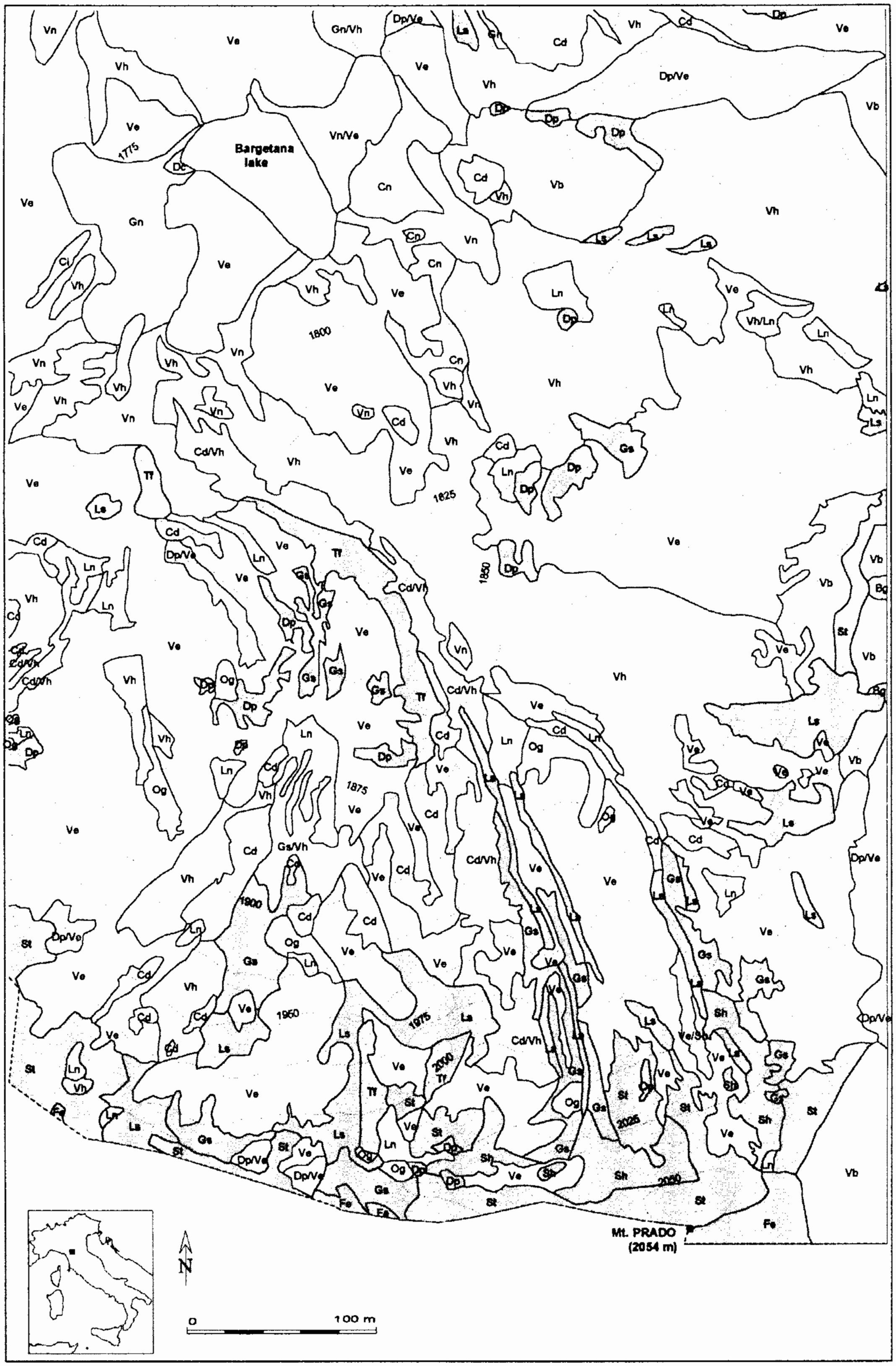

Fig. 1. Vegetation map of the Mt. Prado glacial cirque. Plant communities are listed in Table 1. Two communities (Aa and Cc) are not shown due to scale of the map. Grey patches: communities with the highest frequency of rare species.

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Succession and zonation in the Hawaiian Islands

Mueller-Dombois, Dieter

Botany Department, University of Hawai'i, Honolulu, HI 96822, USA;
Fax +18082541873; E-mail amdhawaii@aol.com

Abstract. Vegetation succession in the Hawaiian Islands is predictable in its montane rain forest biome up to an early stage of soil development. In lowland and seasonal environments, and in more advanced stages of soil development, the influx of alien species often produces changing patterns and processes. An example is the explosive spread of the introduced *Myrica faya* (native to Macaronesia) into a geologically young montane seasonal zone, originally dominated by the native *Metrosideros polymorpha* tree. In more advanced stages of soil weathering, the dieback dynamics of *M. polymorpha* provides entry of new alien dominants. A significant process of change is 'species packing' rather than 'species extinction', although the latter is certainly true for some of the rare species. In the early stages of succession, vegetation zonation is primarily vertical, following the outline of lava flows. As the rock surfaces weather into soils, zonation becomes horizontal, thereby offering an enriched spectrum of habitats for species diversification. In spite of this habitat richness, the Hawaiian flora did evolve only into ca. 1000 vascular plant species. This is the principal reason for the vulnerability of Hawai'i's native ecosystems to alien species invasion.

Keywords: Alien species; Dry forest; Ecological release; Forest dieback; Invasion; Primary succession; Species packing; Stability; Tropical rain forest; Vegetation dynamics.

Introduction

When bringing succession and zonation together under one topic, it is important to remember that succession is a time concept and zonation a spatial concept. Succession, however, is a long-term process, and our human life-span allows only the study of 'glimpses' of successional change. This dilemma has led to the practice of deriving successional information through the study of side-by-side vegetation patterns which originated after major disturbances at different times. This is known as the space-for-time concept in vegetation ecology. Results remain hypothetical.

However, if the disturbances have been similar and their dates are known , and if the habitats are closely comparable, such space-for-time studies may yield useful predictions. Volcanic areas with known substrate origins, as found in the Hawaiian Islands, are particularly suitable for studying chronosequences of vegetation and soil development. These studies began on the lava flows of the Big Island (Hawai'i) and were continued along the island-age sequence (Fig. 1). I will summarize the topic in four sections: primary succession, zonation shift, effects of key invaders, and conclusions on ecosystem stability.

Primary succession in the Hawaiian rain forest

In the windward rain forest environment, new lava flows are invaded by cryptogams and higher plants as soon as the rock surfaces cool. Bluegreen algae and mosses appear immediately but do not become dominant. Instead a lichen, *Stereocaulon vulcani*, often forms a dominant cover on the lava-rock surfaces within five years in the humid lowlands and more slowly in the uplands. Simultaneously some of the cracks among the rock surfaces become invaded by ferns and seed plants. Most abundant among these are individuals of the sword fern *Nephrolepis multiflora* and the endemic tree, *Metrosideros polymorpha* (*Myrtaceae*).

The lichen dominates the scene until the seedlings of *M. polymorpha* reach the young adult stage. This may take from 50 - 100 yr. During that time, several pioneer shrub and forb populations enter the lava fields, some only temporarily. Among the temporary shrubs is *Dubautia scabra* (*Asteraceae*), an endemic mat-forming short-lived perennial. A few individuals of this shrub may enter a new volcanic substrate in one or several localities, then expand rapidly into small cohort populations. After developing a population peak in a few years, most individuals become senescent and begin to die. A subpopulation or next generation may then appear in a neighboring location on the new surface and repeat the growth cycle there. Its dying mats often become favorable places for early successional plants. A similar ephemeral behavior is shown by the endemic shrub *Rumex giganteus* (*Polygonaceae*). Other pioneer shrubs, such as the endemic *Vaccinium reticulatum,* are longer-lived perennials. They also may swarm over only parts of the new surface. Their dispersal depends mostly on berry-feeding birds. A tall fern, an 'almost-tree-fern', *Sadleria cyatheoides,* colonizes by an abundance of wind-driven spores, but establishes only as widely scattered individuals or in small groups. Much depends on the dispersal mechanism and favorable microhabitats. In all cases, woody and herbaceous plant growth develops into only a sparse vegetation cover. That is why the lichen stage can persist for so many years.

A next major change occurs when the indigenous mat-forming fern *Dicranopteris linearis* is spreading itself by fast-growing stolons among the still open-grown and juvenile *Metrosideros* forest. This fern causes the local extinction of the *Stereocaulon* lichen cover. It also prevents further establishment of *Metrosideros* seedlings. Although this fern soon dominates the undergrowth, a few other plants usually are associated with it. They include the tall sedge *Machaerina angustifolia* and the clubmoss *Lycopodium cernuum.* Among shrubs, *Vaccinium calycinum* may be added or replace *Vaccinium reticulatum.* Another heath shrub *Styphelia tameiameiae* as well as the tall *Sadleria* fern may persist.

When the *Metrosideros* forest develops a closer canopy, tree ferns of *Cibotium* spp. begin to penetrate through the weakening *Dicranopteris* mat. The expanding fronds of the tree ferns then aid in the decline of the light-demanding *Dicranopteris.* At that time also, several arborescent shrubs and small trees appear among the tree ferns. They include

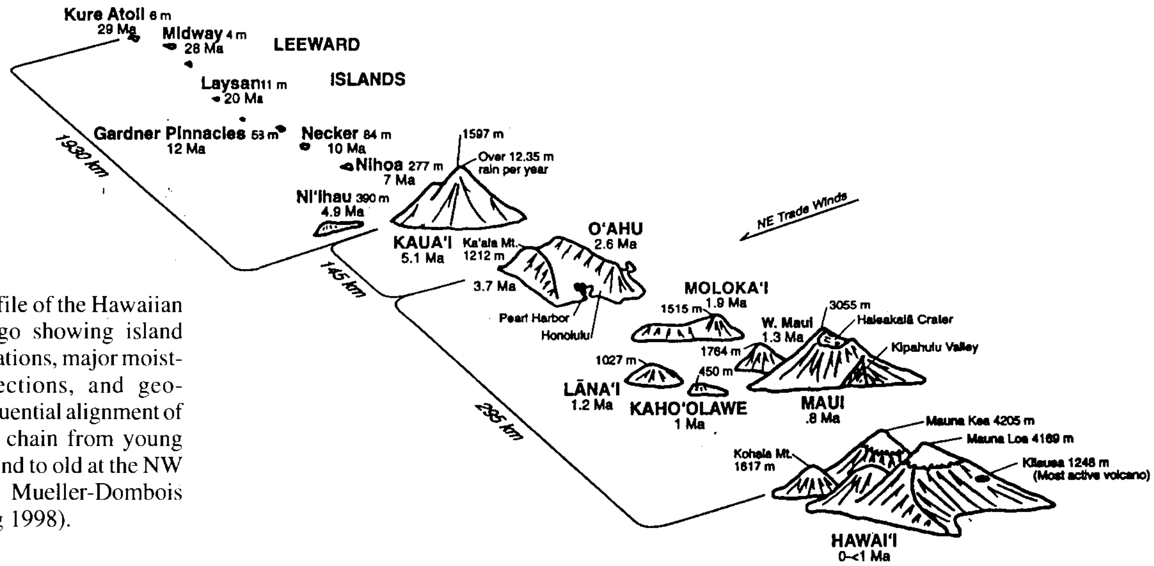

Fig. 1 Profile of the Hawaiian Archipelago showing island ages, elevations, major moist-wind directions, and geochronosequential alignment of the island chain from young at the SE end to old at the NW end (after Mueller-Dombois & Fosberg 1998).

members of the *Rubiaceae*, *Gesneraceae*, *Rutaceae*, *Araliaceae*, *Myrsinaceae*, *Aquifoliaceae* and *Lobeliaceae*, but no saplings of *Metrosideros polymorpha*. Rarely does any member of the associated woody plant families join the *Metrosideros* canopy. The mature Hawaiian rain forest thus develops a monodominant canopy in primary succession together with an almost monodominant tree fern subcanopy.

If a stand-destroying volcanic eruption does not recur, a fifth stage may be added. This is the canopy dieback stage. Eventually, the mature *Metrosideros* forest will reach a point in time when its canopy trees begin to senesce. If in this stage, the forest is subjected to growth-impeding climatic perturbations, its canopy can collapse 'domino-style' over the entire volcanic substrate that gave rise to the forest (Akashi & Mueller-Dombois 1995).

Zonation shift from vertical to horizontal

An important peculiarity of the Hawaiian vegetation is the wide altitudinal range of a number of native forest dominants. This wide altitudinal distribution of native key species creates a vertically oriented zonation pattern, which is related to two factors, 'ecological release', and 'edaphic zonation'. Ecological release is the outcome of successful establishment when the early island plant communities offered little or no competition to the advance of aggressive, indigenous invaders. These species therefore spread over a wide altitudinal range from near sea level inward of the strand zone to the high altitude environment at about 2500 m. The shrubs *Styphelia* and *Vaccinium* climbed even much higher, where they form major components of the alpine heath-scrub below and above 3000 m elevation.

On Mauna Loa, zonation is typically vertical or azonal, following the course of lava flows. The stages in rain forest succession, as indicated by lichen, fern, and seed plant species are essentially similar from sea level to the inversion zone near 2000 m elevation. The only significant differentiation is the rate of primary succession, which is much faster at low elevation than near the inversion zone.

Following primary succession, when lava rocks weather into soils, vegetation zonation becomes more strongly controlled by climate and geomorphological development. The result is a shift to horizontal zonation as evidenced by an altitudinal stratification of vegetation patterns. The topographic vegetation profile (Fig. 2) on the 410 000-yr old windward slope of Haleakalā Mountain on East Maui demonstrates the zonation shift from vertical to horizontal as follows: The leading canopy species, *M. polymorpha*, is distributed from the lowland to the treeline at 2 200 m. There are two overlapping varieties, the pubescent leafed var. *incana* and the glabrous leafed var. *glaberrima*. These varieties have been recognized as having a successional relationship, the pubescent being more prevalent in the early pioneer stages, the glabrous becoming more prevalent on older, more developed soil substrates (Mueller-Dombois 1983a,b; Stemmermann 1983; Kitayama et al. 1995, 1997). In terms of water relations, the pubescent form can withstand soil drying to a greater degree than the glabrous varieties. Thus, the altitudinally wide-ranging *Metrosideros* canopy tree dominates over a broad vertical (altitudinal) zone.

Horizontal stratification is beginning to show (on Fig. 2) by a decreasing size and canopy structure downslope and by differentiating species in the undergrowth. The lowest unit (A1) has gone through a forest dieback on volcanic shield remnants. These shield remnants are frequently flooded and are slowly cut by streams into smaller topographic segments. On the Haleakalā east slope, this is a zone of habitat diversification, which continues upslope to about 1800 m elevation, where the frequently flooded positions are more patchy. Above 1200 m, the shield is still very much intact. There the *Metrosideros* trees are taller and the substrate is more permeable and thus better drained. This improved soil drainage pattern occurs within the cloud-frequented zone up to the inversion zone near 2000 m. Above the inversion layer, the climate becomes abruptly seasonal (with summer-drought). Here, *Sophora chrysophylla*, together with other shrubs, form a subalpine scrub in which *Metrosideros* occurs only as scattered remnant trees left over from a former pioneer stage.

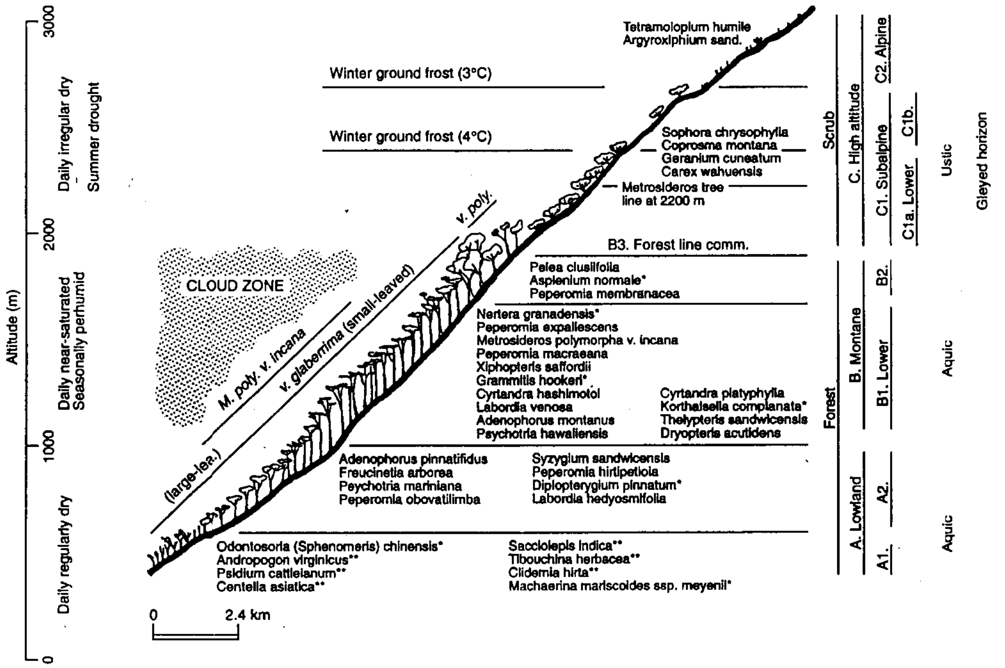

Fig. 2 Topographic vegetation profile of wet slope on Haleakalā Mt., Island of Maui (after Kitayama & Mueller-Dombois 1994, slightly modified). The profile demonstrates the shift from vertical zonation, as indicated by the two altitudinally wide-ranging dominant *Metrosideros* varieties, to horizontal zonation as indicated by the differentiating species in the undergrowth.

It still forms the treeline at 2200 m.

Thus, the altitudinal zones on the tradewind side of Haleakalā are controlled largely by two factors, the geomorphological aging process and the changing climate upslope. These factors produce a horizontal zonation which is reflected in the undergrowth vegetation by a number of differentiating species, many of which are ferns. A native vine, *Freycinetia arborea* (*Pandanaceae*), can be used as a key indicator species, separating lowland from montane rain forest at 1000 m.

Succession and zonation with key alien invaders

The majority of differentiating species, which characterize the forest dieback zone floristically (zone A1 on Fig. 2), are introduced or alien species. Only two of the differentiating species are indigenous. The indigenous fern *Odontosoria chinensis* is strictly a heliophyte that became established in response to the loss of *Metrosideros* canopy. The other is the native sedge, *Machaerina mariscoides*, which is an indicator of both wet soil and canopy openness. In this case, the six alien species strengthen the floristic differentiation of this lowland vegetation zone. The paperbark tree, *Melaleuca quinquenervia* (*Myrtaceae*), native in New Caledonia and North Queensland, is now rapidly spreading through the dieback zone, overlapping with the scrubby recovered growth of *Metrosideros*. *M. quinquenervia* seedlings were planted in parts of the dieback zone in the 1930s to replace the forest cover that had deteriorated through the dieback of the native *Metrosideros* forest.

The best studied example of an alien species causing changes in succession is *Myrica faya* (*Myricaceae*) (Vitousek et al. 1987; Walker & Vitousek 1991; Tunison 1998). The species was introduced around the turn of the century from the Macaronesian Islands to the island of Hawai'i and others. One tree was noted in Hawai'i Volcanoes National Park in the early 1960s. By the late 1960s, the species began to spread explosively throughout the geologically young, open submontane seasonal environment of the Park. This is one of six vegetation zones in this geologically young territory. The spread of *M. faya* was facilitated by two factors, alien birds, particularly the Japanese white eye (*Zosterops japonicus*), and the presence of *Metrosideros* trees. The Japanese white eye feeds on the fruits of *M. faya* and is also attracted by the nectar in the *Metrosideros* flowers. It uses the *Metrosideros* trees as perch trees and *Myrica* often became established near the bases of the *Metrosideros* trees. A third factor favoring *Myrica*, is its ability to fix nitrogen with an actinorrhizal symbiont (*Frankia*) in root nodules. *Myrica* trees grow many times faster than *Metrosideros*. In a decade, numerous *Myrica* trees were able to join the *Metrosideros* canopy.

The aggressive behavior of alien invaders, such as *M. faya*, gave the impression that their distributional advances surpass that of the successful indigenous invaders. We tested this popular notion on the wet slope of Haleakalā mountain by asking the question, "do alien plant species have wider ecological ranges than native species?" (Kitayama & Mueller-Dombois 1995). The answer turned out to be negative.

Although successional alien invaders may have an advantage by being a new ecological species not yet available among the natives, their release in the new island environment is usually limited by their past adaptation to the climatic and edaphic vegetation zones in their home environment. For *M. faya*, this means the species will not spread from the submontane seasonal environment into the warm-tropical lowlands on either the seasonally dry leeward or the year-round moist windward sides. It will also not spread into the subalpine environment. All of these contain *Metrosideros polymorpha* in geologically young areas.

Conclusions regarding ecosystem stability

The Hawaiian Islands represent a large, isolated archipelago. Thus, their species richness, before human contact, was low, allowing for ecological release of indigenous invaders and considerable secondary enrichment through speciation. The number of indigenous colonizers of flowering plants are estimated as 272 species. Less than half of these gave rise to 850 endemic species, resulting in a current estimate of ca. 1000 native Hawaiian species. The total adventive flora is estimated as ca. 4000 species. Of these, 860 species have become naturalized with another 10% of them having assumed distributional dominance that has affected changes in succession and zonation.

Compared to the species richness of similarly sized tropical land areas, Hawaii's inventory of 1000 native species is far below its natural stocking capacity. Although the threat of extinction of rare endemics is real and of great concern, what we witness far more than species extinction is the opposite, namely species packing.

The primary succession from barren lava flow to mature *Metrosideros-Cibotium* rain forest is still functioning well in the volcanically active areas on Mauna Loa and Kilauea without much species packing. On older substrates, the perpetuation of *Metrosideros* as the dominant canopy species through auto-succession in form of chronological monocultures, is declining. An example is the influx of *Melaleuca* after landscape-level dieback of the native forest on the lower wet slope of Haleakalā. Here, the dieback was a natural process, but the invasion of *Melaleuca* was facilitated by human agency. Similarly in the montane seasonal environment of Hawai'i Volcanoes National Park, the presence of *M. faya* is human induced, but its explosive expansion is due to a combination of ecological factors and mechanisms that together amount to a new natural dynamics.

In terms of the MacArthur-Wilson theory (1967), the distant Hawaiian archipelago has become a near-source archipelago. Its original assemblage of species, in spite of almost 90% secondary enrichment through endemism, probably never attained its native species potential under isolation. The assemblage of 1000 species, although distributed over the available habitat spectrum, did not accomplish a full use of available resources. Human-induced disturbances, such as caused by feral goats and pigs, opened up a spectrum of newly available niches. The anthropogenic disturbances are added to the natural disturbances, such as those associated with volcanism, geomorphological development, and climatic perturbations. Moreover, once in a while a new plant species invades that brings its own set of resources. This applies to *M. faya* with its symbiotic N-fixing availability. However, it would not have invaded this habitat, were it not for *Myrica*'s seed dispersal by introduced birds. They in turn were attracted by the nectar in the flowers of the habitats' native key species, *Metrosideros polymorpha*. Now this new alien, *Myrica faya*, fulfills a successional role. It may even exclude the native *Metrosideros* from parts of its habitat spectrum. But *Myrica* will not displace *Metrosideros* completely as long as a wide dynamic habitat spectrum remains available. This includes the formation of new lava flows, which may act as refugia for the low-N tolerant *Metrosideros* tree in the future.

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Zonation and management of mountain forests in the Sierra de Manantlán, México

Olvera Vargas, Miguel
& Figueroa-Rangel, Blanca L.

Instituto Manantlán de Ecología y Conservación de la Biodiversidad, Centro de la Costa Sur, Universidad de Guadalajara, Apartado Postal 108, C.P. 48900, Autlán, Jalisco, México;
Fax +33811425; E-mail molvera@cucsur.udg.mx

Abstract. The present work is a quantitative description of woody species composition and the vegetation status of secondary mixed-oak (*Quercus* spp.) forest in the Sierra de Manantlán, México in Tropical America. The analysis involved 60 circular permanent plots of 500 m^2 each (0.05 ha) and 40 temporary plots. The inventory recorded adult trees, saplings, and seedlings as well as site conditions (altitude, aspect, slope, litter, humus depth, and physiography) and stand conditions (canopy openness, herbaceous and shrub cover). Structural characteristics and some site conditions were remeasured over a four-year period. Based on the results of a classification method (TWINSPAN) we have identified at least seven vegetation types, each dominated by one or two oak species. Canonical Correspondence Analysis (CCA) ordered the plots mainly by differences in altitude and physiography. Stands dominated by *Quercus castanea* are found at the lowest altitudes, while stands dominated by *Q. crassipes*, are found at the highest altitudes. Based on these site conditions and vegetation composition, the study area can be divided in two different management zones. *Q. crassipes* stands can be managed under even-aged methods as shelterwood cuttings and the rest of the stands under uneven-aged methods as selective cuttings.

Keywords: Canopy openness; Classification; Community; Ordination; Physiography; *Quercus*; Selective cutting; Shelterwood cutting.

Introduction

In tropical ecosystems tree species tend to be intermingled, but generally they form particular associations. Sometimes these are easily recognizable in the field, yet often the associations are complicated, and are difficult to discern by simple field checking. The Cerro Grande plateau, located in the southeastern portion of the Sierra de Manantlán, shows a particular physiography with a large topographic and geo-morphological variation. It is apparently an isolated island with no clear connection with the surrounding landscape, not even with the nearby area of Cerro de Enmedio. Although, *Quercus* is clearly the most conspicuous genus on the plateau, *Quercus* species rarely form pure monospecific stands, particularly in wet environments. In the wet habitats the genus, represented by *Quercus candicans*, *Q. rugosa* and *Q. laurina*, shares its niche with other broad-leaved trees in a wide spectrum of physical and biological conditions, while in the driest habitats *Quercus* species tend to form monospecific associations (Figueroa-Rangel 1995).

The present study used both ordination and classification techniques to identify groups based on species composition and stand structure and to identify which site conditions promote differences in species composition among the groups. The aim was to determine the best management option for mixed-oak forests in Cerro Grande.

Material and Methods

Study area

The study was undertaken in Cerro Grande in the Sierra de Manantlán, along the border of the states of Jalisco and Colima in México (19°24'32" - 19°31'02" N; 104°01'09" - 103°57'44" W). Cerro Grande is a calcareous plateau of 450 km^2 with a complex and highly variable relief that generally faces West (Lazcano 1988). Soils are classified as Andosols and a minor part as Cambisols and Luvisols (Anon. 1976). Slopes range from 10 - 60% and the largest part of the forested land stretches between altitudes of 2000 and 2360 m. According to García (1987), the climate of the region belongs to a temperate-subhumid type classified as Ca (w2) (w) (e) g.

Field data

60 circular permanent plots and 40 temporary plots of 500 m^2 were established selectively over several topographic conditions and oak-forest associations. Within each stand, all trees $\geq$ 5 cm DBH (diameter at breast height) were numbered and tagged to record species, DBH, and social status (dominant, codominant, intermediate and suppressed). The number of saplings per species (individuals < 5 cm DBH and > 1.30 m tall) were also registered. Site variables were considered according to Olvera et al. (1996): slope (%), altitude (m), aspect, litter depth (cm), thickness of the humus layer (cm), canopy openness (%), of herb and shrub cover (%), physiographical units, erosion, and grazing pressure.

Data analysis

TWINSPAN (Hill 1979) was used to group the plots into classes based on their floristic composition, considering presence/absence data. Canonical Correspondence Analysis (CCA) was performed on floristic composition of vegetation and site condition data (ter Braak 1990). Two CCA analyses were performed; one using density (number of individuals/ha) of each plot, and another using basal area (m^2) per ha per plot.

Results and Discussion

Classification of vegetation

The 60 plots were divided in seven community types at the 3rd level of division according to TWINSPAN.

1. *Quercus laurina* community (14 plots)

In this community, *Quercus laurina* dominated the canopy together with some individuals of *Q. candicans* and *Oreopanax xalapensis*. Codominant elements were *Abies religiosa* var. *emarginata*, *Clethra* spp. and *Symplocos citrea*. *Ternstroemia lineata* was the most abundant and frequent species in the middle-stratum generally associated with *Cornus excelsa*, *Ilex brandegeana*, *Styrax argenteus* and *Garrya laurifolia*. Saplings of *Ternstroemia lineata*, *G. laurifolia* and *S. argenteus* were found as well.

2. *Quercus rugosa* community (17 plots)

In this community, *Quercus rugosa* was the most abundant species dominating the canopy. As in community 1, *Ternstroemia lineata* was the most abundant and frequent species in the middle-stratum. Associated species in this community were *Arbutus xalapensis*, *Symplocos citrea*, *Xylosma flexuosum*, *Fraxinus uhdei*, *Comarostaphylis discolor* and *Garrya laurifolia*. There were no saplings of the species present in the upper and middle canopy. Although *Q. rugosa* was dominant in the canopy, the most abundant species was *Ternstroemia lineata*.

3. Mixed-oak community (6 plots)

In the canopy of this community, three oak species dominated the canopy (*Quercus candicans*, *Q. castanea* and *Q. crassipes*). They were associated with *Alnus jorullensis*, *Cornus excelsa*, *Symplocos citrea*, and *Arbutus xalapensis* in the middle-stratum of some stands. The sapling community consisted of *Q. castanea* and *Symplocos citrea*.

4. *Quercus castanea* community (3 plots)

In this community, *Quercus castanea* was the most abundant and frequent species and generally a unique element in the canopy, although sometimes *Q. obtusata* codominated. *Acacia pennatula* and *Picramnia guerrerrensis* were present in the lower-stratum. There were no saplings present in these stands.

5. *Quercus crassipes*-*Quercus castanea* community (2 plots)

Quercus crassipes as well as *Q. castanea* dominated the canopy in this community, with *Alnus jorullensis* and *Arbutus xalapensis* in the middle stratum.

6. *Quercus crassipes*-*Pinus leiophylla* community (4 plots)

Quercus crassipes dominated the canopy, along with some individuals of *Pinus leiophylla*. *Q. castanea* codominated in the canopy, while *Alnus jorullensis* and *Prunus serotina* dominated the middle-stratum.

7. *Quercus crassipes* community (14 plots)

Quercus crassipes dominated the canopy, and it was the most abundant and frequent species in the stands. This species was frequently associated with codominant individuals of *Pinus leiophylla* and *P. pseudostrobus*. *Alnus jorullensis* and *Prunus serotina* were present in the middle-stratum. Only *Q. crassipes* saplings were found in the stands.

Relationships between vegetation and site conditions

There were clear differences in results when using density or basal area data to delineate species groups by ordination techniques. For density data, variation according to altitude was highly correlated with Axis 1. Plots dominated by *Q. crassipes* (on the left) were located at altitudes higher than those dominated by other oak species (sites on the right; Fig. 1a). Sites dominated by *Q. crassipes* (at altitudes from 2100 to 2300 m) contained only Holarctic genera such as *Alnus*, *Prunus* and *Pinus*. In Chiapas, in southern México, Quintana-Ascencio & Gonzalez-Espinosa (1993) found these genera growing at altitudes from 2300 to 2450 m, while Kappelle (1995), in Costa Rica, found more tropical genera such as *Nectandra*, *Geonoma*, *Clusia* and *Ocotea* at altitudes 2300 m. Along Axis 2, plots dominated by *Q. castanea*, with the highest herbaceous cover and the highest canopy openness, were separated from the remainder (Fig. 1a). Herbaceous cover was highly correlated with canopy openness, which can be regarded as a result of physiographical attributes of the plots because it is related to light and water availability, which in turns is an allogenic consequence of climate, weather, soil and topography (Smith & Huston 1989).

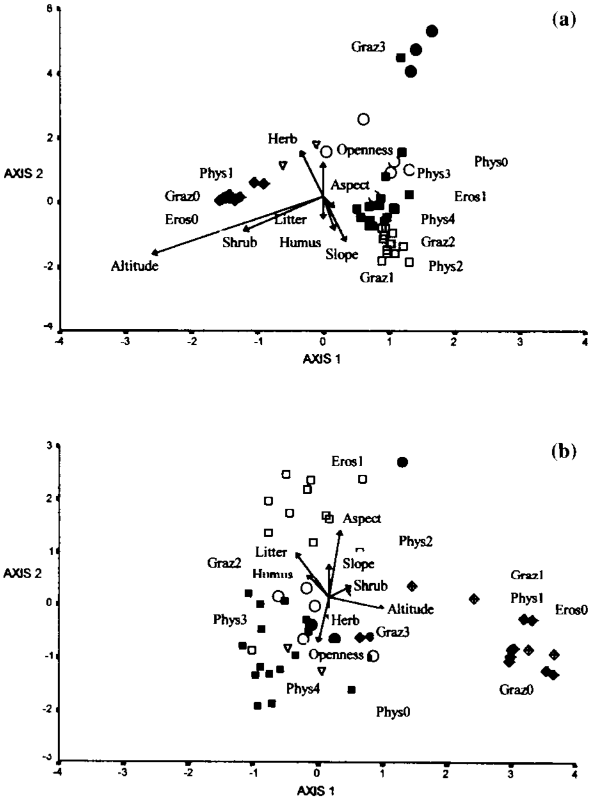

Fig. 1. Ordination diagram with axes 1 and 2 of a Canonical Correspondence Analysis of the 60 oak forest plots and site condition data in Cerro Grande, Mexico; (**a**) using density data, (**b**) using basal area data. ◆ Plots with *Quercus crassipes*. ▽ Plots with *Quercus castanea* and *Quercus crassipes*. ● Plots with *Quercus castanea*. ○ Plots with *Quercus candicans*, *Quercus castanea* and *Quercus crassipes*. ■ Plots with *Quercus rugosa*. □ Plots with *Quercus laurina*.

For basal area data, plots dominated by *Q. crassipes* were distinguished from the remainder of the sites (Fig. 1b), probably because of their location in the driest environments (Olvera & Moreno 1992) and on flat terrains, mostly on plateaus. These conditions were different from the other sites, which were located in upper and middle slopes. Van Rompaey (1993), in a study of African forest, found a relationship between moisture requirements and the establishment of species in their catena position. Species characteristics of wet environments were generally found at lower slopes in the catena, and species characteristics of dry environments were located at the crest. *Q. crassipes*, in this case, dominated the driest sites, presumably because they were located on northern aspects where precipitation is lower due to orographic shade. Along Axis 2, plots with *Q. laurina* were distinguished from the rest of the plots because they were situated on southern aspects, and the rest on northern aspects (Fig. 1b). Southern exposures in Cerro Grande are warmer than northern exposures, because they receive more solar radiation during winter in these latitudes. Also the influence of orographic shade causes higher precipitation in the south than in the north (Martínez et al. 1992), which provides more moisture and better conditions for biomass growth and canopy closure.

Conclusions

In Cerro Grande, the physiography is highly variable, and differences in catenas, aspect, altitude, and topography can be expected in a narrow range. This variability causes a great variation in the species composition of oak forests on a small area. Using classification, seven communities (two of them dominated by *Q. crassipes*) were distinguished and, with ordination, *Q. crassipes* stands were distinguished from the remainder, which would suggest that there are only two communities. Therefore, mixed-oak forests in the study area can be divided in two management zones under two different management alternatives. Those stands dominated by *Q. crassipes* can be managed under even-aged methods like shelterwood cuttings. This method involves cutting in three phases. In the first phase, the oldest trees or the ones with unwanted characteristics should be removed, in the second phase the aim is to promote the necessary conditions for the germination and establishment of oaks (basically controlling the gap size), and the third phase involves the harvesting of the remainder trees. The rest of the stands can be managed under uneven-aged methods like selection cuttings. Applying this method only the mature oak trees or those trees with a minimum diameter should be removed, trying to keep a balanced structure. As this method depends on the recruitment of seedlings into successive age classes, it is very important to prevent animals from grazing in such management areas.

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Vegetation dynamics on lava flows on Mt. Etna

Poli Marchese, Emilia & Grillo, Maria

Istituto di Biologia ed Ecologia vegetale, Università di Catania, Via Etnea 440, I-95128 Catania, Italy;
Fax +39095553273; E-mail polim@tin.it

Abstract. We studied processes of plant colonization on six of the most recent lava flows of the Mt. Etna volcano (Sicily, Italy). The following dynamic-structural stages were identified: 1. Lichen and moss colonies on rocks (*Rhizocarpetea geographici*, *Grimmio-Rhacomitrietea heterostichi*); 2. Herbaceous communities, mostly of the *Tuberarietea guttatae*, which settle both on shallow soils, where they are mostly dominated by dwarf therophyte species and on deeper soils, where they represent steppe characteristics; 3. Shrub communities (*Quercetea ilicis*) established in gullies and dominated by *Calicotome villosa*, *Spartium junceum* and *Pistacia terebinthus* at lower altitudes and by *Genista aetnensis* at higher altitudes; 4. Woodland communities (*Quercetea ilicis*) populating habitats of deep gullies and characterized by *Quercus ilex* and thermophilous deciduous oaks. Our analysis suggests that these dynamic stages belong to the series of Mediterranean evergreen vegetation (*Quercetea ilicis*). The vegetation stages cannot always be related to the age of lava flows, as other factors such as morphology of lava surface or microclimate come into play.

Keywords: Primary succession; *Quercetea ilicis* belt; Sicily.

Nomenclature: for plants follows Pignatti (1982).

Introduction

The flora and vegetation of active volcanoes has attracted a great deal of scientific interest. The study of the pioneer vegetation on lava fields is particularly important given the significance it has for the study of the primary succession (Beardsley & Cannon 1930; Smathers & Mueller-Dombois 1974; van der Maarel et al. 1985; Whittaker et al. 1989; Mueller-Dombois 1992). Numerous authors have dealt with primary succession on active volcanoes. Of particularly importance are the studies carried out in Europe by Fridriksson (1966, 1975, 1992), Fridriksson & Magnùsson (1992), Bjarnason (1991) and others on the Icelandic volcanoes, by Raus (1986, 1988) on the Greek island of Santorini (Thera), by Gonzales et al. (1990) and others on the Canary Islands. In Italy similar studies have been conducted principally on Mt. Vesuvius (Agostini 1975; Mazzoleni et al. 1988, 1989; Mazzoleni & Ricciardi 1993) and on Mt. Etna (Poli 1965, 1970a, 1970b; Poli & Grillo 1975; Poli et al. 1975; Di Benedetto 1983; Poli Marchese et al. 1995). In these papers some aspects of the primary succession related to age and substrate characters were shown.

In the present contribution the main stages of plant colonization on six lava flows located on the southern slopes of Mt. Etna are outlined. Our aim is to briefly characterize structure, floristic composition and dynamics of the vegetation on different lava flows located in the same area.

Material and Methods

Study area

Mt. Etna, situated in the northeast of Sicily (Italy), is a relatively recent volcano formed at the beginning of the Quaternary. Reaching a height of 3370 m and with a basal area of 1500 km^2, the volcanic structure rests on a layer of Pleistocene clays. The geomorphology of Etna is characterized by the presence of more than 200 secondary craters or 'little cones', formed during lateral eruptions, by a large depression – an ancient caldera – on its eastern slope called Valle del Bove, and by numerous lava flows. The volcanic substrate is the result of lava flows of different ages, from prehistoric times until today.

The study area is located on the southern slopes of Mt. Etna spanning an altitude range of 200-1100 m, in the zone most affected by human influence. The area is characterised by both old and recent lava flows. This study was conducted on six, among the more recent flows dating back to 812/1169, 1536, 1780, 1886, 1910 and 1983, respectively (see Romano et al. 1979).

The surface morphology of the lava flows varies according to lava type. The lava may be composed of rough-textured porous clinker-like rubble ('aa' type), of solid smooth-surface ('pahoehoe' type) or of loose fine material such as lapilli and volcanic ash, called 'ejecta' (Romano et al. 1979). The ecological factors on each lava flow vary according to surface morphology and microclimate. This gives rise to a mosaic type arrangement of vegetation (Poli 1970a, 1971).

The macroclimate of the region can be characterized under reference to two meteorological stations: Catania (65 m a.s.l.) and Nicolosi (698 m a.s.l.). The mean annual rainfall at the former site is 626 mm while in the latter it is 1110 mm. The mean annual temperature amounts to 18.0° C and 14.3° C respectively. The climate, with a dry period during summer, belongs to the Mediterranean type. It can be considered thermo-Mediterranean at the Catania station and meso-Mediterranean in Nicolosi.

The vegetation was analysed by means of phytosociological relevés according to Braun-Blanquet (1964) at each of the six lava flows. The relevés were made in areas located at different altitudes and in different microhabitats and substrates. The areas were selected randomly, with a minimum distance of 50 m between each other. The side lava flows areas have not been considered.

The dynamic relationships between the stages were established with the habitat-comparison method, which is based on a comparison of vegetation types of different age, under similar habitat conditions (Braun-Blanquet 1964).

Results

The vegetation composition on the lava flows studied varies markedly according to surface morphology and the age of the lava. There is a relationship between both these factors and the depth of fine material on the substrate, and consequently between the soil depth and the vegetation type. The colonization process occurring on the lava flows studied can be hypothetically summarized as follows:

1. Cryptogamic stages (lava of all ages)

The first macroscopic stage of plant colonization is represented by the lichen and moss synusiae which cover the rough surface and little hollows of the rocks. The lichen vegetation is often dominated by *Stereocaulon vesuvianum*, which at times covers vast areas. The lichen communities all belong to the *Rhizocarpetea geographici.*

In small cavities in the rock, where there is a thin layer of soil, mosses may become established. These are represented for instance by various species of the genus *Rhacomitrium* (*Rh. heterostichum*, *Rh. canescens*). The moss communities belong to the classes of the *Grimmio-Rhacomitrietea heterostichi* and *Ceratodonto-Polytrichetea piliferi* (Poli Marchese et al. 1995).

2. Dwarf therophyte vegetation (lava of all ages except 1983)

The first stage of phanerogamic vegetation is represented by dwarf therophytes which become established on a thin layer of soil or on moss colonies. This vegetation, which is widespread on the various lava flows, has a variable floristic composition (Poli 1970b) with at times *Crassulaceae* species dominating, above all those of the genus *Sedum* (*S. stellatum*, *S. coeruleum*, *S. tenuifolium*, *S. album*, *S. rubens*), further containing many grasses (*Vulpia ciliata, Aira cupaniana, Catapodium rigidum*, *Lamarckia aurea*) and herbs such as *Rumex bucephalophorus*. They characterize pioneer therophyte communities of xerophilous character belonging to the *Tuberarietea guttatae* (according to Rivas-Martínez 1977) and identified at Mt. Etna on various lava flows (Poli 1970b; Poli & Grillo 1975; Di Benedetto 1983; Poli Marchese et al. 1995).

The dynamic role of this stage seems clear in that it represents the first phanerogamic stage on young volcanic substrate. In some areas this vegetation represents an intermediate dynamic stage between the first cryptogamic stages and the following ones dominated by phanerogams.

3. Herbaceous stages (lava of all ages except of 1983)

Where a certain quantity of fine soil has accumulated on the lava surface, herbaceous vegetation made up of xerophilous communities become established. Some of these communities can be considered 'Mediterranean steppe' sensu Giacomini (in Giacomini & Fenaroli 1958). In the areas most affected by human activity these communities are rich in disturbance-tolerant species. Examples include the communities dominated by *Micromeria graeca* or *Trifolium incarnatum,* and a community dominated by *Ferula communis* and *Asphodelus ramosus*.

Between the lava blocks, on deeper soil, discontinuous vegetation dominated by perennial herbs is widespread. Here, an important role is played by *Rumex scutatus, Centranthus ruber, Senecio ambiguus, Helichrysum italicum* and, in some areas, also *Euphorbia characias* and *Scrophularia canina.*

This vegetation belongs to the *Tuberarietalia guttatae* and often contains nitrophilous elements from the *Brometalia rubenti-tectori* communities. In some areas communities belonging to this order have been identified. The presence on the same surface of elements belonging to the two orders cited can be attributed – in agreement with Izco (1977) and other authors – to a transition between the therophyte-rich natural vegetation and those heavily disturbed by human activity. In the areas most affected by pasture activity, species belonging to the *Poetea bulbosae* are widespread (see Poli Marchese et al. 1995).

4. Shrub stages (lava of all ages except 1983)

Isolated shrubs are often found in various types of herbaceous vegetation. They become established in gullies where a greater quantity of humus and fine earth has collected. As colonization proceeds the shrub cover becomes denser until more or less closed-canopy shrubland may develop, which, however, maintains a pioneer character. At lower altitudes the communities are most frequently dominated by *Calicotome villosa, Spartium junceum* and *Pistacia terebinthus.* At higher elevations the shrub stages are mostly dominated by *Genista aetnensis*. This species has an important role in the colonization of the Etna lava flows – it characterizes various vegetation types of very variable floristic composition. Some of the shrubland is characterised by presence of characteristic tree species with a shrub habitus, such as *Quercus ilex* and thermophilous deciduous oaks (such as *Quercus* cf. *virgiliana, Q*. cf. *dalechampii*) and *Rhamnus alaternus.* More mature shrublands, which at times appear as brushwoods, are dominated by *Pistacia terebinthus* and thermophilous deciduous oaks. There are various examples of those found on the oldest lava communities. The various stages of shrub vegetation, even those belonging to the *Quercetea ilicis*, contain species characteristic of the *Tuberarietea guttatae* and *Brometalia rubenti-tectori* communities.

5. Woody stages (absent from the 1886, 1910 and 1983 lava and present on others)

In the deep gullies in the lava flows and where the soil has reached notable thickness there are vegetation types whose composition and structure closely resemble those of woodlands. Of these types of vegetation those characterised by *Quercus ilex* and by thermophilous deciduous oaks are among the most common. They represent an intermediate dynamic stage linking the shrub vegetation and the more mature woodlands of the *Quercetea ilicis.* There are significant woodlands with *Quercus ilex* or other woodland species occurring on the oldest lava flows. These woodlands have a very poor floristic composition; they belong to the *Quercetea ilicis.*

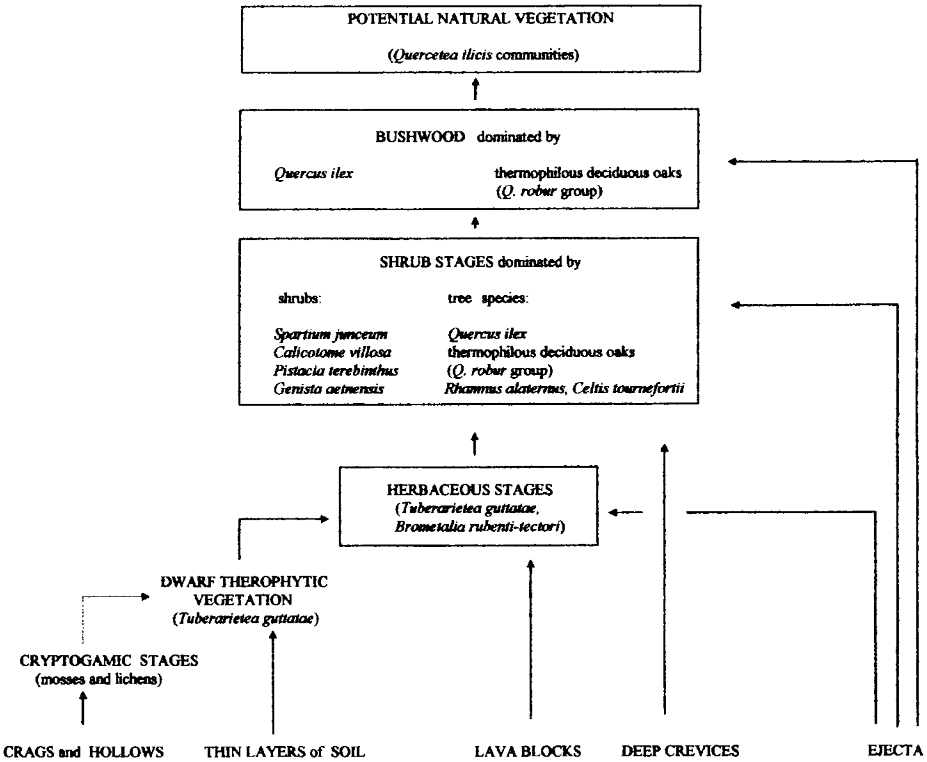

Fig. 1. Primary succession pathways on lava flows on the southern slope of Mt. Etna (crags: perpendicular outcrops).

Discussion

The lava flows on the low southern slopes of Mt. Etna present numerous dynamic stages. They are not uniformly present on all lava flows. For example, the structurally more advanced stages characterized by arboreal vegetation are only present on the oldest lava flows and not on the more recent ones of 1910 and 1983. On lava flows of only 15 yr old none of the stages is present even though in some rocky habitats some lichen or bryophyte species are beginning to appear. The various stages identified belong to the same dynamic series – the series of Mediterranean evergreen vegetation of the *Quercetea ilicis*.

The dynamic stages occurring on each lava flow cannot always be related to the age of the lava as other factors depending on the lava substrate come into play. Of particular importance are the surface morphology and the depth of soil as well as the microclimatic conditions. The morphology of the lava surfaces is irregular. The irregularity, as pointed out by many authors (Bjarnason 1991; Mazzoleni et al. 1989; Mueller-Dombois 1992), allows an accumulation of different soil layers on the various surfaces, giving way to peculiar microclimatic conditions, linked to both sites and exposures of the surfaces themselves. The distinguished categories of the lava surface, such as crags (perpendicular outcrops), depressions and cavities, more or less flat surfaces, lava blocks, and fissures, are thus colonized by different successional stages.

The plant colonization process is also regulated by biotic factors connected with the colonizing species concerned, such as the dispersal type, germination capacity, growth and longevity, as emphasized by Chevennement (1990). Moreover the constant presence of man and his activities (sheep grazing, intense urbanization of the surrounding area, etc.) allows the growth of disturbance-tolerant and ruderal species in the various vegetation stages. This can influence further development of vegetation.

On the basis of the data collected in the area studied we can hypothesize a comprehensive scheme of the succession pathways on the lava fields (Fig. 1). This pathway scheme is in accordance with the tolerance succession model (Connell & Slatyer 1977). This model, which is also applicable to findings of Lebrun (1959), Léonard (1959) and others working on vegetation of volcanoes, is based on the principle that species present in each stage of the succession modify the substrate where they appear, making it more favourable for other species, which become established and then compete with and eventually eliminate the previous one.

This study, which follows others of other lava flows on the lower slopes of Mt. Etna (Poli & Grillo 1975; Di Benedetto 1983; Poli Marchese et al. 1995), provides further information for a description of the plant colonization process on Mt. Etna.

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Main types of vegetation zonation on the mountains of the Caucasus

Zazanashvili, N.*, **Gagnidze, R.**
& Nakhutsrishvili, G.

Institute of Botany of the Georgian Academy of Sciences,
Kojori Road 1, 380007 Tbilisi, Georgia;
**Fax +99532330190; E-mail nzazanashvili@wwfgeo.org.ge*

Abstract. Variation in vegetation zonation on the mountains of the Caucasus is defined first of all by the (1) geographically transitional position of the region between the temperate deciduous broad-leaved forest zone and the latitudinal subtropical zone, (2) position in the contact area of different phytogeographical provinces: Mediterranean, Minor Asian, Iranian, and (3) by the evolutionary history of the Caucasian flora and vegetation (there were two refugia of Tertiary flora in the region during the ice-ages). Basically, there are four types of vegetation zonation on the Caucasus mountains: West Caucasian (Colkhic), East Caucasian, South Caucasian (Front Asian) and Southeast Caucasian (Hyrkanic).

Keywords: Altitudinal profile; Refuge; Vegetation zone.

Introduction

The Caucasus region covers a total area of 500000 km^2 and includes the nations of Armenia, Azerbaijan and Georgia, the North Caucasian portion of the Russian Federation, the northeastern part of Turkey, and a relatively small part of northwestern Iran. It is a region of natural contrasts, and is composed of several prominent orographic elements (Fig. 1). The climate is very variable. Mean annual precipitation in its southwestern part exceeds 2000 mm in the coastal area of the Black Sea; in contrast, it rarely exceeds 150 mm in the southwestern part of the Caspian Sea coast. Mean annual air temperature in the Transcaucasian part of the Black Sea coast and Caspian Sea coast is 15°C declining from south to north and with increasing altitude. The flora and vegetation of the Caucasus are quite diverse, and depend on both the physical features discussed above and the evolutionary history of the ecosystems. First of all, there are two refugia of Tertiary flora in the region, the Colkhic in the catchment basin of the Black Sea and the Hyrkanic in the extreme southeastern end of the Caucasus. Even now, many relict forms still appear as dominants or co-dominants in a number of plant communities.

Concepts

A mountain *vegetation zone* is defined as a combination of zonal primary (climax) formations. A zone may consist of *belts* which differ from each other by the actual combinations of the zone's characteristic formations and separate plant communities (i.e. by their *formation spectrum*). A *type of zonation* is determined by the altitude combination of vegetation zones (*zonal altitudinal profile* - ZAP), which is repeated in the whole area with a certain variation. A *type of zonation* is a general notion which encompasses the most characteristic and common features of certain *sub-types*. Below we will discuss the main types of zonation as clearly exposed on the Caucasian mountains.

Zonation typology

Four main types are distinguished in the Caucasus mountain zonation (Fig. 1).

I. West Caucasian (Colkhic) type.

This type is characteristic of the western sections of the Great Caucasus range and of the Small Caucasus mountain chain, mainly where the Caucasus embraces the Black Sea catchment basin, i.e. to that region, where one of the refugia of hygro-thermophilous representatives of the Tertiary flora existed during the ice-ages. This type was formed under humid conditions (mean annual precipitation is mostly more than 2000 mm, in certain places it even exceeds 4000 mm). The main characteristic of this type is a wide distribution of Colkhic relicts along the whole zonal altitudinal profile, almost from sea level up to 2300 m. Colkhic relicts either form a 2 - 4 m tall dense understorey in different forest types, or they occur as independent shrub communities in certain habitats. Here, in the Transcaucasus (lower subalpine belt) endemic oak and birch elfin woods are found, with *Quercus pontica, Betula medwedewii* and *B. megrelica*; other endemic relicts include *Rhododendron ungernii, R. smirnowii, Epigaea gaultherioides* and *Corylus colchica*.

IA. Humid thermophilous Colkhic broad-leaved forest zone. This zone occurs up to 1000 (1200) m.

IA1. Mixed broad-leavedf forest belt. This belt occurs up to 500 (600) m and includes *Castanea sativa, Carpinus caucasica, Fagus orientalis, Quercus hartwissiana* and *Zelkova carpinifolia*, with a Colkhic understorey including *Rhododendron ponticum, Laurocerasus officinalis* and *Ruscus colchicus* as well as the lianas *Hedera colchica* and *H. helix*. In relatively dry habitats thermophilous hornbeam-oak forests occur with *Quercus iberica, Carpinus caucasica* and *C. orientalis*, in the South Colkhis (from 200 m up we find pine-oak forests with *Quercus dshorochensis* and *Pinus kochiana* as well as Colkhic thickets with *Rhododendron ponticum, Ilex colchica, Laurocerasus officinalis* and *Ruscus colchicus*.

IA2. Chestnut forest belt. This belt is characterized by forests with *Castanea sativa* and *Fagus orientalis*, occurring from 500 - 1000 (1200) m) with a Colkhic understorey; further by thermophilous oak forests and Colkhic thickets (see IA1 with *Vaccinium arctostaphylos*).

IB. Humid beech forest zone. A zone between 1000 (800) - 1400 (1800) m with *Fagus orientalis* forest often with a Colkhic understorey, and dark coniferous/beech forests (see I C) partly with a Colkhic understorey. Colkhic thickets (see IA1 with *R. ungernii, Vaccinium arctostaphylos, Viburnum orientale*).

IC. Nemoral humid coniferous forest zone. This zone, from 1400 (1000) - 1800 (2100) m, includes forests with *Abies nordmanniana, Picea orientalis* and *Fagus orientalis*, partly with Colkhic understorey. Colkhic thickets occur as in I B.

ID. Subalpine elfin wood and meadow zone. This zone occurs from 1800 (1600) - 2400 (2700) m.

ID1. Lower subalpine belt. This belt occurs from 1800 (1600) - 2100 (2200) m and includes *Fagus orientalis, Quercus pontica* and *Betula medwedewii* elfin woods, often with a Colkhic understorey; tall herbaceous vegetation occurs with *Heracleum ponticum* and *Ligusticum physospermifolium.* Other elements include dark coniferous forests; *Rhamnus imeretina, Sorbus subfusca* or *Corylus colchica* thickets; Colkhic thickets (see I B); meadows.

ID2. Upper subalpine belt. This belt, from 2100 - 2400 (2700) m, includes birch/ash-birch elfin woods with *Betula litwinowii* and *Sorbus caucasigena*; *Rhododendron caucasicum* thickets; meadows with *Calamagrostis arundinacea* and *Geranium platypetalum* – on limestone with *Woronowia speciosa* and *Carex pontica.*

IE. Alpine grassland and thicket zone. This zone appears between 2400 and 2900 (3000) m.

IE1. Lower alpine belt. This belt occurs from 2400 to 2750 m and includes grasslands (*Nardus stricta* and *Geranium gymnocaulon*) and *Rhododendron caucasicum* thickets.
IE2. Upper alpine belt. This belt occurs from 2750 to 2900 (3000) m and with grasslands (*Festuca supina, Kobresia schoenoides* and *Geranium gymnocaulon*) and mats (*Cerastium cerastoides* and *Ranunculus svaneticus*); rock and scree vegetation.

IF. Subnival zone. This zone occurs from 2900 - 3700 (4000) m and includes open plant communities (*Cerastium polymorphum* and *Minuartia trautvetteriana*); fragments of mats and grasslands (up to 3000 m).

IG. Nival cryptogam zone. This zone occurs > 3700 m .

II. East Caucasian type

This type is characteristic of the eastern sections of the Great Caucasus range and of the Small Caucasus mountain chain. The climate has continental features over most of the area: mean annual precipitation varies from 600 to 1000 mm limits. Besides, the northern slope of the Eastern Great Caucasus and the Small Caucasus are drier than the southern slope of the Eastern Great Caucasus, which is reflected on the zonation sub-type level. Furthermore, in comparison with the humid Colkhis, corresponding zones are located 100-200 m higher here. Due to the absence of refugia the zonation is relatively simple.

IIA. Thermophilous oak forest zone. This zone occurs up to 1000 (1200) m.

IIA1. Riverside and foothill forest belt. This belt, at < 500-600 (1000) m, includes oak/poplar forests with *Quercus pedunculiflora* and *Populus hybrida,* thermophilous hemixeric hornbeam-oak forests on the slopes (*Quercus iberica, Carpinus orientalis*); arid woodlands (*Pistacia mutica, Juniperus polycarpos*); shibliak (*Paliurus spina-christi, Rhamnus pallasii*).

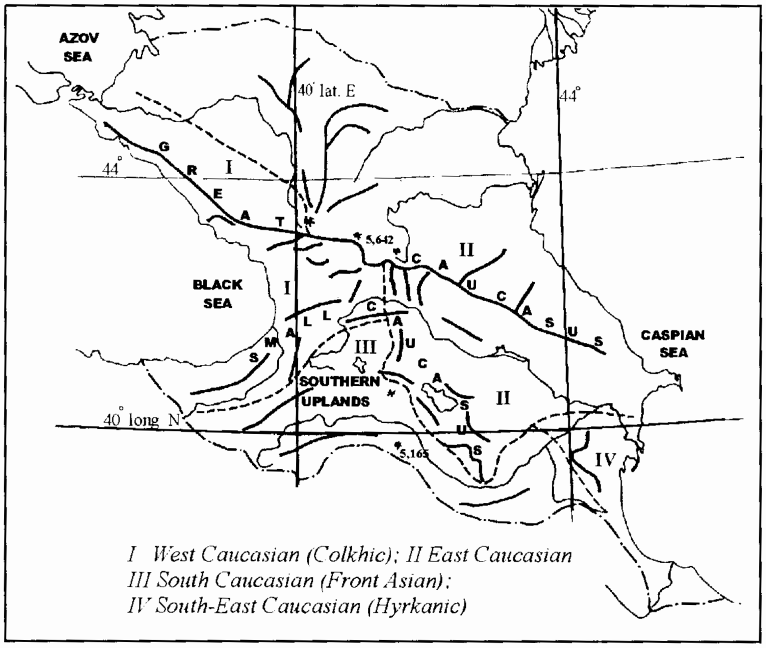

Fig. 1. Main types of mountain zonation in the Caucasus.

IIA2. Lower mountain belt. This belt, from 500 - 1000 (1200) m, includes oak/hornbeam forests (*Quercus iberica, Carpinus caucasica*); beech and hornbeam-beech forests (*Fagus orientalis, Carpinus caucasica*).

IIB. Mesic beech forest zone. This zone occurs from 1000 - 1800 (2000) m.

IIB1. Middle mountain belt. At 1000 - 1500 m this belt includes *Fagus orientalis* and *Pinus kochiana* forests.

IIB2. Upper mountain belt. This belt, at 1500 - 1900 (2000) m, includes *Fagus orientalis* forests; *Quercus macranthera* forests; *Pinus kochiana* forests.

IIC. Subalpine elfin wood and meadow zone. This zone occurs between 1900 (2000) and 2500 (2700) m.

IIC1. Lower subalpine belt. This belt, at 1900 - 2200 m, includes *Quercus macranthera, Pinus kochiana* and *Acer trautvetteri* woodlands; elfin woods (*Betula litwinowii, B. raddeana*); tall herbaceous vegetation (*Heracleum sosnowskyi, Aconitum orientale*); low open juniper communities (*Juniperus hemisphaerica*) on the rocks and scree; *Rhododendron caucasicum* thickets; meadows (*Agrostis planifolia, Geranium ibericum*); meadow steppes (*Festuca ovina, Carex humilis*).

IIC2. Upper subalpine belt. This belt, at 2200 - 2500 (2600) m, is characterized by birch/ash-birch elfin woods (*Betula litwinowii, B. raddeana, Sorbus caucasigena*); *Rhododendron caucasicum* thickets; meadows (*Festuca woronowii, Betonica macrantha*).

IID. Alpine grassland and thicket zone. This zone occurs between 2500 and 3000 (3200) m.

IID1. Lower alpine belt. This belt, found between 2500 and 2800 m, includes grasslands (*Festuca woronowii, Carex tristis* and *Kobresia capilliformis*); *Rhododendron caucasicum* thickets.

IID2. Upper alpine belt. This belt, from 2800 - 3000 (3200) m, includes grasslands (see IID1, with *Kobresia schoenoides*) and mats (*Sibbaldia parviflora, Carum caucasicum*)

IIE. Subnival open zone. In this zone, at 3000 - 4000 m, open plant communities with *Cerastium kasbek* and *Tripleurospermum subnivale* occur, with fragments of mats and grasslands (up to 3300 m).

IIF. Nival cryptogam zone. This zone is found at > 4000 m.

III. South Caucasian (Front Asian) type

This type is characteristic of the uplands and mountains of the Southern Caucasus mainly composed of volcanic sediments. Here representatives of the Caucasian relict flora do not occur: Anatolian-Iranian components predominate in the plant communities floristic composition; the typical forest zones are not characteristic of the zonal altitudinal profile which is formed in xerothermic, continental conditions: the mean annual precipitation varies within 250 -500 mm limits and increases in high-mountain regions. In comparison with humid regions in the Caucasus the corresponding zone limits are situated 300 - 400 m higher. The typical zonal altitudinal profile is as follows:

IIIA. Desert zone. This zone, at <800 m, includes dwarf semi-shrub deserts (*Artemisia fragrans, Salsola* spp. with ephemeroids); deserts with *Halocnemum strobilaceum* and *Suaeda microphylla* on saline soils; thorn-cushions (*Astragalus microcephalus*).

IIIB. Xeric grass and semi-shrub zone. This zone, at 800 (1200) - 1600 m, includes tomillares (*Thymus kotschianus, Scutellaria* spp.); friganoids (*Ambliopogon* spp., *Caccinia rauwolfii*); thorn-cushions (*Astragalus microcaphalus, Onobrychis cornuta*); steppes (*Stipa* spp., *Festuca valesiaca, Carex humilis*).

IIIC. Hemi-xeric woodland zone. This zone, at 1600 - 2300 (2400) m, includes *Quercus macranthera* woodlands; low woodlands (*Pyrus* spp., *Acer hyrcanum, Juniperus polycarpos*); hemi-xeric shrublands (*Cotoneaster* spp., *Sorbus graeca*); steppes (*Stipa tirsa, Festuca valesiaca*); thorn-cushion steppes (*Astragalus* spp., *Onobrychis cornuta*); meadow steppes (*Festuca ovina, Carex humilis*).

IIID. Subalpine zone. In this zone, between 2300 and 2800 (2900) m, we find *Quercus macranthera* woodlands; steppes (*Festuca valesiaca, Sesleria phleoides*); meadows (*Bromopsis variegata, Koeleria caucasuca*); meadow steppes (*Festuca valesiaca, Bromopsis variegata*); thorn-cushions (*Astragalus aureus, A. lagurus, Onobrychis cornuta*).

IIIE. Alpine zone. This zone, at 2800 - 3400 (3600) m, includes alpine grasslands (*Festuca woronowii, F. chalcophaea, Alopecurus aucheri, Carex tristis*), mats (*Sibbaldia parviflora, Alchemilla erythropoda*); rock and scree vegetation.

IIIF. Subnival open zone. Between 3400 and 4200 (4400) m open plant communities occur with *Draba araratica, Poa araratica* and *Saxifraga hirculus.*

III G. Nival cryptogam zone. Here this zone is found at > 4200 m.

IV. Southeast Caucasian (Hyrkanic) type

This type is characteristic of the extreme southeastern part of the Caucasus, southeast Azerbaijan and the northwest Iranian mountains along the Caspian Sea coast. Here the other refugium from the Tertiary flora, the Hyrkanic refugium, occurs. There is more difference than similarity between the Colkhic and Hyrkanic refugia. In the Hyrkanic area evergreen species are less widely distributed and are of less phytocoenotic importance. Besides, if relicts are spread from sea level to alpine belt in Colkhis, communities in Hyrkanic area, where relicts appear as dominants and co-dominants, reach only up to 1000-1200 m. Due to local climatic peculiarities, the lower zones of the mountains are more humid than the upper zones: the mean annual precipitation in the sub-mountain area is 1700 mm (expressed by summer minimum), while the mean annual precipitation above 2000 m is 300-400 mm.

IVA. Humid thermophilous Hyrkanic broad-leaved forest zone. This zone occurs at altitudes < 1000 (1200) m.

IVA1. Mixed broad-leaved forest belt. This belt is found up to 600 m and includes several oak forests with *Quercus castaneifolia, Parrotia persica, Zelkova carpinifolia, Albizzia julibrissin, Diospiros lotus* and other tress and with shrubs/semi-shrubs such as *Ilex hyrcana, Ruscus hyrcanus* and *Danaë racemosa* and lianas (*Smilax excelsa, Hedera pastuchovii*). An other forest type is characterized by the thermophilous *Quercus castaneifolia*.

IVA2. Oak forest belt. This belt occurs from 600 to 1000 (1200) m and includes *Quercus castaneifolia* forest (see above), beech and beech/hornbeam forests (*Fagus orientalis, Carpinus caucasica*) and *Quercus iberica-Carpinus caucasica* forests.

IVB. 1000-1600 (1800) m - mesic beech forest zone: – *Fagus orientalis* forests.

IVC. Steppe and xeric dwarf semi-shrub zone. From 1600 to 2300 (2500) m we find steppes with *Stipa* spp. and *Festuca valesiaca*; thorn-cushions (*Astragalus aureus, Onobrychis cornuta*); - meadow steppes (*Festuca valesiaca, Carex humilis*).

Discussion and Concluding remarks

The typology of the mountain zonation in the Caucasus as described here is related to that of Stanukovich (1973). If the Colkhic altitudinal profile is interpreted as a subtropical forest - forest - dark coniferous forest - meadow-shrub zone, the Colkhic zonation type can be linked not only to Scandinavian, Alpine and Carpathian zonations, but to other region types as well. Similarly the Eastern Caucasian type could be linked to the Central Asian group type (cf. Gagnidze 1970).

Another case of over-complication of the Caucasus mountain zonation typology (e.g. Shiffers 1955) is connected with (1) lack of attention to common features of different but geographically close regions and (2) the fusion of the notions of actual and natural potential vegetation; for instance, numerous types of secondary vegetation in deforested areas in the North Caucasus may complicate the zonal pattern.

The occurrence of refugia has greatly influenced the Colkhic type of zonation; in other cases relict – including evergreen hygro-thermophilous – elements may not be so diverse. Analogies for a Colkhic-type zonation can be found in areas characterized by transitional 'laurineous forests' (Klötzli 1988) or 'warm evergreen *Fagus* forests' (Fujiwara 1998), particularly in the northern parts of the Southeastern United States and the Southern Andes (Hildebrand-Vogel et al. 1998) as well as in some other regions. Similar relations could be found with the Hyrkhanic refugial type, but as mentioned above, evergreen elements are less distinctive in this type. If we compare the Colkhic and Hyrkanic types with European mountain zonation types (Ozenda 1994), the convergentional features point rather to the southern Alps.

The South Caucasian type could be united with the Southeast Anatolian-West Iranian group of zonation types. The issue of the East Caucasian type requires an additional investigation: this type, among other Caucasian types, has a transient position.

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Classes of synanthropic vegetation in urban open spaces of Potchefstroom, South Africa

Cilliers, S.S.[1]* & Bredenkamp, G.J.[2]

[1]*Section Botany, School of Environmental Sciences and Development, Potchefstroom University for C.H.E., Potchefstroom 2520, South Africa;* [2]*Department of Botany, University of Pretoria, Pretoria 0002, South Africa;*
**Fax +27182992799; E-mail plbssc@puknet.puk.ac.za*

Abstract. A first syntaxonomical account of phytosociological classes of urban open spaces was completed. Data were used from six separate phytosociological studies which include railway and roadside embankments, vacant lots, pavements, parking areas, wetlands and other natural areas. Plant communities in South African urban areas were given formal names according to the International Code for Syntaxonomic Nomenclature. A synoptic table consisting of 99 synthetic columns, each representing a plant community described in six separate studies, was compiled using MEGATAB. TWINSPAN was used to analyse the synoptic data and subsequently Braun-Blanquet procedures were implemented to classify the communities in a hierarchical system, from which phytosociological classes were identified. Two classes representing synanthropic vegetation namely the *Stellarietea mediae* R.Tx et al. ex von Rochow 1951 and the *Alternanthero pungentis-Cynodontetea dactyli* Cilliers & Bredenkamp – with three orders and seven alliances - were identified and are discussed in this paper. Only one association was described in each alliance to validate the higher syntaxon names. The classification of the newly described class serves as a basis for further investigations to, amongst other aspects, identify other associations in this class. Using Detrended Correspondence Analysis ordination the contribution of certain habitat and anthropogenic variables in the establishment of the different syntaxa is discussed.

Keywords: Braun-Blanquet method; MEGATAB; Syntaxonomic classification.

Introduction

Urban ecological research with the emphasis on urban vegetation studies is of increasing practical importance (Pyšek 1995). Applications of these studies include urban land management, planning and nature conservation (Sukopp & Weiler 1988) and the use of synanthropic plants as bio-indicators in monitoring the quality of urban environments (Sukopp & Werner 1983; Franceschi 1996). Description of urban vegetation is usually linked with the phytosociological approach, and more specifically formal syntaxonomy (Pyšek 1995).

Although the importance of urban vegetation studies is realized in South Africa (Poynton & Roberts 1985; Roberts & Poynton 1985) a formal syntaxonomical classification of urban open space vegetation was never attempted before. In a recently completed series of studies in the Potchefstroom Municipal Area in different land use areas such as railway reserves, parks, pavements and parking areas, vacant lots, road verges, urban wetlands and other natural areas (Cilliers & Bredenkamp 1998, 1999a, b, 2000; Cilliers et al. 1998, 1999), synanthropic vegetation was included.

The main objective of this study was to compile a phytosociological synthesis and establish a formal syntaxonomy for urban open spaces in the Grassland Biome of South Africa. The six studies of different land use areas mentioned above, were used, but emphasis is placed on synanthropic vegetation.

Material and Methods

Potchefstroom is one of the main centres in the North West Province of South Africa. It is situated in the Grassland Biome (Rutherford & Westfall 1994) and more specifically in the Dry Sandy Highveld Grassland (Bredenkamp & van Rooyen 1996). The study area includes all urban open spaces in the Potchefstroom Municipal Area and is situated between 27°00' and 27°07' E and 26°40' and 26°44' S.

Six separate phytosociological studies had been carried out in the study area, comprising the classifications of the following stratification units in different land use areas:

1. Railway line reserve areas (Cilliers & Bredenkamp 1998);
2. Intensively managed sites which include parks, pavements and parking areas (Cilliers & Bredenkamp 1999a);
3. Vacant lots in residential, commercial and industrial areas (Cilliers & Bredenkamp 1999b);
4. Wetland areas (Cilliers et al. 1998);
5. Road verges of the six main entrance roads into Potchefstroom, along an urban-rural gradient (Cilliers & Bredenkamp 2000); and
6. Natural and semi-natural areas on the city margin and fragments inside the city (Cilliers et al. 1999).

Combination of the six data sets resulted in a large, rather unmanageable data set. The three-step procedure for analysing large data sets proposed by Bredenkamp & Bezuidenhout (1995) was therefore followed. Step 1 was already completed in each of the six studies, which resulted in phytosociological tables and vegetation classifications. A total of 99 plant communities, sub-communities and variants were identified, informally named and described. Step 2 comprises the compilation of synoptic tables using MEGATAB (Hennekens 1996) and then re-entered into a combined data set. TWINSPAN (Hill 1979a) was used to analyse the combined synoptic data and subsequently Braun-Blanquet procedures were used to classify the 99 vegetation units in a hierarchical system. From the hierarchical classification higher syntaxa, including classes were identified. To validate the higher syntaxa, an association was described for each of the higher syntaxa, but these are not discussed in this paper. An alteration to step 3 was made. Instead of constructing separate phytosociological tables for each phytosociological class, as was proposed by Bredenkamp & Bezuidenhout (1995), the large synoptic table was divided into a separate synoptic table for each class, which was reorganized separately from each other, to identify the lower syntaxa in each class. Only the synoptic table for one of the classes of synanthropic vegetation is included in this paper (Table 1) and not the large synoptic table (Cilliers 1998) nor the synoptic tables for the other classes. The matrix of the synoptic table show the constancy values and the average cover-abundance values in brackets (Mueller-Dombois & Ellenberg 1974). Detrended Correspondence Analysis (Hill 1979b) was applied to the large synoptic data set to determine possible gradients in vegetation. A step-by-step ordination technique was used. Of the five separate ordinations only step 5 (Fig. 1) is included in this paper.

Results and Discussion

Communities belonging to two classes of synanthropic vegetation were recognized in the study area.

1. *Stellarietea mediae* R. Tx. et al. von Rochow 1951

The *Stellarietea mediae* which consists of annual, herb-rich ruderal and agrestal communities in Europe (Mucina 1997) is represented by two communities in Potchefstroom. These communities probably belong to the European order of the *Sisymbrietalia* J. Tx.. ex W. Matuskiewicz 1962. Those represent a new alliance for South Africa – the *Malvo neglectae-Sisymbrion orientalis* Cilliers & Bredenkamp.

This alliance consists of short-lived, species-poor communities occurring in pavement cracks (Cilliers & Bredenkamp 1999b) or along south-facing walls on vacant lots (Cilliers & Bredenkamp 1999a) inside the city. The soil can be regarded as the synanthropic soil form, Witbank (Anon. 1991). Although this alliance may establish throughout the year, it is much more conspicuous during or just after the winter months, when there is a decline in management of pavements and vacant lots. The differential species of the *Malvo neglectae-Sisymbrion orientalis* Cilliers & Bredenkamp are the annual, European forbs *Malva neglecta* and *Sisymbrium orientale*.

2. *Alternanthero pungentis-Cynodontetea dactyli* Cilliers & Bredenkamp

This newly described class includes 37 informally described plant communities, sub-communities and variants of ruderal vegetation in the study area, always associated with some type of disturbance (Cilliers 1998; Cilliers & Bredenkamp 1998, 1999a, b, 2000; Cilliers et al. 1998, 1999). Although the soil type can be regarded as the synanthropic Witbank soil form (Anon. 1991), different alkalinity levels, clay contents, gravel contents, water contents and soil compaction levels were recorded for the different syntaxa of this class.

The differential species are the prostrate perennial forb *Alternanthera pungens* and the erect annual forb *Conyza bonariensis* introduced from South America (Table 1).

The following lower syntaxa were described in this class:

2.1. *Plantagino lanceolatae-Modioletalia carolinianae* Cilliers & Bredenkamp inside the city in areas which are intensively managed and where direct human impact such as trampling, mowing, weeding and the use of chemicals, are high, but where adequate water is available.

2.1.1 *Medicaginion lupulinae* Cilliers & Bredenkamp is associated with frequently mown areas inside the city which are relatively wet, on lawns in parks (Cilliers & Bredenkamp 1999a), along road verges (Cilliers & Bredenkamp 2000), and occasionally in wetland areas (Cilliers et al. 1998). Some of the communities in this alliance are more conspicuous in winter when no mowing take place, and other communities are restricted to areas under trees, which are protected from frost in winter.

2.1.2 *Ipomoeo purpureae-Paspalion dilatati* Cilliers & Bredenkamp is also situated in wet areas which are frequently mown inside the city, but particularly on soils with a high clay content (> 40 %) and which are highly compacted (> 4.5 kg/m^2).

2.1.3 *Setario sphacelatae-Urochloion mosambicensis* Cilliers & Bredenkamp is restricted to the highly disturbed parts of road verges on the city margin, on sandy soils in ditches which may be seasonally waterlogged, but also in drier parts such as the edges of the road shoulders on compacted, somewhat gravelly soils. This alliance seems to include different stages of succession of the verges of newly constructed roads in the study area (Cilliers & Bredenkamp 2000).

2.1.4 *Eragrostio lehmannianae-Guilleminion densae* Cilliers & Bredenkamp is associated with high levels of trampling on pavements (with or without paving stones and slabs) (Cilliers & Bredenkamp 1999b), vacant lots (Cilliers & Bredenkamp 1999a) and some of the children's playgrounds inside the city (Cilliers 1998) and also on the highly compacted road shoulders along the entire urban to rural gradient of the six main entrance roads to Potchefstroom (Cilliers & Bredenkamp 2000). Although some of these areas are mown as well, mowing takes place less frequently than in the areas occupied by the *Medicaginion lupulinae* (alliance 2.1.1).

2.2 *Enneapogonetalia cenchroidis* Cilliers & Bredenkamp is associated with compacted skeletal soils in dry and hot conditions along railway lines (Cilliers & Bredenkamp 1998) and roads (Cilliers & Bredenkamp 2000) in the study area. It also occurs on derelict land on the city margin on mixtures of soil and building debris which were dumped more than four years ago (Cilliers 1998). This order is also situated on older rubbish dumps which were covered by a layer of topsoil (Cilliers 1998).

2.2.1 *Enneapogonion cenchroidis*

2.3 *Conyzo bonariensis-Argemonetalia mexicanae* Cilliers & Bredenkamp consists of short-lived communities in which annual plants are dominant. It is situated in very dry and hot conditions, on compacted soils or on heaps of soil and building debris, which were recently dumped (not more than 4 yr ago) on vacant lots inside the city (Cilliers & Bredenkamp 1999b) or on natural and semi-natural areas on the city margin (Cilliers 1998; Cilliers et al. 1999), as well as on very gravelly areas next to railway lines (Cilliers & Bredenkamp 1998).

2.3.1 *Solanion elaeagnifolii* Cilliers & Bredenkamp occurs mainly on heaps which consist of a mixture of soil and building debris.

2.3.2 *Argemonae mexicanae-Salsolion kali* Cilliers & Bredenkamp is unique to those gravelly areas between railway lines in the study area, which are sometimes subjected to the use of herbicides (Cilliers & Bredenkamp 1998).

A DCA-ordination of the synoptic relevés of the *Alternanthero pungentis-Cynodontetea dactyli* was undertaken (Fig. 1). The synoptic relevés of the three orders and the four alliances of one of the orders (2.1) are restricted to specific areas on the diagram (Fig. 1). On ordination axis 1, the *Enneapogonetalia cenchroidis* (order 2.2) and the *Conyzo bonariensis-Argemonetalia mexicanae* (order 2.3) are separated from the *Plantagino lanceolatae-Modioletalia carolinianae* (order 2.1) as they are situated in drier, hotter habitats, in soil with a high percentage gravel in areas which are not mown and where not much trampling take place. These two orders (2.2 and 2.3) can be distinguished from each other on ordination axis 2 on the basis of soil compaction levels, percentage of introduced therophytes and alkalinity levels in the soil. The four alliances of the *Plantagino lanceolatae-Modioletalia caroliniane* (Order 2.1) can be clearly distinguished from each other (Fig. 1). Although not very clearly, the *Medicaginion lupulinae* (alliance 2.1.1) is separated from the other alliances (2.1.2, 2.1.3 and 2.1.4) on ordination axis 1, as mowing occurs more frequently and trampling levels and percentage of gravel in the soil are high. The *Eragrostio lehmannianae-Guilleminion densae* (alliance 2.1.4) which is situated in the centre of the diagram differs from two of the other alliances (2.1.1 and 2.1.3) by the high levels of trampling. The *Setario sphacelatae-Urochloion mosambicensis* (alliance 2.1.3) occurs at the top of ordination axis 2 and can be distinguished from the other alliances (2.1.1, 2.1.2 and 2.1.4) in that soil compaction is high and that a low percentage of introduced therophytes occur.

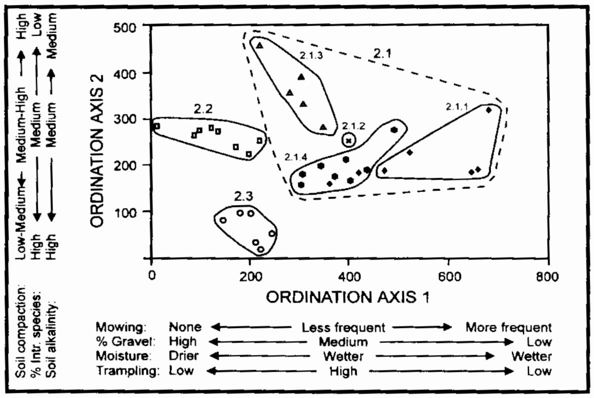

Fig. 1. Detrended Correspondence Analysis of the *Alternanthero pungentis-Cynodontetea dactyli* (reduced data set after the removal of synoptic relevés of the other phytosociological classes) of urban open spaces in the Potchefstroom Municipal Area, North West Province, South Africa (numbers of syntaxa refer to those in text).

The ruderal communities described in these two classes have the ability to establish in areas which are unsuitable for any of the other 12 phytosociological classes in the Potchefstroom Municipal Area (Cilliers 1998). These areas are trampled or frequently mown or have high soil alkalinity or contain dumps of soil or building debris, and this class contributes, therefore, to the total species diversity of urban open spaces in Potchefstroom. Knowledge of the existence and distribution of the *Alternanthero pungentis-Cynodontetea dactyli* is further important in that they contain declared weeds or invaders, which could possibly be better controlled if the communities in which they exist, are better understood (Vincent & Bergeron 1985). Due to the long history of urbanization in Europe, ruderal communities have been the subject of many studies over the past 30 yr. According to Mucina (1989) changes in traditional human activities such as abandonment of keeping domestic animals near houses, new ways of managing road verges, reclamation of dung hills and rubbish tips, lead to the endangerment of certain ruderal communities in Europe, and some means must be found to preserve them. Conservation of ruderal communities in South Africa, especially in cities and towns, seems a far-fetched idea at the moment, probably because of the presence of noxious species and the so-called aesthetic conflict as described by Gilbert (1989). More scientific knowledge on the floristic composition and dynamics of ruderal communities and the phenology of the species in these synanthropic communities, may perhaps lead to the realisation that some of these communities should also be conserved in urban open spaces in South Africa.

The present study serves as a basis for further detailed syntaxonomic investigations. Although an attempt was made to establish a hierarchy in each of the phytosociological classes, all the associations present in the study area were not formally described. A satisfactorily description of all the associations can only be achieved if the original relevés representing a specific class are combined in a single phytosociological table (Step 3 of the procedure for the analysis of large phytosociological data sets proposed by Bredenkamp & Bezuidenhout 1995). The identification and description of classes, orders and alliances in the present study and the future identification and description of all the associations in the study area, form the basis for the use of the deductive method of classification. The deductive method of classification (Kopecký et al. 1995; Dostálek 1996) was proposed to develop and supplement the classification procedures of the Braun-Blanquet approach (inductive method of classification) as it sometimes

Table 1. Part of a synoptic table of the *Alternanthero pungentis-Cynodontetea dactyli Cilliers* & Bredenkamp (in press) in urban open spaces in the Potchefstroom Municipal Area, North West Province, South Africa (numbers of syntaxa refer to those in text).

Synreleve number	17	21	22	20	91	16	48	28	96	47	52	53	54	55	5	11	12	13	14	15	18	46	6	7	69	71	93	94	51	72	95	8	9	98	99	97	73
Number of releves	1	8	11	1	3	9	3	4	3	14	4	4	15	13	4	7	10	3	5	1	1	10	10	8	12	10	4	3	2	1	2	4	6	3	6	6	4
Orders	2.1																						2.2									2.3					
Alliances	2.1.1							2.1.2		2.1.3					2.1.4								2.2.1									2.3.1					2.3.2
Alternanthero pungentis- Cynodontetea dactyli																																					
**Cynodon dactylon*	5(4)	1(+)	1(3)	5(+)	5(3)	5(3)	5(4)	4(2)	5(2)	5(3)	4(1)		5(3)	4(3)	5(3)	1(+)	5(3)	5(3)	5(4)	5(3)	.	4(3)	4(3)	5(3)	5(3)	3(2)	5(4)	5(3)	3(3)	.	3(1)	5(3)	5(3)	5(3)	5(3)	3(1)	2(1)
**Alternanthera pungens*	5(1)	.	1(3)	.	2(+)	3(+)	5(+)	.	.	2(3)	2(+)	4(1)	3(+)	2(3)	4(2)	1(1)	4(+)	5(3)	1(+)	5(3)	5(+)	3(3)	5(2)	5(2)	3(2)	2(2)	2(2)	2(1)	2(+)	.	3(+)	3(1)	3(2)	3(+)	1(+)	3(2)	.
**Conyza bonariensis*	.	1(+)	2(+)	.		2(+)	.	5(+)	.	2(+)	.		1(+)	.	4(+)	3(3)	4(1)	5(1)	4(1)	.	5(+)	1(+)	2(+)	3(+)	3(2)	.	2(1)	2(+)	.	5(+)	.	5(2)	5(2)	5(2)	1(+)	5(2)	4(+)
**Verbena bonariensis*	.	2(+)	1(+)	.	2(+)	2(+)	2(+)	2(+)	3(+)	1(+)	.	2(+)	1(+)	1(1)	3(+)		.	2(+)	.	.	5(+)	1(+)	1(+)	3(1)	2(3)	1(+)	2(2)	2(2)	.	.	.	.	.		.	1(+)	2(1)
Plantagino lanceolatae-Modioletalia carolinianae																																					
**Modiola caroliniana*	5(+)	2(3)	2(2)	5(+)	2(1)	4(1)	3(+)	5(+)	2(1)	2(+)	.	.	1(+)	.	2(1)	.	1(1)	2(+)	2(3)	.	5(3)	.	1(+)	2(+)	.		.		.	.	.	.	.	.	.	.	.
**Plantago lanceolata*	5(3)	2(3)	.	.	5(2)	2(1)	2(+)	2(+)	2(+)	2(1)	2(+)		2(+)	1(+)	3(+)	.	1(1)		1(+)	5(+)	5(3)	1(+)	1(1)		.		.		.	.	.	.		.	.	.	.
**Taraxacum officinale* group	.	5(2	2(2)	5(1)	3(+)	5(3)	2(+)	.	2(2)	1(+)	.	.	1(+)	1(+)	4(+)		.	.	2(+)	.		.	1(+)	2(+)	.		.		.	.	.		1(+)	.	.	.	.
**Gomphrena celosioides*	.	.	.	.	2(1)	4(1)		.	2(+)	3(+)	.	4(+)	2(+)			.	3(2)	3(+)	2(+)	.	5(+)	3(2)	1(+)	2(+)	.	.	.	2(+)	.	.	.	.		.	.	.	.
Chloris pycnothrix		.	1(1)	5(+)		5(2)	.		.	3(2)	.	3(+)		1(+)	2(3)	1(3)	.	.		.	5(3)	4(3)	2(1)	2(3)	.	.	2(+)		.	.	.	.		.	.	.	.
**Paspalum dilatatum*	5(3)	.		5(+)	5(3)	5(2)	2(+)	2(+)	3(2)	2(2)	.	.	1(1)	.			1(1)	.	5(3)			1(+)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Digitaria ternata	.	3(2)		5(1)	2(+)	4(1)		.	2(1)				2(2)	2(1)	.	1(+)	.		.		5(1)	1(+)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
**Chamaesyce hirta*	.	.		5(1)	2(4)	5(3)	5(2)			2(3)	.		.		.	2(1)	2(+)		.	.	5(+)	2(2)	1(+)	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Medicaginion lupulinae																																					
**Medicago lupulina*	5(-)	5(4)	2(3)	5(1)	2(1)	2(1)	.		.								1(+)				5(+)																
**Sonchus oleraceus*	5(+)	2(+)	1(+)	.	2(+)	.	2(+)									2(+)	1(+)				5(+)	1(+)											1(2)				2(1)
Oxalis pes-caprae	.	2(1)	5(2)			4(2)	.														5(+)																
Ipomoeo purpureae-Paspalion dilatati																																					
**Ipomoea purpurea*								4(1)	3(+)														1(+)				2(+)				2(+)						
**Melilotus alba*								2(3)	2(+)						2(+)										1(+)		2(+)										
Setaria pallide-fusca							2(+)	2(+)	2(+)																												
**Guilleminea densa*			1(1)			3(2)				3(2)	2(+)	5(+)	2(+)	2(1)	3(1)	3(2)	5(3)	5(3)	5(3)		5(+)	3(2)	5(3)	4(1)	1(1)	.	3(1)	3(+)	3(+)				1(+)				
Tragus berteronianus										2(+)	2(+)	4(+)	2(2)	.	.	1(1)					5(+)	1(+)	1(+)	1(+)	1(1)	1(+)		2(+)									
Chamaesyce inaequilatera			1(+)			1(1)				1(+)	.	.	1(+)	1(+)		2(+)	3(2)	3(3)	2(+)		5(+)		1(+)			1(+)	2(+)	1(+)									
Eragrostis trichophora										2(+)	2(+)	2(+)	1(+)	1(4)								1(+)	1(+)				2(+)	3(+)					1(3)				
Setario sphacelatae-Urochloion mosambicensis																																					
Setaria sphacelata					2(+)				2(+)	2(2)	2(1)	2(1)	2(1)	2(1)											1(+)	1(+)									1(2)		
**Eragrostis tef*										1(1)	5(3)	3(1)	1(1)	1(1)																							
Pogonarthria squarrosa									2(1)	1(1)	2(1)	3(1)	1(1)	1(1)																							
Hermannia depressa										1(1)	.	2(1)	1(3)	1(1)	2(+)																						
**Dactyloctenium aegyptium*										1(1)	2(+)		1(+)	2(+)																							
Corchorus asplenifolius										1(+)		2(+)	1(+)	1(+)							5(+)			2(+)											1(+)		
**Ambrosia psilostachya*					1(1)			1(+)		2(+)	1(+)		1(+)	1(1)									1(+)	2(1)													
Melinis repens										2(+)		3(+)	1(+)												1(+)	2(+)											4(+)
Ipomoea obscura										1(3)	2(+)	2(+)																									
Chamaecrista biensis										1(+)		3(+)		1(3)																							
**Bidens pilosa*								4(+)		1(+)			1(+)	1(+)								1(+)															
**Boerhavia erecta*							2(+)			1(1)			1(+)	.			1(1)						4(2)	1(+)	3(3)	3(2)	3(1)	5(+)	.	5(+)		3(+)	2(+)	2(2)			2(+)
**Atriplex semibaccata*							3(+)		.	1(+)					2(+)								2(3)	1(1)	1(1)			5(+)	2(+)			3(1)	5(3)	5(3)	2(+)	.	2(+)
Enneapogonion cenchroidis																																					
Enneapogon cenchroides										1(3)													4(3)	4(3)	5(3)	4(3)	5(3)	3(3)	3(4)	5(+)	3(4)						5(2)
Setaria verticillata								2(+)															1(+)	1(+)			4(3)				3(+)					1(+)	
Eragrostis chloromelas																							1(3)	1(+)	1(+)					5(+)							
Conyzo bonariensis-Argemonetalia mexicanae																																					
**Argemone mexicana*		1(+)					2(+)									1(+)				5(1)			1(+)				2(+)					3(1)	4(2)	2(1)	3(+)	.	4(3
**Lactuca serriola*															2(1)	1(+)																5(2)	5(3)	5(1)			2(3)
**Tragopogon dubius*																1(+)							1(+)									3(1)	5(3)	2(+)			4(2)
Solanion elaeagnifolii																																					
**Solanum elaeagnifolium*									2(1)				1(+)	.	3(+)										1(1)	2(1)						4(+)	4(3)	5(1)	5(4)	2(3)	
**Chenopodium*									2(1)								1(+)															5(1)	4(3)		1(3)	3(5)	
Argemonae mexicanae-Salsolion kali																																					
**Salsola kali*																									1(+)						2(+)						4(1)
** = introduced species**																																					

failed to solve classification problems (Pyšek 1995). Vegetation in man-made habitats consists of species with wide ecological amplitudes, which develop towards more uniform vegetation types without recognisable characteristics (Sukopp & Werner 1983). These synanthropic vegetation types are very difficult to be typified at the association level and are, therefore, simply ignored (Pyšek 1995).

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The colonization of alien plants by native phytophagous insects

Frenzel, Mark, Brändle, Martin & Brandl, Roland

UFZ - Centre for Environmental Research Leipzig-Halle, Department of Community Ecology, Theodor-Lieser-Str. 4, D-06120 Halle, Germany;
Fax +49 345 5585329; E-mail fre@oesa.ufz.de

Abstract. We investigate colonization patterns of native phytophagous insects on alien tree genera in Germany and on herbaceous alien cabbage plants (*Brassicaceae*) in Poland. Compared to native trees, alien tree genera are poor in species. Variation in insect species richness across these trees is best explained by the time of presence in Germany. In contrast to trees, the insect fauna on alien species of *Brassicaceae* is not impoverished. This is explained by host expansions mediated by secondary chemistry. We conclude that factors influencing insect communities on alien plants are similar to the processes influencing insect communities on native genera.

Keywords: *Brassicaceae*; Germany; Invasion; Neophyte; Poland; Species richness; Tree.

Introduction

The invasion of alien organisms in new biogeographic regions triggered by human activities is considered as one of the major threats to biodiversity (reviews in Drake et al. 1989). However, the invasions of aliens may be viewed as large-scale experiments. The analysis of the invasion process, the build up of biotic interactions in the new area (Leclaire & Brandl 1994) and the evolutionary consequences triggered by these new interactions provide important clues to understanding the organization of communities. However, biological invasions are not restricted to anthropogenic communities. Invasions have always been important during the history of biogeographic regions. For example, after the Pleistocene the complex invasions of species triggered the assemblage of recent communities in Central Europe. Nevertheless, the scale of invasions caused by humans is unique in the history of biotas.

The most important type of biotic interaction in terrestrial systems is the relationship between plants and insects. The colonization of alien plants by native insects may help to understand the factors influencing the composition of phytophagous insect communities. In general, the colonization process depends on temporal and spatial patterns of the invasion, the characters of the plant (distributional range, plant chemistry, morphology and phenology) and the pre-adaptations of the insect fauna (Strong et al. 1984). Thus, the colonization of aliens by native phytophages may vary considerably. Certain aliens, e.g. *Opuntia* cacti in southern Africa, have recruited not even one African insect species, although they have been present in South Africa for 250 yr (Moran 1980). Other aliens, e.g. crops like cacao or sugarcane assembled a diverse fauna within a few years (Strong et al. 1977).

Plants which invaded Europe prior to 1500 AD with the spread of farming are called archaeophytes, whereas neophytes are defined as recent invaders since the discovery of America (1500 AD). For the purpose of the present study, we define alien plants as all species that have been spread by man, combining archaeophytes and neophytes. In our study we compare species richness and composition of phytophagous insect communities on alien *versus* indigenous trees and herbs in Europe. Species which reached Central Europe without human influences are indigenous or native species.

Methods

Trees

We extracted data from published studies (a list is available on request) about phytophages of 25 indigenous and six alien tree genera occurring in Germany. We investigated the same insect taxa (orders and families) as Kennedy & Southwood (1984) in their study about the richness of phytophagous communities on trees in Great Britain. Similarly to Kennedy & Southwood, we defined tree genera in Germany as alien if they have been introduced by man since the Roman empire. To explain the variation in species richness of insect communities between alien tree genera, we compiled a set of independent variables: (1) host presence (time span a tree has been present in Germany; after Kowarik 1992) (2) host distribution on a biogeographic scale (native geographic range of the tree genus across the Palearctic realm after Meusel & Jäger 1992; number of 50 km × 50 km grids) and (3) taxonomic isolation of the host (total number of tree species within the genus).

Brassicaceae

The data about phytophagous insects on *Brassicaceae* (all herbaceous species) were extracted from a study performed in Poland, covering 139 plant species within 56 genera (Lipa et al. 1977). Here we classify plants as indigenous, archaeophytic or neophytic as listed in Frank & Klotz (1990). As an additional category we call plants not occurring naturally in Poland but grown by Lipa et al. for the purpose of their study as 'planted species'. We compared the species richness of 29 phytophagous insect families feeding on indigenous and neophytic host plant species.

Results

Compared to native tree genera, insect communities on alien trees are impoverished (Fig. 1a; *t*-test of log-transformed data: $p<0.001$). In contrast, the richness of phytophages on *Brassicaceae* shows no consistent decrease from indigenous to 'planted species' (Fig. 1b). Surprisingly, species richness on 'planted species' is even larger compared to the three other categories (ANOVA with subsequent multiple comparison test by least significant difference, $p < 0.01$).

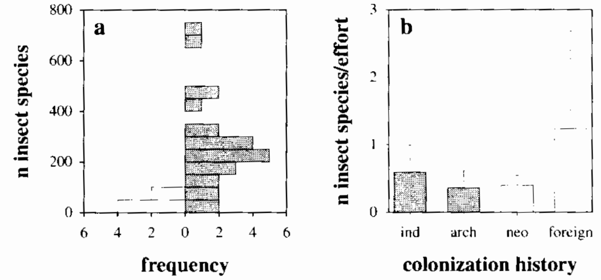

Fig. 1. Comparison of species richness of phytophagous insects on alien (white bars) and native (shaded bars) trees and *Brassicaceae*. **a.** Frequency distribution of species richness compiled from the literature of six alien and 25 native tree genera in Germany. **b.** Mean species richness of insects (corrected for sampling effort; see Frenzel & Brand 1998) on *Brassicaceae* in Poland; ind = indigenous plants ($n = 30$), arch = archaeophytes ($n = 12$), neo = neophytes ($n = 16$) and planted = planted species ($n = 46$). Error bars give standard deviations.

Species richness on alien tree genera is well correlated with the time span since introduction to Germany (Table 1, Fig. 2a). In contrast, host distribution and taxonomic isolation have no influence on species richness of phytophages (Table 1). However, because of the small sample size our analysis is not very powerful. The correlation between species richness and time of host presence is not apparent in the data of Kennedy & Southwood (1984) for insects on alien trees in Great Britain (Fig. 2b).

Species composition of phytophages on tree genera and species of *Brassicaceae* was compared by correlating the mean species richness of phytophagous taxa (insect orders and families on trees, insect families on species of *Brassicaceae*) across native *versus* alien taxa. For both trees and *Brassicaceae*, we found a significant correlation (Fig. 3a, b). However, the explained variance is much lower in trees than in *Brassicaceae* ($p = 0.03$). The high correlation in the *Brassicaceae* with a regression slope of about one (reduced major axis slope = 0.91; 95% confidence interval of slope = 0.79-1.05) indicates that the fauna on alien *Brassicaceae* is a representative sample of the fauna on native *Brassicaceae*.

Table 1. Alien tree genera in Germany. Coefficients of determination (r^2) for the correlation between host presence, host distribution and taxonomic isolation of alien tree genera and insect richness. Significant results (two-tailed) in bold.

Parameter	Transformation	n	r^2	P
Host presence	Log	6	**0.73**	**0.029**
Host distribution	Arcsine	6	0.00	> 0.3
Taxonomic isolation	Log	6	0.03	> 0.3

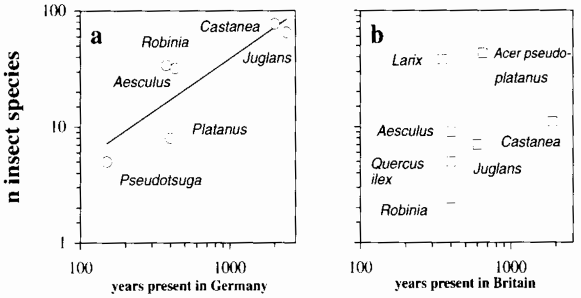

Fig 2. a. Species richness of phytophages on alien tree genera *versus* time of presence in Germany ($r^2 = 0.73$, $p = 0.029$). **b.** The same plot with species richness of insect communities on alien trees in Great Britain ($r^2 = 0.01$; $p = 0.79$; data from Kennedy & Southwood 1984).

Discussion

There are several general hypotheses to explain variations of phytophagous species richness between host plants (Strong et al. 1984). In decreasing order of importance these are (1) the species-area relationship, (2) the time of presence of a host in an area (host age hypothesis), (3) the leaf anatomy, (4) the taxonomic isolation, and (5) the plant architecture. In case of the tree data we were able to test the species-area relationship, host age and taxonomic isolation and we found clear support for the host age hypothesis (Birks 1983): the richness of insects feeding on alien hosts increases with the time since introduction. However, the data of Britain show that this pattern is not consistent across Europe, which suggests that the colonization process is triggered by a set of factors that vary with geography. Besides time, the colonization of trees may depend on pre-adaptations within the species pool of native insects. Host switches between closely related tree species are more likely since congeneric species contain similar plant secondary components (Strong et al. 1984). In Britain the alien species *Acer pseudo-platanus* has a close native relative, *Acer campestre*. This may explain the exceptionally high number of phytophagous insect species recorded on the alien *Acer* species (Fig. 2b).

In contrast to trees, the host age hypothesis does not explain the species richness on alien *Brassicaceae*: there is no decrease in species richness from natives to 'planted species'. The biological background for the rapid colonization of

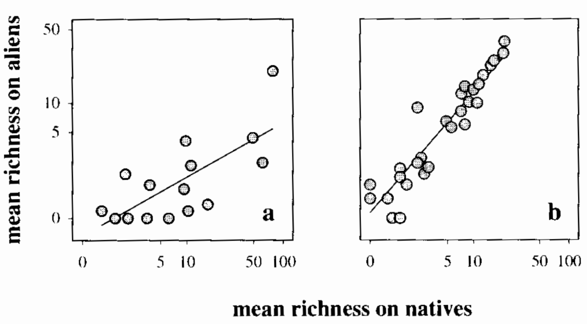

Fig. 3. Correlation of mean species richness of phytophagous taxa on native *versus* **a.** alien tree genera – log(x+1) transformed data; $r^2 = 0.52$; $p = 0.002$) and **b.** alien species of *Brassicaceae* – log(x+1) transformed data; $r^2 = 0.88$; $p < 0.0001$.

alien *Brassicaceae* may be similar to that responsible for the richness of phytophages on *Acer pseudo-platanus* in Great Britain. Glucosinolates are secondary compounds characteristic of *Brassicaceae* and widely distributed among this family. Insect species adapted to glucosinolates may easily shift not only between host plant species, but even between genera (Frenzel & Brandl 1997). Thus, the colonization process of alien *Brassicaceae* is triggered by preadaptations within the available pool. This hypothesis also explains the differences in the correlation pattern of the taxonomic composition of the insect faunas on alien and native hosts between trees and *Brassicaceae* (Fig. 3).

In conclusion, our preliminary analysis shows that the accumulation of insects on alien hosts is moulded by the same factors as phytophagous communities on native plants. Our results clearly show that the ecological processes associated with the invasion of aliens are not specific to them. Thus, the conception of threats caused by invasions of aliens depends mainly on the human perspective.

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Effects of disturbance on floristic patterns of *Quercus pyrenaica* forests in central Spain

Gavilán, Rosario G.[1]*, Escudero, Adrián[2] & Rubio, Agustín[3]

[1]*Departamento de Biología Vegetal II, Facultad de Farmacia, Universidad Complutense, E-28040 Madrid, Spain;*
[2]*Departamento de Biología, E.U.T.I. Agrícola, Universidad Politécnica, E-28040 Madrid, Spain;*
[3]*Departamento de Silvopascicultura, E.T.S.I. Montes, Universidad Politécnica, E-28040 Madrid, Spain;*
**Fax +34913941774; E-mail: rgavilan@eucmax.sim.ucm.es;*

Abstract. A matrix of 252 relevés representing five associations of *Quercus pyrenaica* forests in central Spain was analysed for effects of disturbance on floristic patterns within these woodland communities. Two data matrices were constructed: (A) including relevés with a large share of characteristic *Querco-Fagetea* species; (B) remaining relevés. These matrices were analysed by means of multivariate and univariate statistical methods. Higher homogeneity, in terms of number of species, and a lower number of invasive plants were found in sub-matrix A representing well-developed forests. Disturbance in the canopy layer may affect the herb layer composition, which can become invaded by species from other communities (*Prunetalia spinosae* and *Festucetea indigestae*). In the case of the *Arbuto-Quercetum pyrenaicae*, typical of the Mesomediterranean Belt, they were separated in the second sub-matrix, probably because the association was described taking into account species that appear when the canopy layer is more open.

Keywords: Canonical Correspondence Analysis; Classification; Disturbance; Phytosociology; Species richness.

Introduction

Quercus pyrenaica forests in central Spain occur at medium and low altitudes, most frequently in the Supramediterranean Belt. Usually, these forests have been used for several purposes, to extract wood for heating, grazing by domestic animals, meadow management for winter fodder and even conversion to conifer stands. This extensive management is different within a geographical area, mainly due to different forms of land ownership . Consequently, today it is difficult to find good examples of mature forests.

Most vegetation studies on these forests have been made from a phytosociological perspective (Rivas-Martínez et al. 1991), and in central Spain five associations have been described (Table 1). Thus many relevés are available, and our main purpose was to ascertain the level of difference in the floristic composition between five forest communities in relation to disturbance. To achieve this we have constructed two matrices, one with relevés that represent well-developed, mature forest (A), and another one (B) representing perturbed forests.

Material and Methods

We collected 252 – both own and published– phytosociological relevés (Table 1) and analysed these by calculating the total number of species and the share of the *Querco-Fagetea, Prunetalia spinosae* and *Origanetalia vulgaris* species in every relevé. Although the orders *Prunetalia* and *Origanetalia* are considered to belong to the *Querco-Fagetea*, we preferred to treat them separately, since they are considered secondary successional communities (in the case of *Prunetalia)* or forest fringe communities (in the case of *Origanetalia*). The whole data set was divided into two sub-matrices considering the richness in typical forest plants (those of *Querco-Fagetea*) as a characteristic of a mature forest. Thus sub-matrix A included relevés that have at least 20 species and 40% of *Querco-Fagetea* elements if present in the eastern part of the territory (Sierras de Ayllón y Guadarrama and surroundings regions) or at least 30% if found in the western part. This lower level chosen in western territories is due to the generally lower richness in *Querco-Fagetea* elements of the mature forests. These levels have been chosen following our experience in such communities in these regions (Gavilán 1994). Finally, the relevés without such characteristics were included in sub-matrix B. The two sub-matrices comprised 72 (A) and 180 relevés (B), respectively.

The total matrix was firstly analysed by Principal Component Analysis. Then the two first axes were submitted to a Kolmogorov-Smirnov test (Sokal & Rohlf 1995) in order to check the homogeneity of the relevé distributions. This resulted in a significance (2-tailed test; $P=0.0037$) for the second axis.

The remaining tests were applied to the two sub-matrices separately following a two-step approach. First, we carried out a classification by means of a Hierarchical Clustering using minimum variance – which minimizes the sum of squared distances to the cluster centroids, forming compact, circular clusters (Lapointe & Legendre 1994). The Similarity Ratio was used as a resemblance measure. Species values were standardized by their range in order to give equal weight to the species (Podani 1994).

Subsequently, the classification scheme was revised by a constrained ordination approach. This last step led to an environmental interpretation of the floristic variability, which underline the hierarchical classes. In order to search such environmental trends we conducted a Canonical Correspondence Analysis (CCA; ter Braak & Šmilauer 1998).

Table 1. List of associations of *Quercus pyrenaica* forests in central Spain (Rivas-Martínez 1987). Alt: altitudinal range (m); (N= north; S = South; E = East W = West; BB: bioclimatic belt (MM: Mesomediterranean; SM: Supramediterranean).

Forests	Abbr	Alt	Exposure	BB
Arbuto unedonis-Quercetum pyrenaicae	AQp	450-800	S, W	MM
Genisto falcatae-Quercetum pyrenaicae	GQp	700-1000	N, W	SM
Holco mollis-Quercetum pyrenaicae	HQp	900-1050	N/S, W	SM
Luzulo forsteri-Quercetum pyrenaicae	LQp	900-1300	N/S, E	SM
Festuco heterophyllae-Quercetum pyrenaicae	FQp	1500	N, E	SM

An environmental matrix was compiled using the available information included in the original tables. These variables were altitude, inclination, exposure, area, cover, number of species and location expressed into two numerical variables, longitude and latitude.

Results

Frequency analysis (Figs. 1a, b) showed a wider range of the number of species in sub-matrix B (48) than in A (28). The maximum is also much higher: 47 in sub-matrix A and 59 in sub-matrix B, the average is lower: 30 in sub-matrix A and 26 in B, and the variance is much higher: 40 in A and 92 in B, indicating a lower homogeneity of sub-matrix B.

When the composition of plants in each sub-matrix is analysed (Fig. 2a, b), sub-matrix A has a larger proportion of species belonging to the *Querco-Fagetea* (*Prunetalia* and *Origanetalia* included), but also a larger proportion of *Quercetea ilicis* species. However, invasive plants from prairies and nitrophilous perennial vegetation (*Molinio-Arrhenatheretea* and *Artemisietea vulgaris,* respectively) are quite similar. The higher presence of species belonging to Mediterranean perennial pastures of the *Festucetea indigestae* (*Jasiono-Koeleretalia, Hieracio-Plantaginion radicatae*) in sub-matrix B is important.

The classification of sub-matrix A showed six groups of relevés that approximately matched the associations and biogeographic units described for the territory (Rivas-Martínez 1987). The two main branches of the dendrogram separated the eastern associations (FQp and LQp, from the western ones (HQp, GQp, AQp; see Table 1 for abbrevia-

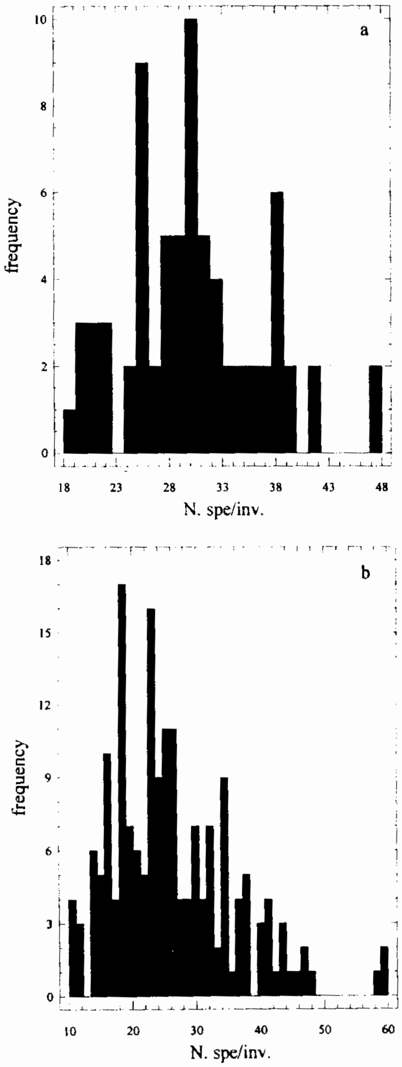

Fig. 1. Frequency distribution of species number per relevé in matrix A (**a**) and matrix B (**b**).

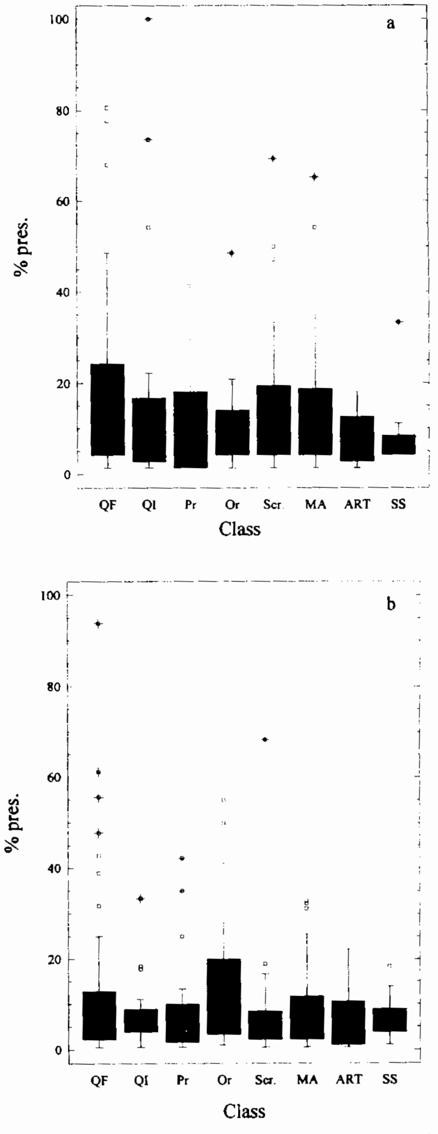

Fig. 2. 50th percentile of the phytosociological distribution of species as to their percentage presence in sub-matrix A (**a**) and sub-matrix B (**b**). QF = *Querco-Fagetea*; QI = *Quercetea ilicis*; Pr = *Prunetalia spinosae*; Or = *Origanetalia virentis*; Scr. = Scrub and shrubland classes (*Cytisetea, Calluno-Ulicetea, Cisto-Lavanduletea*); MA = *Molinio-Arrhenatheretea*; ART = *Artemisietea vulgaris*; SS = *Festucetea indigestae.*

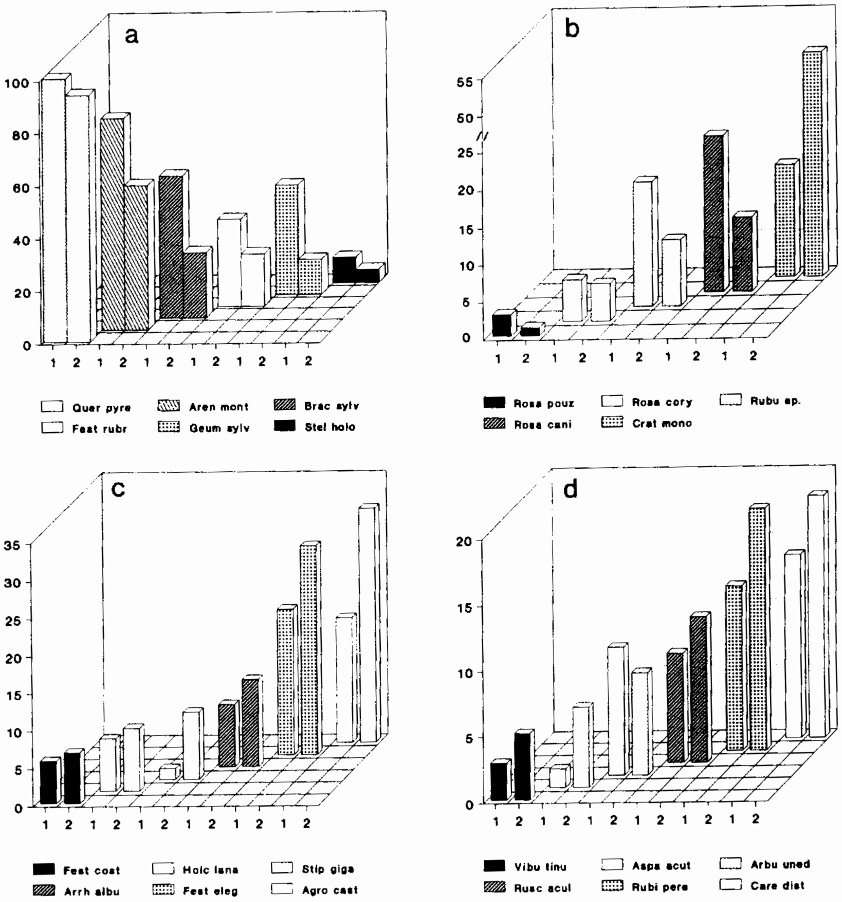

Fig. 3. Percentage of some species differentiating sub-matrix A (1) and sub-matrix B (2). **a.** *Querco-Fagetea* (including *Origanetalia*); **b.** *Prunetalia*; **c.** perennial pastures (*Molinio-Arrhenatheretea*; *Artemisietea vulgaris* and *Festucetea indigestae*); **d.** *Quercetea ilicis*. Quer pyre = *Quercus pyrenaica*; Aren mont = *Arenaria montana*; Brac sylv = *Brachypodium sylvaticum*; Fest rubr = *Festuca rubra* group; Geum sylv = *Geum sylvaticum*; Stel holo = *Stellaria holostea*; Rosa pouz = *Rosa pouzinii*; Rosa cory = *R. corymbosa*; Rosa cani = *R. canina*; Crat mono = *Crataegus monogyna*; Fest cost = *Festuca costei*; Holc lana = *Holcus lanatus*; Stip giga = *Stipa gigantea*; Arrh albu = *Arrhenatherum album*; Fest eleg = *Festuca elegans*; Agro cast = *Agrostis castellana*; Vibu tinu = *Viburnum tinus*; Aspa acut = *Asparagus acutifolius*; Arbu uned = *Arbutus unedo*; Rusc acul = *Ruscus aculeatus*; Rubi pere = *Rubia peregrina*; Care dist = *Carex distachya*.

tions). It is interesting to note that AQp relevés are hardly separated from the others; they are usually characterized by the presence of a group of sclerophyllous Mesomediterranean *Quercetea ilicis* species, such as *Asparagus acutifolius, Rubia peregrina, Viburnum tinus* and *Ruscus aculeatus*, that not appear in other associations of Suprameditterranean distribution.

In sub-matrix B no separation of groups following a biogeographical or phytosociological pattern was detected, probably due to the higher presence of plants from other communities like *Molinio-Arrhenatheretea, Artemisietea vulgaris* and other syntaxa. In contrast with sub-matrix A, there is a group well characterized floristically by sclerophyllous elements of the *Quercetea ilicis* (AQp), as mentioned above.

The CCA of both matrices was highly significant ($P < 0.001$) as indicated by a Monte Carlo test (250 repetitions) in which the trace was used to build the F-ratio statistic. The ordination results for the two data sets are similar. The correlation of environmental variables with the axes is similar as well (Table 2). There are some differences however since sub-matrix B produces lower correlation values than A, particularly for the second axis. Altitude is the best correlated environmental variable with the first axis. In sub-matrix A, except exposure and number of species, the other variables reach correlation values over 50%, either positive or negative. In sub-matrix B, only latitude and inclination reach this value. The higher correlation of cover and area in sub-matrix A can be related to the more homogeneous floristic composition of the relevés. The second axis is related to inclination, area, longitude and latitude in sub-matrix A, while number of species and latitude are the only variables with correlation over 0.40 in sub-matrix B.

From a biogeographical point of view, the ordination of sub-matrix B is clearer than that of A, but in both cases the group of relevés with a Luso-Extremadurense position (*Arbuto unedonis-Quercetum pyrenaicae*) remains separated in the most positive part of the axes, clarifying the former classification in sub-matrix A.

Table 2. Eigenvalues and inter-set correlations of environmental variables with the first two CCA axes in sub-matrices A and B.

	A-CCA1	A-CCA 2	B-CCA 1	B-CCA 2
Eigenvalues	0.329	0.181	0.385	0.199
Altitude	-912	-27	-888	-186
Inclination	-521	618	-554	294
Aspect	61	138	52	297
Cover	-593	43	-446	-339
Area	-510	535	-368	-196
No. of species	206	-62	34	-522
Longitude	-528	487	-186	333
Latitude	-525	588	-655	409

Discussion

The effect of disturbance in deciduous forest from central Spain could be understood in terms of species richness in a similar way as in other studies (Vetaas 1997). Following the classical view of richness and disturbance (Odum 1971; Rao et al. 1990), sub-matrix A appeared to be slightly richer as to mean number of species than B. It is well-known that disturbance may increase species richness (Connell 1978; Petraits et al. 1989). Some relevés of sub-matrix B show the highest number of species, the range in number of species being much higher than in A.

Disturbance has also been related to stability (van der Maarel 1993); sub-matrix B showed less stability since the number of species per relevé is more variable. Besides, the number of species is highly correlated with the second CCA axis of sub-matrix B, separating relevés with higher richness. This can be understood as a measure of instability within that sub-matrix.

Disturbance is frequently caused by the partial or total substitution of the natural canopy of *Quercus pyrenaica* by stands of *Pinus sylvestris* or *P. pinaster* (depending on the altitude). These types of deciduous forest are light-dependent communities (Kobe et al. 1995; Walters & Reich 1996). Any management of the canopy layer modifies the light pattern and the floristic composition of the herb layer (Fig. 3a), such that it is invaded by other species from communities of *Prunetalia spinosae* (see *Crataegus monogyna* in Fig. 3b) or *Festucetea indigestae* (Fig. 3c).

The CCA ordination showed better correlation with environmental variables in sub-matrix A. The higher correlation of altitude, longitude and latitude with the first axis can be related to an east-west geographical gradient – the Sistema Central mountains range from higher altitudes in the eastern part to lower in the western areas. Likewise the high correlation of inclination together with longitude and latitude in the second axis could be related to the higher average altitude of the northern plateau with respect to the southern, i.e. a north-south geographical gradient (Gavilán & Fernández-González 1997).

From a purely phytosociological point of view, classification showed the necessity of floristically good sets of samples for ascribing relevés to a particular association. Classification remains unclear in sub-matrix B, except for *Arbuto unedonis-Quercetum pyrenaicae* forests, which are better separated in B. The lack of separation in sub-matrix A is due to the absence of species from the *Quercetea ilicis* (Fig. 3d), usually differentiates this association. This absence could be explained by a more developed canopy layer. Consequently, it means that some potential vegetation types have been phytosociologically described taking into account the floristic composition of non well-developed forests.

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Landscape structure in the green belt around the metropolitan area of Seoul, Korea

Lee, C.-S.[1*], Hong, S.-K.[2], You, Y.-H.[2], Kim, J.-E.[1] & Moon, J.-S.[1]

[1]*Faculty of Environment and Life Sciences, Seoul Women's University, Seoul 139-774, Korea;* [2]*Center for Ecological Research, Seoul Women's University, Seoul 139-774, Korea;*
[*]*Fax +8229705822; E-mail leecs@swift2.swu.ac.kr*

Abstract. An attempt to clarify the landscape structure of urban areas was carried out in the green belt around Seoul, Korea's capital. By means of aerial photographs and a field survey, a vegetation map including the land-use pattern was made. With this vegetation map and the phytosociological survey the landscape structure was described. Landscape elements identified were: (1) Secondary forest, (2) Agricultural field, (3) Introduced plantation, and (4) Other elements including urbanized area, graveyard, and bare rock. Secondary forest was composed of *Quercus mongolica*, *Q. variabilis*, *Q. acutissima*, *Q. aliena*, *Pinus densiflora*, and *Alnus japonica* communities. Plantation was composed of *Robinia pseudoacacia*, *Populus tomentiglandulosa*, *P. rigida*, *Larix leptolepis*, *Pinus koraiensis* and *Castanea crenata*. Patches near to human settlements located in the lower zones of the mountains were fragmented and small but they became larger towards the higher mountain zones. Mt. Cheonggye having fewer patches shows anthropogenic disturbance of lower intensity than that of the other two mountains. On the other hand, in the case of Mt. Acha, patches due to geomorphologic conditions such as bare rock and steep slope were added to the vegetation patch, while characteristics of parent rock less susceptible to human impact mitigated differentiation of patch. In floristic composition of *Q. mongolica* community distributing in the upper part of each mountain, that of Mt. Cheonggye, in which artificial interference is rare, showed a difference with those of study areas different in parent rock and disturbance regime. But that of *R. pseudoacacia* community located in lower area of mountain, in which artificial interference is frequent was similar to each other.

Keywords: Anthropogenic disturbance; Landscape ecology; Urban forest; Vegetation type.

Introduction

Forests around urban areas have been utilized as locations for obtaining timber, fuel, organic fertilizer, and feed of livestock as well as land-use of diverse types. Hence, even though a forest was recognized as homogeneous by aerial photographs, its internal structure appeared to be heterogeneous due to human interference (Küchler & Zonneveld 1988; Nakagoshi & Rim 1988; Nakagoshi et al. 1992).

From a landscape ecology viewpoint, a study of urban forest could be contribute to understanding the cultural landscape. Moreover, urban forest is not only important because of its species-richness (Hudson 1991; Saunders & Hobbs 1991; Spellerberg et al. 1991), but also because it forms a buffer against influences from the urbanized areas (Bradley 1995). Furthermore, urban forest is important for recreation (Adams & Dove 1989; Bradley 1995).

In this paper, we describe the distribution of landscape elements in urban area of Seoul, the capital of the Republic of Korea (Fig. 1). Secondly, we compare the landscape structure in terms of kinds, numbers, and sizes of patches in the landscape, and discussed the characteristics of anthropogenic disturbance causing the structural differences in these landscapes. Finally, we compared landscape quality regarding species composition in relation to parent rock and disturbance regime.

Methods

Boundaries of landscape elements divided by vegetation structure and land-use patterns were certified by aerial photographs. In the present study, monochrome aerial photographs (scales 1:5000 and 1:7000) taken in the winter of 1996 were used for recognizing vegetation types and landscape boundaries. The landscape attributes recognized by aerial photographs were overlapped on topographic maps scale 1:25000. The smallest area of each patch (or landscape element) is 25 m × 25 m. Smaller patches were neglected, because their size and shape would be uncertain on a topographic map at scale 1:25000 (Nakagoshi et al. 1992). Vegetation mapping and analysis of the map were completed by use of Geographic Information System (GIS) supported by ArcView (ESRI 1996). Vegetation patches and other land-use patterns identified as landscape elements by aerial photography were confirmed by field survey and phytosociological analysis (Braun-Blanquet 1964; Mueller-Dombois & Ellenberg 1974). To compare landscape elements under different disturbance regimes and natural conditions, Detrended Correspondence Analysis (DCA; Hill 1979) was applied. Species scores were transformed into percent cover values. In the *Quercus mongolica*- and *Robinia pseudoacacia* communities, which are dominant elements in secondary forests and plantations, respectively, only species with a frequency $\geq 10\%$ were included.

Numbers and areas of landscape patches were determined using GIS.

Results and Discussion

Characteristics of the landscape structure in the study area

The landscape element types identified from the vegetation map are summarized in Table 1. Landscape element types of Mt. Cheonggye were identified as secondary forest elements derived from natural succession, introduced elements for rehabilitation of degraded forest ecosystems, agricultural elements, graveyards, and others including urbanized areas, graves, and bare rock (Table 1).

Secondary forests included *Q. mongolica*, *Q. variabilis*, *Q. acutissima*, *Q. aliena* and *Pinus densiflora* communities.

The dominant landscape elements among them were the *Q. mongolica* community and *Q. acutissima* community in uplands and lowlands, respectively. The *Q. acutissima* community is a typical secondary forest element established near human settlements in Korea (Lee 1998). It is an essential landscape element in the typical rural landscape pattern of Korea (Lee 1998). *Q. mongolica* is a typical late successional species linked to the climatic climax forest in Korea. *Q. mongolica* forest is considered a climax forest (Lee 1997).

Introduced landscape elements were composed of *Robinia pseudoacacia*, *Populus tomentiglandulosa*, *Pinus rigida*, *Larix leptolepis* and *Castanea crenata*. The dominant element here was *Robinia pseudoacacia* plantation. *R. pseudoacacia* was introduced in Korea from North America for the rehabilitation of devastated forest in the late 19th century. It is an early successional leguminous species.

Agricultural elements include croplands and paddy fields. Urbanized areas were restricted on the lower parts of the mountainous area. Graveyards also appeared as a specific landscape element even though their area is small.

The landscape element types on Mt. Daemo had a distribution pattern similar to those in the Mt. Cheonggye area, but the *Alnus japonica* community and bare rock occurred only on Mt. Daemo while the *Q. aliena* community was absent there.

Mt. Acha differed from the other two areas. Here a large public cemetery occurred and the *P. densiflora* community was widely distributed because of the extent of shallow coarse soil, typical of areas with granite bedrock .

In addition, *Q. variabilis* and *Q. aliena* secondary forest communities and the introduced *Populus tomentiglandulosa* community were not found on Mt. Acha. On the other hand, pear orchards were common. This is related to the history of Seoul, which had been the Capital of the Chosun Dynasty from 1392 to 1945 and was maintained as the Capital of Korea after 1945 (Fig. 1). Post-war urbanization proceeded mainly towards the south of the centre of Seoul. Especially since the 1970s there was a rapid expansion. Large areas of pear orchard located on hillocks and lowlands bordering the mountains were urbanized (Fig. 1).

The number and size of patches

The total number of patches was highest on Mt. Cheonggye. The number of patches and total area of the three mountains was positively correlated, but the number of patches per unit area was correlated negatively with total area. In other words, the number of patches per unit area in the smaller Mt. Daemo area was larger than that of the other two mountains with a largere area.

In the Mt. Cheonggye area the total number of patches was highest in the category introduced elements. On Mt. Daemo and Mt. Cheonggye the total number of patches of introduced elements was highest, with a larger exent of agricultural elements in the latter area. On Mt. Acha there were more secondary forest elements. Plantation of many small patches became an important cause of landscape fragmentation in all three areas. Other elements, agricultural elements and secondary forest elements contributed to further landscape fragmentation on Mt. Cheongge, Mt.

Table 1. The configuration of landscape elements identified from vegetation maps of three mountains. N = Nr of patches.

Landscape element type	Mt. Cheonggye			Mt. Daemo			Mt. Acha		
	N	Area	*N*/1000ha	*N*	Area	*N*/1000ha	*N*	Area	*N*/1000ha
Secondary forest elements									
Pinus densiflora	17 (5.7)	131.3 (2.9)	129.5	3 (1.2)	12.8 (1.0)	235.3	10 (7.9)	218.1 (16.1)	45.9
Quercus mongolica	5 (1.7)	1684.3 (37.9)	3.0	3 (1.2)	97.2 (7.5)	30.9	6 (4.7)	58.0 (4.3)	103.4
Q. variabilis	4 (1.3)	441.9 (37.6)	9.1	2 (0.8)	38.7 (3.0)	51.7	- -	- -	-
Q. aliena	1 (0.3)	1.2 (0.0)	847.5	- -	- -	-	- -	- -	-
Q. acutissima	27 (9.1)	412.7 (9.2)	65.4	24 (9.8)	268.4 (20.6)	89.4	20 (15.8)	72.1 (5.3)	277.5
Alnus japonica	- -	- -	-	1 (0.4)	2.3 (0.2)	431.0	1 (0.8)	1.0 (0.1)	1030.9
Subtotal	54 (18.1)	2671.3 (59.6)	20.2	32 (13.4)	419.3 (32.1)	76.3	37 (29.2)	349.1 (25.7)	106.0
Introduced elements									
Pinus rigida	16 (5.4)	100.4 (2.2)	159.3	60 (24.4)	139.3 (10.7)	430.6	4 (3.1)	99.7 (7.4)	40.1
Pinus koraiensis	8 (2.7)	16.5 (0.4)	485.4	11 (4.5)	6.3 (0.5)	1751.6	7 (5.5)	13.3 (1.0)	525.9
Robinia pseudoacacia	35 (11.8)	439.6 (9.8)	79.6	40 (16.2)	202.9 (15.5)	187.1	21 (16.5)	343.2 (25.3)	61.2
Populus tomentiglandulosa	14 (4.7)	22.7 (0.5)	617.3	17 (6.9)	49.9 (3.8)	340.5	- -	- -	-
Larix leptolepsis	16 (5.4)	69.8 (1.6)	229.2	3 (1.2)	6.9 (0.5)	435.4	2 (1.6)	53 (0.4)	380.9
Castanea crenata	15 (5.0)	169.3 (3.8)	88.6	6 (2.4)	4.1 (0.3)	1467.0	5 (3.9)	51.8 (3.8)	96.6
Subtotal	104 (35.0)	818.3 (18.3)	110.0	137 (55.6)	409.5 (31.4)	334.6	39 (30.6)	513.2 (37.8)	76.0
Agricultural elements									
Orchard	- -	- -	-	- -	- -	-	9 (7.1)	50.4 (3.7)	178.6
Crop land	9 (3.1)	34.2 (0.8)	263.2	11 (4.5)	95.4 (7.3)	115.3	- -	- -	-
Paddy field	27 (9.1)	493.2 (0.8)	54.7	24 (9.8)	86.2 (6.6)	278.5	2 (1.6)	9.6 (0.7)	207.7
Subtotal	36 (12.1)	527.4 (11.8)	68.3	35 (14.3)	181.6 (13.9)	192.7	11 (8.7)	60.0 (4.4)	18.3
Other elements									
Graveyard	9 (3.1)	11.3 (0.3)	799.3	15 (6.1)	10.8 (0.8)	1394.0	2 (1.6)	172.0 (12.7)	11.6
Urbanized area	58 (19.5)	449.4 (10.0)	129.1	23 (9.4)	282.4 (21.6)	81.4	17 (13.4)	233.3 (17.2)	72.9
Bare rock	- -	- -	-	3 (1.2)	2.4 (0.2)	1265.8	21 (16.5)	29.2 (2.2)	719.4
Subtotal	67 (22.6)	460.7 (10.3)	145.4	41 (16.7)	295.6 (22.6)	138.7	40 (31.5)	434.5 (32.0)	92.1
Total	297 (100)	4477.6 (100)	58.3	246 (100)	1305.9 (100)	188.4	127 (100)	1356.8 (100)	93.6

The value in parenthesis is percentage of number and size of patch.

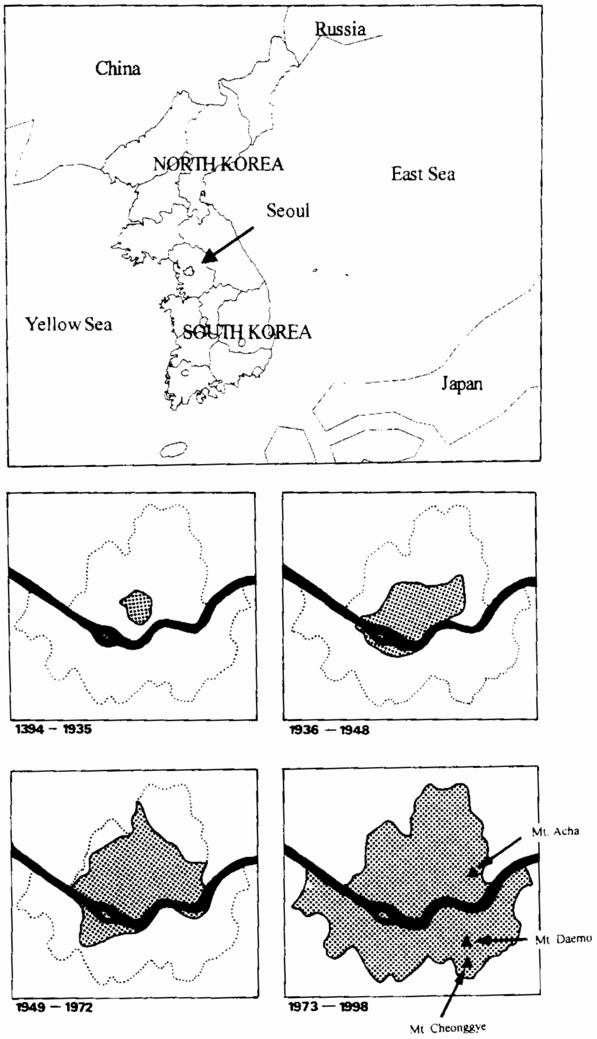

Fig. 1. Changes in the extent of the Seoul Metropolitan area and location of study sites.

Daemo and Mt. Acha, respectively. Even though Mt. Acha is visited by many people, this has not led to landscape fragmentation. On the other hand, the appearance of bare rock fragments contributed to the landscape fragmentation on Mt. Acha. Landscape patches located in the upland of the mountains were largely related to bare rock (16.5%). The number of patches also reflects the occurrence of vegetation boundaries caused by topographical and geological features (Zonneveld 1995). However, in the case of Mt. Cheonggye and Mt. Daemo there was no or only a little fragmentation by bare rock. The gneiss bedrock on Mts. Cheonggye and Daemo shows a relatively rapid weathering and is composed of finer particles as compared with granite, and hence it leads to a larger soil depth and fine soil, which is favourable for plant growth (Lee & Kim 1987). On the other hand, such soil conditions are more susceptible to human disturbance. Many landscape patches of Mt. Daemo actually reflect severe anthropogenic disturbance. Although many people visit Mt. Acha, this area has better adapted soil conditions, related to the granite bedrock.

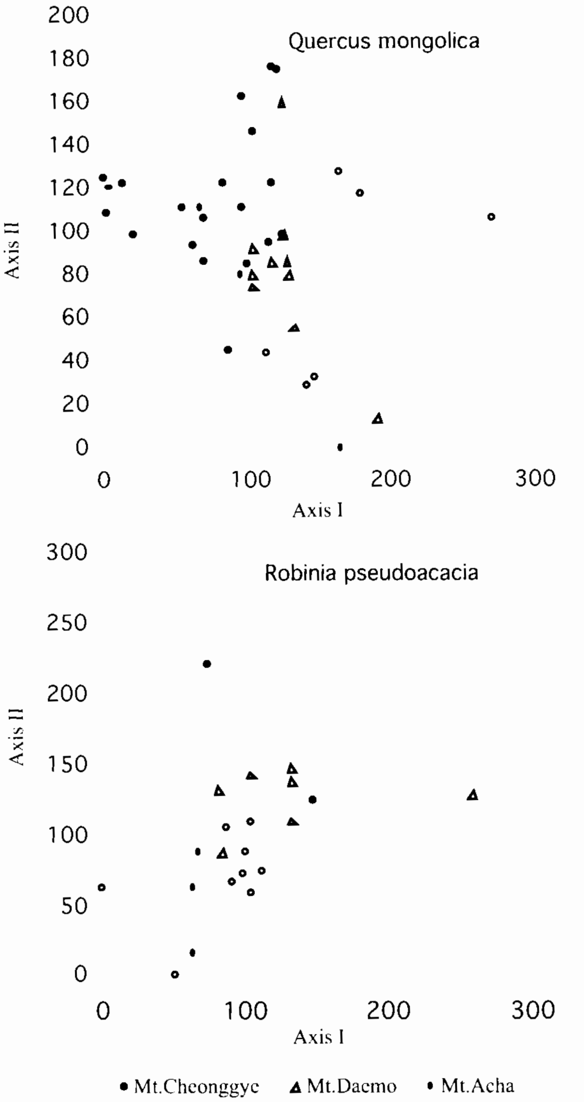

Fig 2. Ordination of stands of the *Quercus mongolica* and *Robinia pseudoacacia* communities on the three mountains.

The number of landscape patches decreased toward the top of the mountains, while most patches, including patches of introduced elements such as plantations, were concentrated around the urbanized and agricultural areas, which are located in the lowlands.

Floristic composition of the study areas

The stand ordination of *Q. mongolica* community, the dominant secondary forest element, showed that stands along axis I were arranged in the order Mt. Cheonggye, Mt. Daemo, Mt. Acha (Fig. 2). This arrangement is related to the soil characteristics. Differences in floristic composition between Mt. Cheonggye and Mt. Daemo can be related to differences in human interference. Mt. Cheonggye is farther away from the principal residential area, in which apartment complexes are concentrated (see Fig. 1). Moreover, Mt. Cheonggye is larger in area and higher in elevation (Table 1).

The main habitat of the *R. pseudoacacia* community is found at the mountain foot. Therefore, sites of this community would be under severe human impact on all three mountains and this might contribute to the fact that *R. pseudoacacia* stands on the three mountains have a similar floristic composition.

Effects of anthropogenic disturbance on urban landscape pattern

On Mt. Cheonggye introduced elements hardly appeared within the matrix of secondary forest, which is different from the situation in the other two mountains. The distribution pattern of landscape element types on Mt. Daemo was similar to that of Mt. Cheonggye. But patches of introduced elements frequently appeared in the matrix of secondary forest. In addition, introduced elements, especially *R. pseudoacacia* and *P. rigida* plantations, which were restricted to lowland sites in the Mt. Cheonggye area, were also distributed above mid-slope.

The distribution pattern of landscape element types on Mt. Acha was similar to that in the other two mountain areas, but the dominant element in secondary forest was the *P. densiflora* community. On the other hand, the distribution pattern of landscape element types on Mt. Acha was similar to that of Mt. Daemo regarding introduced elements, especially patches of *R. pseudoacacia* and *P. rigida* plantations appearing above mid-slope. Such a similarity can be related to the fact that both Mt. Daemo and Mt Acha are located more closely to the principal residential area, and are smaller in size and lower in elevation as compared with Mt. Cheonggye.

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The distribution of native and exotic species along an imposed fertility gradient in a New Zealand grassland

Svavarsdóttir, Kristín

Soil, Plant and Ecological Sciences Division, Lincoln University, Canterbury, New Zealand; Present address: Soil Conservation Service, Gunnarsholt, 851 Hella, Iceland;
Fax +3545539715; E-mail kristin_sv@landgr.is

Abstract. Plant community responses to fertilization were studied in a tussock grassland in Canterbury, New Zealand. The objective of this paper is to determine whether there are different responses of the exotic and native species to the fertilization. The vegetation at the study site initially had a uniform cover primarily of native species, with a minor component of exotic species. An experiment with sown legumes and a one-off fertilizer application (P and S) of various levels was established in 1979. 13 yr later a strong inorganic P-gradient was still found in the soil, corresponding to the phosphate application rates. Species richness decreased along the gradient mainly due to a decrease of native species. Exotic species richness showed no trend along the P-gradient. The native grasses, *Festuca novae-zelandiae* and *Poa colensoi*, were abundant at low P-levels but decreased from 100 kg P/ha. *P. colensoi* mostly disappeared at 400 kg P/ha. *Agrostis capillaris* and *Poa pratensis* (both exotic) had the reverse pattern; they increased greatly at 100 and 200 kg P/ha respectively. Fertilizer applications to counteract nutrient losses in tussock grasslands need to be used carefully if a management goal is to maintain the native components of the community.

Keywords: Field experiment; Native grassland; Phosphate; Species richness; Tussock grassland; Vegetation structure.

Introduction

Tussock grasslands are the native grasslands of New Zealand and they cover large areas of the South Island montane zone. These grasslands have been greatly affected by humans (Wardle 1991). Their distribution expanded after Maoris arrived in New Zealand ca. 1000 yr ago and cleared large areas of the forest. Another wave of destruction came when Europeans arrived with their livestock last century and large areas of these grasslands were burnt and grazed. There are indications that pastoralism during the last 150 yr has resulted in less fertile systems (McIntosh 1997).

In recent decades, there has been an attempt to increase the productivity of some of these grasslands, especially short tussock grasslands that grow at lower elevation. The main technique has been to improve the soil nutrient status by introducing legumes and applying phosphate fertilizer to promote legume growth (Douglas & Allan 1992). Much work has been done to assess the performance of legumes and a few palatable species (e.g. Scott et al. 1990; Davis 1991), while the impact on the whole ecosystem has often been neglected. Old field experiments offer an opportunity to assess such impact. In this paper, an old field experiment, in which fertilizer had not been reapplied since its establishment 13 yr earlier, was studied to determine whether there were different long-term responses of the exotic and native species to fertilization of a short tussock grassland.

Methods

Experimental site

The experiment site is situated in a short tussock grassland in the South Island, New Zealand on 43° 38' S, 171° 07' E. Prior to experimentation, the site had initially a uniform vegetation with native species dominating (*Festuca novae-zelandiae* the characteristic species), but some exotic species were present (Davis 1991). The elevation is 680m, and the annual precipitation is 880 mm.

In 1979, the New Zealand Forest Research Institute set up the experiment, looking at the establishment of different legumes along a P-gradient (Davis 1991). The experiment used a two-factor split-plot design; nine different P-rates (from 0 to 800 kg P/ha) were applied at the plot level, and nine different species of legumes, plus a control, at the subplot level. Basal fertilizer, with S, K and Mg, was applied to all plots.

Data collection

In each plot (2.3 m × 4 m), all species were recorded and their cover visually estimated. Six cover classes were used (< 1%; 1-5%; 6-25%; 26-50%; 51-75%; 76-100%).

Ten soil cores (25 mm diameter, 150 mm depth) were sampled from each plot. The soil cores from a plot were bulked together, air dried at 25 °C, and analysed for phosphorus (P) (ignition technique; Blakemore et al. 1987), pH in water (Blakemore et al. 1987), and total nitrogen (N) and carbon (C) using a mass spectrometer (Europe Scientific Ltd, UK).

Data analysis

Species richness was determined as number of species for each of three groups of species: native species, exotic species, and all species. ANOVA was used to determine the dependence of species richness on the legume and phosphate treatments and their interactions. In this paper only the effects of the P-gradient are discussed.

Individual species responses were studied using generalized additive models (GAM; Hastie & Tibshirani 1990). Species cover data of two native grasses (*Festuca novae-zelandiae* and *Poa colensoi*) and two exotic grasses (*Poa pratensis* and *Agrostis capillaris*) were fitted to measured soil variables. These species represent well the patterns observed in the experiment. The variables were fitted in the order: inorganic P, total N, C:N ratio, and pH. Analyses were carried out using S-Plus version 3.2 (Anon. 1993).

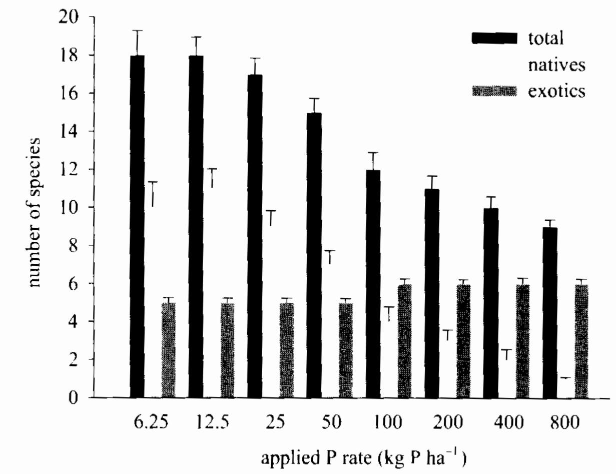

Fig. 1. Species richness for native, exotic, and all species, 13 yr after phosphate fertilizer was applied. Mean of recorded species is shown for each P-rate. Error bars are SE.

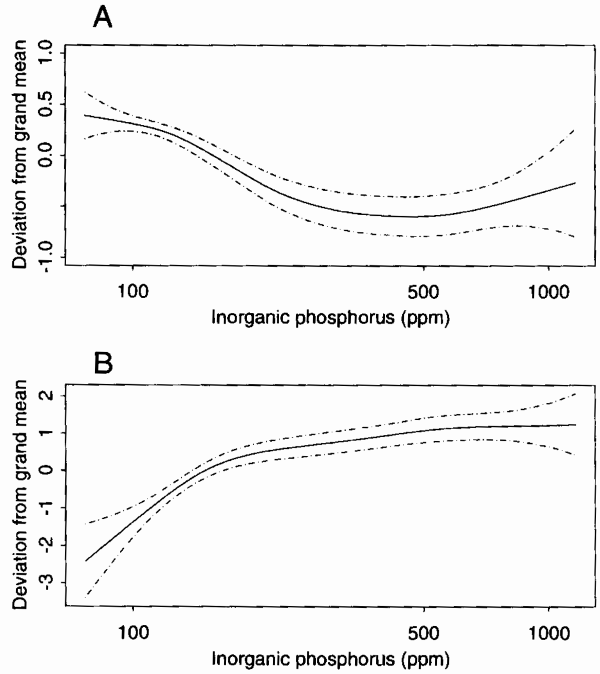

Fig. 2. Species response for the native grass, *Festuca novae-zelandiae* (**A**), and the exotic grass, *Poa pratensis* (**B**), to inorganic soil P. The graph shows results of GAM models and the y-axis presents the deviance from the grand mean of species cover.

Results

Total number of species decreased along the P-gradient (Fig. 1). This trend was due to changes in the number of native species, they decreased as the applied P-rate was higher (Fig. 1). The species richness of natives was 10 species at the lowest rate of fertilizer (6.25 kg P/ha) and one species at the highest rate (800 kg P/ha). The number of exotic species was almost constant along the whole P-gradient (Fig. 1; mean 5.5, s.d. = 0.53, $n = 8$).

Of the measured soil variables, inorganic P was the variable that was best explained by the initial P-treatments ($p < 0.001$), i.e. a strong imposed P-gradient in the soil was still apparent 13 yr after the treatments were applied. Inorganic P in the soil accounted for most of the explainable variation for all four species (Table 1, see change in deviance). The native tussock grasses, *Festuca novae-zelandiae* (Fig. 2A) and *Poa colensoi* (similar trend; data not shown), were abundant at low P-levels, but decreased along the P-gradient. Both grasses occurred as a minor component of the vegetation sward in plots which had received 100 kg P/ha or more 13 yr before. The exotic grass, *Poa pratensis* occurred sparsely in plots at low P-levels, but became the main species at high P-levels (Fig. 2B), dominating the sward. *Agrostis capillaris* had the same pattern (data not shown), but increased its cover at lower P-rates than *Poa pratensis* and did not reach such high cover levels at the highest P-rates.

Discussion

The structure of the vegetation changed greatly along the imposed P-gradient. At low P-levels many species occurred (often with low cover levels), while only very few species of high cover levels occurred in the high P-level plots. This decrease in species richness, and increase in

Table 1. Summary of generalized additive models (GAMs) for the two native grasses, *Festuca novae-zelandiae* (*Fes nov*) and *Poa colensoi* (*Poa col*), and the two exotic grasses, *Poa pratensis* (*Poa pra*) and *Agrostis capillaris* (*Agr cap*). D dev = stepwise change in deviance with addition of a variable; $p(\chi^2)$ = probability test using chi-square distribution (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns = not significant); inorg P = inorganic P in the soil; N = total nitrogen in the soil; C:N = carbon:nitrogen ratio in the soil.

	Fes nov		*Poa col*		*Poa pra*		*Agr cap*	
variable	D dev	$p(\chi^2)$	D dev	$p(\chi^2)$	D dev	$p(\chi^2)$	D dev	$p(\chi^2)$
+ inorg P	74.3	**	140.7	***	404.6	***	112.4	***
+ N	4.5	*	8.4	ns	25.6	***	0.0	ns
+ C:N	7.3	**	7.8	**	22.1	***	20.2	***
+ pH	0.4	ns	5.5	*	5.1	*	8.4	**

dominance by a few species, with increasing fertility is a widely known pattern (see review by di Tommaso & Aarssen 1989). The pattern of the total species richness in the current study was driven by the native species while the number of exotic species was similar along the gradient. The higher nutrient status as a consequence of the fertilization created conditions more favourable to the exotic grasses than the native species originally dominating. Thus, competition is likely to play a role here in determining the species richness (e.g. Grime 1988; Tilman 1988) with the exotic species stronger competitors than the natives at higher fertility. However, seed availability in an area also contributes to which species invade experimental plots (e.g. Eriksson 1993). As the tussock grasslands are low nutrient systems (Wardle 1991) the seed source in the surrounding area was unlikely to be suitable for the plots with higher fertility. The few exotic grasses were the only successful species at those higher levels.

In conclusion, decrease in species richness was due to a decrease of only native species that coincided with a change in the structure (cover dominance) of the vegetation. Consequently, fertilizer applications to counteract nutrient losses in these grasslands depend on the land use, and need to be used carefully if a management goal is to maintain the native components of the community.

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Patterns of structure and diversity across a tropical moist forest chronosequence

Denslow, Julie S.

Department of Biological Sciences, Louisiana State University, Baton Rouge, LA 70803 USA; present address USDA Forest Service, Institute of Pacific Islands Forestry, 23 E. Kawili St., Hilo, HI 96720, USA;
Fax +18089338120; E-mail julie.denslow@gte.net

Abstract. Patterns of structure and diversity are described from a chronosequence established in the Barro Colorado Nature Monument, Panama. The BCNM is a mosaic of secondary forests reflecting two centuries of agriculture and the establishment of forest preserves. Structure and composition were studied in 10 stands: two each had been farmed or pastured 20, 40, 70, and 100 yr previously; two old-growth stands likely never had been farmed intensively. Data from BCNM are compared with those published by Saldarriaga et al. (1988) from an oligotrophic site on the upper Rio Negro, Venezuela. Changes in stand structure across the BCNM chronosequence are consistent with the four phase model of secondary succession (establishment, thinning, transition, steady state). Growth is rapid and stand basal area reaches old-growth values within 70 - 100 yr. In contrast, growth at Rio Negro is slow; only 2/3 of the total basal area characteristic of old-growth stands was established at 80 yr. Sapling densities in both sites decline with forest age, increasing somewhat in older stands of BCNM but remaining low at Rio Negro. In neither site does tree diversity increase asymptotically toward a maximum in old-growth forest or peak at intermediate stand ages. These data suggest that tropical forest successional patterns may not be influenced strongly by the dominance of a few pioneer species as often seems to be the case in temperate forest successions, but reflect the availability of a diverse, easily dispersed regeneration pool.

Keywords: Panama; Secondary forest; Succession; Tropical moist forest; Venezuela.

Nomenclature: Croat (1978).

Introduction

Tropical forests long have provided insight and inspiration to plant ecologists because the high productivity, structural complexity and species diversity help provide a framework within which to place less complex or diverse communities. Similarly tropical moist forest successions should provide a valuable perspective on successional processes. Patterns of tropical forest successions may differ from those observed in temperate ecosystems for several reasons. Canopy closure is likely to be rapid following disturbances due to long growing seasons and high productivity. As a result, light levels near the ground are quickly reduced and the impacts of canopy opening on microclimates are buffered (Denslow et al. 1998). The temporal window of high resource availability thus may be considerably shorter in moist tropical forest than in many temperate successions. Diversity of potential colonists is high; patterns of tropical successions may be influenced less by the morphological, physiological or life history attributes of dominant species than temperate successions (e.g. Oliver & Larson 1996). In addition the predominance of bird and bat dispersal syndromes among most tropical trees and shrubs (Howe & Smallwood 1982) reduces dispersal limitations to seedling establishment at all successional stages. Here I discuss patterns of forest structure and diversity revealed in a long chronosequence from Barro Colorado Nature Monument, Panama in the context of a model of secondary succession based predominantly on temperate data sets. I also compare these patterns with those published by Saldarriaga et al. (1988) for a Venezuelan chronosequence on nutrient-poor oxysols.

A widely recognized model of succession (Peet 1992; Oliver & Larson 1996) recognizes four phases of succession: establishment, thinning, transition, and steady state. During the first phase, many seedlings establish under conditions of high resource availability following a stand-destroying disturbance. Tree growth increases competition for canopy space and leads to the death of suppressed individuals during the thinning phase. The eventual senescence of the early cohort of canopy trees during the transition phase (Peet 1992) or understory initiation phase (Oliver & Larson 1996) increases both structural heterogeneity of the stand and resource availability to seedlings. Finally, the steady state phase describes the gap-mosaic of old-growth forest, a combination of gap-formation and gap-filling processes which produce high spatial and structural heterogeneity (Brokaw 1985; Oliver & Larson 1996). Species diversity is seen to be correlated with these stand structural changes being low in young stands but increasing with stand development and with the establishment of a gap mosaic stand structure.

Methods

Forests on Barro Colorado Island are classified as tropical moist forests (Foster & Brokaw 1982). Mean annual rainfall is ca. 2500 mm distributed between a long wet season and a strong 4-month dry season (January-April). Stands sampled in this study occurred on oxisols and alfisols, both of which are relatively rich in available N and P (Yavitt & Wieder 1988) .

Forests of the Panama Canal watershed provide an unusual opportunity for a study of secondary succession. The vicinity of the Barro Colorado Nature Monument has been the focus of intense human activity for the last 200 yr, first, as a route west for settlers immigrating from the Atlantic coast of North America to California, then as the site of French and American activity during the construction of the canal in the early 1900s, and subsequently for the production of fruit, meat, and dairy products. Throughout this period portions of the watershed have been brought under protection from further exploitation. Most recently the Barro Colorado Nature Monument was established in 1979 to provide long-term protection of Barro Colorado Island, a field laboratory of the Smithsonian Tropical Research Institute, as well as several neighboring mainland peninsulas. The BCNM today is a patchwork of second-growth vegetation dating from different periods of agricultural activity and ranging in age from old fields to forests fallowed more than 100 yr ago. Old-growth forest covers about half of Barro Colorado Island as well as portions of the peninsulas; it is likely to be at least 500 yr old and probably was never cleared for agriculture (Piperno 1990). Contemporaneous descriptions, oral histories, and aerial photographs were used to identify stands of different ages (Denslow & Guzman 2000).

10 stands were selected for study, two each representing forests of ca. 20, 40, 70, 100 yr in fallow as well as two old-growth (500-yr) stands. Study stands were at least 10 ha in area (most were considerably larger). Vegetation in these 10 stands was sampled using a series of nested quadrats arranged contiguously along two 160-m transects (except one transect in one 20-yr stand). Trees > 5 cm DBH were sampled in a total of 32 10m × 10m quadrats. Shrubs and saplings < 5 cm DBH and > 1 m tall were sampled in 64 5 m × 5 m quadrats. All individuals were identified to species and dbh was measured for trees > 5 cm DBH.

These data are compared to results of a study published by Saldarriaga et al. (1988) on a chronosequence on the upper Rio Negro in southern Venezuela and Colombia. While the vegetation in both regions is classified as tropical moist forest, annual rainfall is higher (ca. 3500 mm) on the Rio Negro and soils are extremely nutrient-poor (oxisols and ultisols). Saldarriaga et al. (1988) studied 19 secondary stands ranging in age from 9 to 80 yr as well as four stands identified as mature forest. Stems > 1cm DBH were sampled in three 10m × 30m plots in each stand. Published data are reanalysed here for comparisons with the BCNM study.

One-way analysis of variance (PROC GLM; Anon. 1990) and simple linear regression (PROC REG; Anon. 1990) were used to compare stand characteristics among age classes.

Results

Old-growth forest structures at BCNM and Rio Negro provide a context within which to compare successional patterns. While total stand basal areas of the two sites are similar (basal areas of trees > 5 cm DBH ($\bar{x}$ ± sd) : BCNM: 27.6±4.42 m^2/ha; Rio Negro: 32.1±3.01 m^2/ha), densities of trees >10 cm DBH are higher at Rio Negro (569±33.4 trees/ha) than comparable forest at BCNM (460±55.2 trees/ha; $t = 2.8051$; df = 4; $p < 0.05$).

Agewise differences among stand structural characteristics in the BCNM chronosequence were not statistically significant (Figs. 1 and 3a). However, in view of scarce information available on tropical forest successions and an interest in temporal patterns as well as stand differences, I compare trends among agewise means at BCNM with data from the Rio Negro chronosequence to develop hypotheses about tropical forest successions. Differences in total basal area and stem densities of trees >10 cm dbh across the BCNM chronosequence (Fig. 1) suggest that growth rates are rapid. By 20 yr densities of trees >10 cm DBH reach or exceed tree densities in old-growth stands and by 70 yr total stand basal area does as well. Densities of recruitment size classes (saplings and small trees 5-20 cm DBH) are somewhat higher in older stands than in intermediate age classes (Fig. 3a). Seedlings (20-100 cm height) follow the same pattern (data not shown).

Stand structural changes in the Rio Negro chronosequence (Fig. 2) reflect the lower productivity of these nutrient-limited forests. Total stand basal area (trees > 5cm DBH) increases consistently throughout the chronosequence ($r^2 = 0.65$; $p < 0.01$; $n = 22$), but during the first 80 yr of succession stand basal area reaches only 2/3 that of old-growth forest. Variation in density of trees >10 cm DBH is high within all secondary forest age classes, although trends among means suggest that growth is slow and that recruitment into the 10-cm size class continues to be an important component of succession in older stands (Fig. 2b). Although data for sapling sizes comparable to those for BCNM were not available for Rio Negro, densities of small saplings (1 - 10 cm DBH) were similarly higher in the young than in old stands at Rio Negro (Fig. 3b). At Rio Negro, progressive canopy closure appears to reduce establishment conditions for small saplings. Relatively low sapling densities in old-growth stands suggest that canopy turnover rates in old stands may be low at Rio Negro.

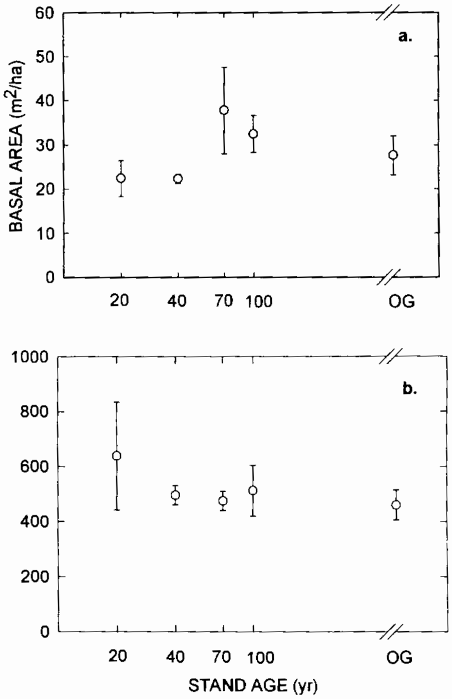

Fig. 1. Patterns of basal area and tree densities across the BCNM chronosequence. ($\bar{x}$ ± sd). **a.** Total stand basal areas of trees >5 cm DBH ($F = 1.69$; n.s.; d.f. =4,5). **b.** Densities of trees > 10 cm DBH ($F = 0.96$; n.s.; d.f. = 4,5). Points represent means and standard deviations of two replicates at each age class.

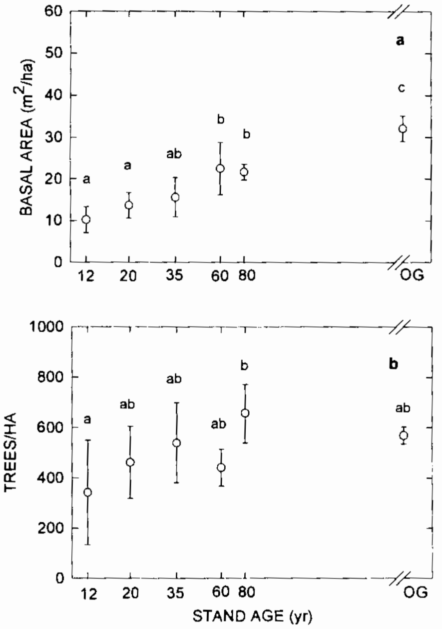

Fig. 2. Patterns of basal area and tree densities across the Rio Negro chronosequence. **a.** Total stand basal areas of trees > 5 cm DBH. ($\bar{x} \pm$ sd); F =17.54; $p < 0.001$; df = 5,17. **b.** Densities of trees > 10 cm DBH. Each age class is represented by the mean and standard deviation of 3 - 4 stands (F =2.53; $p < 0.10$; df = 5,17). Data from Saldarriaga et al. 1988.

Species richness of BCNM trees (> 5cm DBH) shows little variation across stand ages (data not shown). Among small saplings (1 m tall to 5 cm DBH), the number of species sampled declined during the first 100 yr but were somewhat higher in old-growth stands (Fig. 4a). Sample sizes from the Rio Negro chronosequence are small and variation within stand age classes is large; however, observed tree species richness did not vary as a function of stand age (Table 1 in Saldarriaga et al. 1988). In both sites, stem density is an important correlate of species diversity. Species richness of Rio Negro trees (r^2=0.38, $p < 0.05$, n = 23) and BCNM saplings (r^2=0.74, $p < 0.05$; n = 9, Fig. 4b), but not BCNM trees, were a significant positive function of stem density.

Discussion and Conclusions

Old-growth forest at BCNM is tall (main canopy at 30-40 m with emergents approaching 50 m; Knight 1975) and growth rates are high (1.5-8.4 mm/yr for trees >1 cm DBH, estimated from Condit et al. 1995). At Rio Negro, the forest stature is low (<25 m, Uhl & Murphy 1981) and growth rates are slow (ca. 1 mm/yr; Murphy & Jordan unpubl.). Although stand basal areas of the two forests are comparable, tree densities are higher at Rio Negro than at BCNM. Uhl & Murphy (1981) concluded that high stem densities, low basal area, low stature, and low growth rates in the Rio Negro forests were due to the oligotrophic nature of the

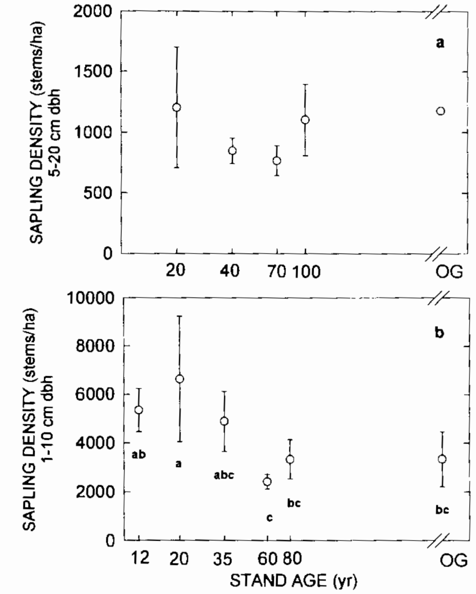

Fig. 3. a. Sapling densities across the BCNM chronosequence (F = 0.90; n.s.; df = 4,5). Saplings are 5 - 20 cm DBH. Each point represents the mean and standard deviation of two replicates at each age class. **b.** Sapling densities across the Rio Negro chronosequence (F = 4.63; $p < 0.01$; df = 5,17). Saplings are 1 - 10 cm DBH. Each age class is represented by the mean and standard deviation of 3 - 4 stands. Data are from Saldarriaga et al. 1988.

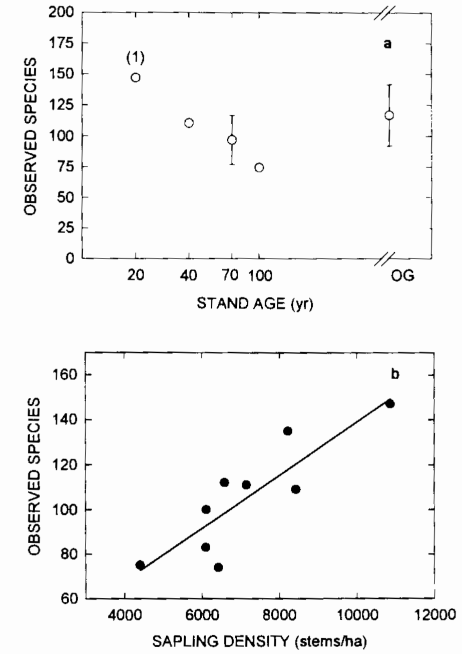

Fig. 4. Numbers of species recorded among saplings 1 m tall to 5 cm DBH in the BCNM stands. **a.** Changes in species richness as a function of stand age. Each age class is represented by the mean and standard deviation of two stands, with the exception of the 20-yr stand for which data from only one stand are included (f= 2.84; d.f. = 3,4; ns). Error bars on 40 and 100 yrs stands are small. **b.** Regression of species richness on density (r^2 =0.74; n = 9; $p < 0.05$).

site. Comparison with old-growth forest on the BCNM suggests that the Rio Negro sites are also more oligotrophic than those in Panama.

The changes in forest structure during tropical succession shown in these two chronosequences are largely consistent with the patterns summarized by Peet (1992) and Oliver & Larson (1996), although early patterns of change in basal area, stem density and species richness were not included at either site. These two tropical chronosequences illustrate the importance of site productivity for the patterns and rates of secondary succession. Basal area accumulation appears to be slow and asymptotic in the Rio Negro sequence reflecting low soil nutrient availabilities. The BCNM chronosequence more closely approaches the shifting mosaic model (Peet 1992) in which biomass of old-growth stands is somewhat less than the maximum exhibited by intermediate aged stands prior to thinning. In any case, basal areas characteristic of old-growth forests are reached by 70 yr in the more productive site. Diversity of canopy trees within young secondary stands is relatively high at both sites, so it is unlikely that these patterns arise solely from the behavior of one or a few common species, as they might in less species rich temperate communities. The pattern is similar to that observed by Brown & Parker (1994) for a mesic temperate forest chronosequence in Maryland.

Both chronosequences suggest that stand turnover rates vary as a function of stand age as evidenced by changes in density of regeneration size classes. At BCNM, stand turnover appears to increase in older stands (80 - 100 yr), suggesting a degree of synchrony in the mortality of canopy trees, which might come about from senescence of an even-aged cohort of a common species, senescence of species sharing similar demographic patterns, or as a function of increasing intensity of competitive interactions among growing trees. At Rio Negro, sapling densities are lower in old than in young stands. Although there is some indication of increased stand turnover at 80 yr, sapling recruitment appears to be limited in older stands. Establishment sites may be scarce in old stands because of space occupied by accumulated dead wood, large boles of canopy trees, and dense clumps of understory palms as well as by shade cast by understory shrubs and treelets.

Species richness within regeneration sizes class is strongly correlated with stem density and thus linked to stand structure within the BCNM sequence. For example, both density and species richness of saplings 1 m tall to 5 cm DBH decline throughout the first 100 yr. Nevertheless, species richness of small saplings are higher in old-growth than in 100-yr secondary stands, suggesting that important structural and compositional differences between old-growth and old secondary forests remain. Low dispersal limitations, high stand heterogeneity, and high diversity likely contribute to a species-rich seed rain and diverse regeneration pools in the oldest stands. Unlike secondary forests in many tropical landscapes, the stands studied at BCNM are bounded not by pasture but by contiguous secondary and primary forest. Dispersal of seeds from proximate sources is likely less limited under these circumstances than under the more usual conditions of fragmented forests in an agricultural landscape (Dalling & Denslow 1998). As a result species diversity is high and successional patterns reflect shared characteristics of many species rather than the dominance of a few.

At neither site is there evidence of an asymptotic approach to maximum species diversity in old-growth stands as suggested by some succession models (Peet 1992; Drury & Nisbet 1973) or a maximum at intermediate ages as suggested by the intermediate disturbance hypothesis (Connell 1978). Tropical forests may more closely follow plankton models of community structure in which high diversity and efficient dispersal provides a species-rich regeneration pool at all stand ages. While the relatively harsh environmental conditions characteristic of abandoned pastures (Uhl et al. 1988) may limit early establishment to high-light requiring, stress-tolerant species, understory light and soil environments do not vary strongly as a function of stand age following canopy closure (Nicotra et al. 2000; Denslow & Guzman 2000) and appear to be within the tolerance range of most rain forest trees and shrubs (Denslow 1987). In the absence of strong environmental selection among the regeneration pool of species, diversity is constrained primarily by opportunity (availability of establishment sites) and composition of the propagule pool. Few species dominance is most likely to be important in the earliest stages of tropical succession (< 15 yr), when seed stocks are limited by dispersal or habitat fragmentation, or when site degradation arrests the process of seedling establishment.

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Tree seedling development in a tropical dry forest in Costa Rica

Gerhardt, Karin

Department of Plant Ecology, Uppsala University, Villavägen 14, SE-752 36 Uppsala, Sweden;
Fax +4618553419; E-mail: karin.gerhardt@ebc.uu.se

Abstract. Tropical dry forests have been fragmented by deforestation and changes in land use. Knowledge of the dynamics of these forests is poor. In northwestern Costa Rica, tree seedling dynamics in abandoned pastures and secondary dry forests were studied by planting them under different light and root competition regimes. Survival and growth was measured regularly between 1989-1993. This study reports the long-term sapling development five years later. The effects of the initial experimental conditions showed that particularly removal of root competition by trenching improved survival on a long-term basis.

Keywords: Tropical dry forest; Seedling establishment; Guanacaste; Conservation area, Long-term effect, *Hymenaea courbaril*; *Swietenia macrophylla*.

Introduction and Study area

Tropical dry forests once constituted ca. 40% of the lowland forests in the tropics (Murphy & Lugo 1986). Rapid deforestation and conversion to farm or grazing land during the last centuries have left only fragments of the original forest and mostly secondary vegetation. Less than 1% of the original forest remains in a relatively undisturbed condition, which makes them more threatened than tropical rain forests (Janzen 1993).

Guanacaste Conservation Area (105000 ha), the study area in northwestern Costa Rica, consists of abandoned pastures, semi-deciduous dry forest fragments and secondary forest regrowth. The seasonal (5-7 months) rainfall varies between 800 and 2500 mm annually. The pastures are slowly being re-invaded by woody species through natural regeneration and by exclusion of fires and other human activities. Active restoration through tree planting was initiated in the end of the 1980s. I carried out an intensive study on seedling survival and growth of common tree species, experimentally planted in different ecological conditions. They were measured monthly between 1989 and 1993 (Gerhardt 1993, 1996) and remeasured in January 1998.

The hypothesis in 1989 was that the long dry season limit belowground resource availability for seedling establishment, compared with tropical rain forests where light is the main limiting factor. By experimentally changing those resource levels (soil moisture availability, nutrient and light levels) insights could be gained about mechanisms for seedling development in these forests (Gerhardt 1996). In this paper the impact of the initially manipulated resource levels on the long-term (post-treatment) development of those seedlings/saplings were examined.

Material and Methods

Two common tree species were monitored in this study. *Hymenaea courbaril*; an evergreen, slow growing, animal-dispersed tree and *Swietenia macrophylla*, a deciduous, fast growing, wind-dispersed tree. In the original study four species were included (Gerhardt 1993, 1996), but only two species remained until 1998.

Two secondary vegetation types were studied: abandoned pasture and approx. 40-yr old forests. Nursery-raised 4-month old seedlings were planted in either in tall *Hypharrenia rufa* (unmown) pasture or in regularly mown pasture, monitored between 1989 and 93 (Gerhardt 1993). The grass was then left for free development. Two forest sites were used; one with deciduous trees dominating (deciduous site) and one containing both deciduous and evergreen trees (semi-evergreen site). In both sites canopy heights varied between 5 and 12 m. Seedlings had been planted in a 2 × 2 factorial design. The canopy was either intact (Th_0), or thinned (Th_1), where shrubs, understorey trees and tree branches had been removed (Table 1). Circular trenches (using polythene plastic) were placed around the seedlings to decrease root competition (Tr_1), or left untrenched as a control (Tr_0) (Gerhardt 1996). Daily rainfall, soil conditions (nutrients and soil physical factors), soil moisture (weekly), light conditions in the forests at different seasons (Table 1), monthly seedling survival, height and diameter increment (every 6 month) and defoliation/herbivory was measured 1989-1993. (For results see Gerhardt 1993, 1996, 1998.) In July 1993 trenches were removed and the canopy was allowed to develop to the original stage. Five years later the surviving saplings/treelets (survival, height and diameter) were remeasured.

Results and Discussion

Pasture trial (1989-93/93-98)

The highest seedling mortality was caused by dry season drought, particularly during the first dry season (Table 2). Growth was initially low during the first three years. Mowing effects were confounded by large soil variation, but mown grass appeared to be somewhat more favourable for seedling development than the unmown grass (Table 2 and Gerhardt 1993).

Mortality during the post-treatment period (1993-1998) was much lower for the plants that had developed in mown (M) than in unmown (U) conditions, *H. courbaril*: M 8% versus U 29%, *S. macrophylla* M 3% versus U 17%. Thus, initial mowing had improved survival in a longer time perspective. Survival rates were similar in both species, but *S. macrophylla* had higher growth rate than *H. courbaril* (Table 2).

Forest trials (1990-1993/1993-1998)

Seedling mortality was low in the rainy season but did generally increase in the late dry season, particularly the first year (Gerhardt 1996). Survivorship was higher in the pasture than in the forest both at an annual rate, and at 7.5 yr.

Table 1. Forest light conditions in the two forest sites in percentage of photosynthetic active radiation (PAR). Th = thinning treatment, Tr = trenching treatment.

Treatment	Wet season 1991	Dry season 1991	
Th_0Tr_0	6 - 8%	Deciduous site	40 - 50%
		Semi-evergreen site	30 - 40%
Th_1Tr_0	35 - 40%	Deciduous site	60 - 70%
		Semi-evergreen site	55 - 65%
Th_0Tr_1	6 - 8%	Deciduous site	40 - 50%
		Semi-evergreen	30 - 40%
Th_1Tr_1	30 - 40%	Deciduous site	60 - 65%
		Semi-evergreen	40 -65 %

(Tables 2 and 3). Thinning and trenching did affect the survival and growth during the first three years of measurement (Table 3; Gerhardt 1996). Mean growth rate was much lower in the forest than in the pasture (Tables 2 and 3). Herbivory contributed to decreased survival and growth during the first years (Gerhardt 1998).

After 7.5 yr it was clear that trenching had had long-term positive effects for both species (using the 1993 surviving plants as a new cohort and comparing with survival in 1998) (Table 4). Sapling survival was twice as high for those that had been located within a trench. This indicates that establishment and early development in tropical dry forest vegetation is favoured by decreased root competition (for water and nutrients) and that the effects are long-term, although trenching had little effect in the semi-evergreen site initially (Table 3; Gerhardt 1996). Trenching may have allowed the development of a larger, more effective, root system. Both trenching and thinning had a positive effect on growth (Table 4).

Table 2. Mean mortality and growth of *Hymenaea courbaril* and *Swietenia macrophylla* in pasture trials from 1989-1998. M = mown pasture, U = unmown/natural pasture.

Annual mortality	Treatments pooled			Survival at 8.5 yr	
At year	1	3	8.5		
H. courbaril	30%	15%	4.0%	M 47%	U 30%
S. macrophylla	47%	16%	4.5%	M 32%	U 24%
Annual growth	**Height increment**			**Height at 8.5 yr**	
At year	1	3	8.5		
H. courbaril	3 cm	5 cm	25 cm	165 cm	
S. macrophylla	10 cm	15 cm	50 cm	340 cm	
Diameter increment				**Diameter at 8.5 yr**	
H. courbaril	0.2 cm	0.2 cm	0.7 cm	3.8 cm	
S. macrophylla	0.4 cm	0.6 cm	2.0 cm	10 cm	

Table 3. Secondary forest experiment mortality and growth from 1990 to 1998.

Annual mortality (treatments pooled)				
At year	1	3	7.5	Survival 1998
H. courbaril				
Deciduous site	33%	16%	11%	22%
Semi-evergreen site	10%	11%	11%	37%
S. macrophylla				
Deciduous site	60%	30%	12%	8%
Semi-evergreen site	20%	16%	13%	25%
Annual growth - height increment				
H. courbaril (all branches)				Total stem height 1998
Deciduous site	5 cm	2 cm	-	62 cm
Semi-evergreen site	6 cm	9 cm	-	95 cm
S. macrophylla				
Deciduous site	13 cm	15 cm	22 cm	162 cm
Semi-evergreen site	9 cm	13 cm	18 cm	147 cm

Conclusions

Competition for belowground resources appear to play a significant role particularly when resources are seasonal (soil moisture), and that increasing light levels during the dry season increases water and plant stress. In a Ghanaian dry forest shady places are reported to be more favourable than open areas (Lieberman & Li 1992). Root competition that affects seedlings is also reported by Fisher et al. (1991) in a moist forest and Coomes & Grubb (1998) in a nutrient-poor rain forest. Most studies in tropical rain forests have found no effects on trenching (Denslow et al. 1991; Grubb unpubl.).

The results from this study show that the initial microsite conditions, particularly belowground, affect tree seedling establishment in a seasonally dry forest. And although not necessarily measurable initially, they may play an important role in the further development of the juvenile trees.

Acknowledgements. I greatly acknowledge the fieldwork assistance during 1998 of Felix Carmona Mendes.

Table 4. Treatment effects on survival (S) and growth (G) using ANOVA analysis (significant at $p < 0.05$), during the first period 1990-1993 and the second period 1993-1998 in the forest trial. + indicates significant effects. Th = thinning treatment, Tr= trenching treatment.

Species	Site	Treatment	S 90-93	S 93-98	G 90-93	G 93-98
H. courbaril	Deciduous	Th			+	+
	Tr	+	+	+	+	
	Semi-evergreen	Th	+		+	+
	Tr		+	+	+	
S. macrophylla	Deciduous	Th			+	+
	Tr	+	+	+	+	
	Semi-evergreen	Th			+	+
	Tr		+	+	+	

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Vegetation changes in a Sahelian valley system in Burkina Faso

Lykke, Anne Mette

Department of Systematic Botany, University of Aarhus, Nordlandsvej 68, 8240 Risskov, Denmark;
Fax +45 8942 4747; E-mail lykke@biology.au.dk

Abstract. Sahelian valley systems ('bas-fonds') are key stone ecosystems in the sense that they harbour dense, species-rich vegetation in an otherwise dry environment. Many of the woody valley species are highly appreciated by local people, because they provide construction-wood, fruits, medicine, and livestock fodder. In this study two methods, interviews with elderly local people and vegetation sampling are used to gain information about vegetation changes of the woody vegetation in a valley system in northern Burkina Faso, West Africa. According to local Fulani people (former nomads) the valley vegetation is highly degraded today, the vegetation used to be dense a few decades ago, but it is now open and lacks regeneration; many species are declining, and some have become locally extinct. Vegetation data support the local information; size class distributions reveal that most woody species have few young individuals and weak rejuvenation, and many of the locally appreciated species are rare. Through interviews and vegetation studies it is possible to assess the state of most of the ca. 60 woody species that grow in the area which is important for the planning of natural management strategies.

Keywords: Degradation; Fulani people; Sahel.

Nomenclature: Lebrun & Stork (1991-1997).

Introduction

The Sahel is well-known for its environmental problems as degradation and desertification in the Sahel have been frequently debated political issues. The degradation problems concern both soil, herbaceous vegetation, and woody vegetation. This study, however, focuses on the woody vegetation, an extremely important element of the Sahelian ecosystems that has been particularly affected by thinning and compositional changes during the last decades (e.g. Geerling 1985; Sinclair & Fryxell 1985; Cross & Barker 1991; Breman 1992; Stiles 1995a). A degradation of the woody vegetation affects local societies directly as woody plants serve essential functions by providing livestock fodder (Le Houérou 1989), by sustaining and ameliorating soil and grass components of the ecosystem (Dunham 1991; Solbrig 1993; Belsky & Canham 1994), and by providing a variety of daily used products such as food, medicine, firewood, and construction materials (e.g. von Maydell 1990).

Despite the fact that trees and shrubs are both severely declining and extremely useful to local people in the Sahel, management of the woody vegetation has received little attention in west African arid and semi-arid areas (von Maydell 1995). Also the newest theories for rangeland management in disequilibrium systems (e.g. Behnke et al. 1993; Scoones 1996) largely ignore problems concerning assessment and management of woody resources. The aim of this study is therefore to specify floristic changes of woody plants in order to provide data that can be used as a basis for management strategies. Species level information on vegetation changes can be gained from vegetation investigations and from local knowledge, which today is a widely recognized source for information on natural resource questions (Gadgil et al. 1993; Meffe & Carroll 1994; Stiles 1995b).

The field studies took place in a typical Sahelian area and included (1) interviews with elderly local people and (2) vegetation sampling with focus on valley systems ('bas-fonds'). Valley systems are key stone ecosystems in the Sahel as they are relatively humid with a comparatively dense, tall, species-rich, and productive vegetation in an otherwise dry environment. Valley systems are highly important for maintaining biodiversity in the Sahel, and they are recognized by local people as the most important vegetation type for extraction of wild products (Lykke 1998).

Study site

The study took place in the region of Gorom Gorom, Oudalan province, in northern Burkina Faso (Fig. 1). The landscape is characterized by large stretches of planes interrupted by valley and dune systems. The word 'valley' is used in a broad sense to include floodplains and banks of seasonal streams with a vegetation that is clearly different from that of the neighbouring plane. The planes are covered by grassland and shrubland vegetation, the dunes are dominated by grasslands and open spaces, and the valleys hold vegetation types ranging from forest to grassland.

The rainy season lasts about three months (June-September) with irregular, sporadic, and unpredictable precipitation, as is typical for the Sahel. From 1958 to 1996 average precipitation in Gorom Gorom was 403 mm/yr. Two major droughts occurred in this period, one in the early 1970s and one during the 1980s. The area is mainly inhabited by people from the ethnic groups of Fulani (Peulh/Rimaibe), Bella, Touaregs and Sonrai. Following the tradition in the Sahel, rangelands are communal lands. During the last 30 yr many nomadic pastoralists have settled down in order to supplement their income by agriculture, and today most people live as agro-pasturalists (Reenberg & Fog 1995). Many families, though, supplement their income by migratory work.

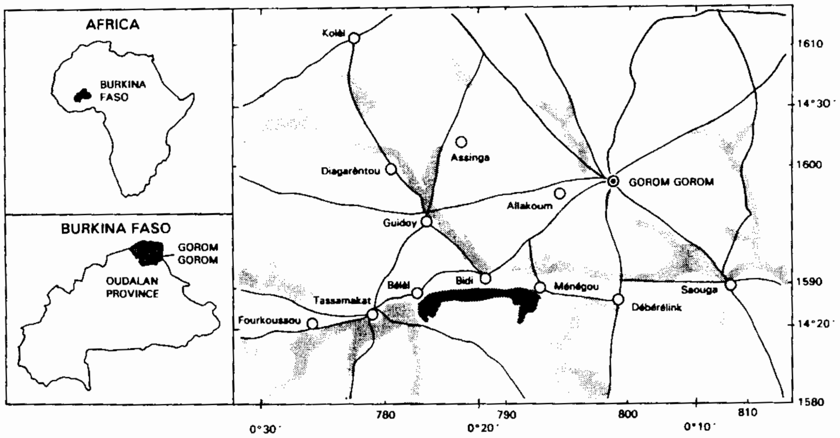

Fig. 1. Location of study area in the vicinity of Gorom Gorom in the Oudalan Province. The investigated valley system is indicated in light gray and a seasonal water pool in dark gray.

Methods

Information was derived from two different methods: interviews with elderly local people and investigations of woody plants in valleys.

11 Fulani villages at walking distance from a valley were selected for interviews (Fig. 1). Information about vegetation changes and increasing/declining species was collected through semi-structured interviews with 21 groups of people (11 groups of men and 10 groups of women) including from one to about 15 people, but mainly three to six persons. People were asked to mention increasing/declining species through free-listing techniques. The semi-structured interviews were followed up by structured interviews with 100 people from five of the villages. People were asked individually to classify each of 59 species according to their status as increasing/declining (declining species were categorized as slightly, moderately, or severely declining).

Vegetation was described on the basis of stratified random sampling. 15 sites were sampled along valleys to cover well-protected valley vegetation. 10 random points were located at each site through random number techniques. This made a total of 150 random points. At each point a 20 m × 20 m plot was investigated for woody plants <5 cm DBH (diameter at 1.3 m height) (referred to as regeneration). At each point plotless sampling was carried out by the point quarter method (Cottam & Curtis 1956): (1) four quadrants were located by a random method; (2) the distance to the nearest tree or shrub ≥ 5cm DBH and ≥ 10 cm DBH in each quadrant was measured; (3) DBH of the nearest tree or shrub ≥ 5 cm DBH and ≥ 10 cm DBH in each quadrant was measured. The densities from plotless sampling were calculated according to Pollard (1971) and Krebs (1989).

Results and Discussion

Local knowledge

Former nomads of the Sahel are obvious informants for detailed information about environmental change, because of their close relation with and dependence on the surrounding natural resources. Most people knew nearly all of the ca. 60 woody species that occur in the area (Lykke 1998). And consistency in the information given independently by different people rendered credibility to local peoples observations. It is a general view among local people that the vegetation of the area had experienced a severe degradation and they gave detailed descriptions about changes in species abundances. The word 'degradation' is here used to describe a vegetation change where the biological potential has been reduced to an inferior state, reversibly or irreversibly, to such a degree that the system's ability to satisfy particular uses has declined (Stiles 1995a).

The valley systems were described as the most severely affected by degradation. The valley vegetation was dense few decades ago, but today it is open in most places and young trees are sparse. The period of border conflicts between Burkina Faso and Mali (1974), which coincided with a severe drought period, was generally cited as the time when a severe dieback of woody plants started and when the abundant regeneration of woody plants ceased.

Acacia tortilis is generally said to increase in the area, but local people consider all the remainder species of woody plants as declining (with the exception of *Balanites aegyptiaca*, *Faiherbia albida* and *Leptadenia pyrotechnica* in certain areas). The following species were most frequently mentioned when local people were asked to name the most declining species (the number in parentheses gives the number of groups of people, out of 21 groups, who mentioned the species): *Grewia bicolor* (19), *Adansonia digitata* (16), *Grewia villosa* (9), *Pterocarpus lucens* (9). A total of 25 species were mentioned (Lykke et al. 1999). During free-listing techniques people generally mentioned

Table 1. Estimation of the degradation status of woody species assessed by structured interviews.

Severely declining (or extinct) (estimated by > 70%)	Severely declining[1] (estimated by 50-70%)	Slightly or moderately declining[1] (estimated by 50-90%)	Slightly declining species (estimated by > 90%)
Cadaba farinosa	*Grewia villosa*	*Ficus sycomorus*	*Leptadenia hastata*
Grewia tenax	*Ximenia americana*	*Leptadenia pyrotechnica*	*Bauhinia rufescens*
Khaya senegalensis	*Guiera senegalensis*	*Hyphaene thebaica*	*Feretia apodanthera*
Capparis sepiaria	*Pterocarpus lucens*	*Diospyros mespiliformis*	*Dicrostachys cinerea*
Kigelia africana	*Acacia senegal*	*Ziziphus mucronata*	*Azadirachta indica*
Grewia flavescens	*Phoenix dactylifera*	*Calotropis procera*	*Piliostigma reticulatum*
Commiphora africana	*Acacia ehrenbergia*	*Sclerocarya birrea*	*Anogeissus leiocarpa*
Vitex doniana	*Grewia bicolor*	*Flueggea virosa*	*Acacia seyal*
Boscia senegalensis	*Andira inermis*	*Tamarindus indica*	*Combretum micranthum*
Stereospermum kunthianum		*Maerua angolensis*	*Acacia tortilis*[2]
Boscia angustifolia		*Combretum glutinosum*	*Balanites aegyptiaca*
Celtis toka		*Faidherbia albida*	*Ziziphus mauritiana*
Gardenia ternifolia		*Combretum aculeatum*	
Crateva adansonii		*Acacia nilotica*	
Maerua crassifolia		*Acacia ataxacantha*	
Boscia salicifolia		*Mitragyna inermis*	
Dalbergia melanoxylon			
Acacia polyacantha			
Adansonia digitata			

[1] Species with geographic differences; [2] *Acacia tortilis* was, as the only species, generally defined as increasing.

common, conspicuous and useful species: the two *Grewia* species have edible fruits and are important browse species, *Adansonia digitata* has edible fruits and leaves and is useful for various purposes, and *Pterocarpus lucens* is valued for browse and for high quality construction wood. People, however, forget rare and less used species when asked through free-listing techniques. When directly questioned about the status of each single species during structured interviews, local people gave information about many species not mentioned during free-listing techniques. This is the case for *Cadaba farinosa*, *Grewia flavescens*, *Maerua crassifolia*, which were considered severely declining by more than 80% of the people, and for *Celtis toka*, *Stereospermum kuntianum*, and *Vitex doniana* which were said to be locally extinct.

A large consistency was found among peoples answers, 19 species were mentioned as severely declining (or extinct) by more than 70% of the people, and 12 species were mentioned as slightly declining (or in the case of *Acacia tortilis* increasing) by more than 90% of the people. For the remainder 25 species there were geographic differences; many species were consistently or mainly mentioned as severely declining by people from some villages whereas they were mentioned as slightly or moderately declining by people from other villages (Table 1). E.g. *Diospyros mespiliformis*, *Ficus sycomorus*, *Andira inermis*, *Sclerocarya birrea* and *Hyphane thebaica* were said to be severely declining around some villages, whereas they were only indicated as slightly declining around other villages. In this way it is possible to get an indication of local variations on the basis of structured interviews.

Vegetation studies

Information on density and number of species sampled per site is given in Table 2. Remarkably few woody plants were sampled in the size class from 5 - 10 cm DBH. The most abundant species ≥ 10cm DBH were *Diospyros mespiliformis*, *Piliostigma reticulatum* and *Anogeissus leiocarpa*, *Balanites aegyptiaca* and *Mitragyna inermis*, which accounted for 80% of all individuals. Except for *Balanites aegyptiaca*, however, they were regenerating sparsely. Five species accounted for 75% of the regeneration; *Acacia tortilis* was most abundant followed by *Feretia apodanthera*, *Guiera senegalensis*, *Combretum aculeatum*, and *Balanites aegyptiaca*. Other (mostly rare) species did not regenerate (Table 2). The valley vegetation is invaded by species that are otherwise typical of the planes, mainly *Acacia tortilis*, and in the four sites with low density of woody plants ≥ 10 cm DBH, *Acacia tortilis* and *Balanites aegyptiaca* dominated the regeneration. This is an example of a change to a more drought adapted vegetation type which was described to be a typical consequence of heavy livestock grazing/browsing (Skarpe 1992).

Vegetation data generally support local information. Size

Table 2. Average number of individuals per ha, based on sampling of 0.6 ha for regeneration, 13 ha for plants ≥ 5 cm DBH and 14 ha for plants ≥ 10 cm DBH.

	Regeneration	≥ 5 cm DBH	≥ 10 cm DBH
Diospyros mespiliformis	147	8.8	8.3
Piliostigma reticulatum	58	6.8	6.7
Anogeissus leiocarpa	15	6.2	6.4
Balanites aegyptiaca	377	6.8	6.2
Mitragyna inermis	60	5.2	4.6
Acacia seyal	128	3.2	3.0
Acacia tortilis	550	1.8	1.7
Pterocarpus lucens	0	0.8	0.8
Combretum glutinosum	2	0.8	0.8
Acacia nilotica	33	0.5	0.4
Tamarindus indica	0	0.4	0.4
Bauhinia rufescens	22	0.4	0.4
Combretum micranthum	153	0.8	0.3
Andira inermis	5	0.2	0.2
Crateva adansonii	2	0.1	0.1
Sclerocarya birrea	0	0.1	0.1
Gardenia ternifolia	0	0.1	0.1
Acacia senegal	0	0.1	0.1
Acacia ataxacantha	3	0.1	0.1
Hyphaene thebaica	8	0	0
Guiera senegalensis	405	0.1	0
Grewia bicolor	13	0	0
Flueggea virosa	18	0	0
Feretia apodanthera	437	0	0
Faiderbia albida	3	0.1	0
Dalbergia melanoxylon	3	0	0
Combretum aculeatum	383	0	0
Total	2827	43	41

class distributions reveal that most woody species have few young individuals and many of the locally appreciated species are rare. *Acacia tortilis*, in contrast to most other species, seemed to have a good and constant rejuvenation, whereas *Pterocarpus lucens* and *Tamarindus indica* practically lack regeneration. At presently size class distributions are analysed in more detail. Many species, however, are so rare that it is difficult to get reliable data through vegetation sampling.

Earlier studies of the vegetation in the Oudalan province showed that many trees died and large areas were degraded in the period from 1955 to 1974 (Krings 1980; Lindqvist & Tengberg 1993). Lindqvist & Tengberg found a recovery of depressions in the last decade, but this was not supported by the present study. Degradation problems of the woody vegetation similar to those described in the present study were earlier reported from the region (Ganaba & Guinko 1996).

Conclusions

Nomads of the Sahel do not have traditional practices for vegetation conservation as migratory routes earlier ensured a natural restoration of the vegetation in a Sahel with less people and less livestock. Today this is no longer possible, and new practices are required to allow the woody vegetation disturbance-free periods to regenerate. Nomadic people, however, posses important knowledge about the environmental changes that have occurred in this century which is useful for assessing the status of the woody vegetation as a basis for restoration and sustainable use.

Long-term vegetation data are rarely available, but static vegetation data are important to quantify and specify the natural resources that are available to local people. A large consistency was found in the information given by different people, but also in local information and information derived from vegetation studies. A combination of interviews and vegetation studies is therefore considered a reliable method for assessing the status of woody species as a basis for management strategies.

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Planting experiments for the restoration of tropical rain forest in Southeast Asia and a comparison with laurel forest at Tokyo Bay

Miyawaki, A. & Meguro, S.

Japanese Center for International Studies in Ecology (JISE), 231-0023 Yamashita-cho, Yokohama, Japan; Fax +81456517692; E-mail miyawaki@jise.or.jp

Abstract. Since 1990 we have conducted a restoration project in the tropical rain forest of Borneo, Malaysia. The dominant trees of the potential natural vegetation of the area (including members of the families *Dipterocarpaceae, Myrtaceae, Lauraceae* and *Sapotaceae*) were planted. We compared the best plots in Malaysia with plots from mesic laurel forest in Japan. The Borneo plots had better initial establishment and higher growth rates than plots in the laurel forest at Tokyo Bay. Restoration of forest in the tropics is important as a means of carbon fixation.

Keywords: Borneo; Degraded land; *Dipterocarpaceae*; Fixation of carbon dioxide; Growth performance; Seedling.

Nomenclature: J.A.R. Anderson (1980).

Introduction

Reforestation has been proposed as a means of solving present global environmental problems. Many restoration projects have recently been initiated in degraded forests. Tropical forest restoration is an especially urgent issue because of the rapid disturbance taking place in the tropical landscape. Among other purposes, restoration would promote the survival of biodiversity.

There have been many restoration projects in Japan, eastern China, Southeast Asia and Latin-America (Miyawaki 1992, 1993, 1999). Here we report on a restoration project in the tropical rain forests of Southeast Asia. We compare our findings in these forests with results from a warm temperate forest.

Site and Methods

The site we used is located at Universiti Putra Malaysia Bintulu Campus on Sarawak State, Malaysia (Borneo Island), about 2 km inland from the sea coast. Slope steepness is 30°. Soil texture is dominated by silt. We varied the following experimental factors: soil moisture, soil type, sun light intensity, microtopography, nutrients, and planting density. Species used were *Dipterocarpaceae* (the main emergent trees that generally form the canopy tree layer in tropical rainforests in Southeast Asia), and other families of the potential natural vegetation (e.g. *Myrtaceae, Lauraceae, Sapotaceae*). 330 000 seedlings of 92 species from 20 families were planted, and 25 permanent plots were established. Here we describe the results from a typical quadrat, PQ 203 (Meguro & Miyawaki 1997).

The permanent quadrat, 11 m × 20 m, was established on barren land abandoned after shifting cultivation and covered mainly with the grass *Ischaemum magnum*. In 1992, the weeds on the permanent quadrat were cut, fallen trees and wooden boards were positioned horizontally on the slope to prevent soil erosion and to trap fallen leaves, and potted seedlings which had been collected from the mature forest floor near the project site were planted. The soil moisture was moderate to wet and soil nutrition was rich. We measured the basal diameter and height of all trees. We have previously published growth data of *Dipterocarpaceae* species (Meguro & Miyawaki 1997). Here we compare our results to those from a permanent quadrat at Tokyo Bay.

At the time of planting, the following species were present (with numbers of stems in parentheses)

Shorea ovata (155)
Shorea dasyphylla (93)
Dracontmelon dao (20)
Baccaurea macrocarpa (10)
Baccaurea lanceolata (5)
Baccaurea bracteata (2)
Parashorea smythiesii (1)
Shorea mecistopteryx (116)
Shorea leprosula (43)
Sandoricum koetjape (20)
Eurycoma longifolia (10)
Calophyllum sclerophyllum (3)
Eugenia hoseana (1),
Shorea parvifolia (1).

Reforestation using the same planting method was conducted on a man-made island in Tokyo Bay so that we could compare establishment and growth rates of a warm temperate and a tropical site. The site was established at Ohgishima in 1983. The top soil was 30 cm deep. The permanent quadrat was 3 m × 22 m on almost flat ground. Species used were laurel and other broad-leaved evergreen trees that formed the canopy of the potential natural vegetation there. Species and numbers of stems on the permanent quadrat were:

Persea thunbergii (23)
Pasania edulis (4)
Myrica rubra (3)
Castanopsis cuspidata var. *sieboldii* (10),
Quercus glauca (3)
Quercus phillyraeoides (4).

Results and Discussion

Elongation and diameter growth at Borneo are shown in Figs. 1 and 2. Growth behaviour at the species level was discussed in Meguro (1998) and Meguro & Miyawaki (1997, in press). *Sandoricum koetjape* and *Dracontmelon dao* were the fastest growing species in this quadrat during the first five years. *Shorea leprosula* was the fastest among the *Dipterocarpaceae*. *S. ovata* and *S. mecistopteryx* were more shade tolerant than *S. leprosula*. The tallest tree grew more than 10 m and the tree with the largest basal diameter was over 20 cm at the base after five years. By contrast, the slowest growing tree was only 1.1 m in height and 1.1 cm in basal diameter.

Average height and basal diameter were 5.7 m and 5.6 cm in this plot. Of course growth rates vary with species, richness of soil, and other environmental conditions. For example, *S. leprosula* is not likely to grow on dry soils, *Dryobalanops beccarii* prefers dry soils, and *Tristania* spp. prefer sandy soils (Anderson 1980; Meguro & Miyawaki 1997, in press).

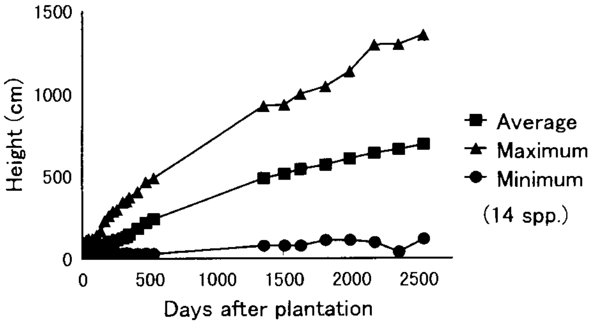

Fig. 1. Height growth curve at Sarawak/Borneo.

We next compare our tropical plot with observations from the temperate restoration project. Ogawa et al. (1965) have shown that weight of branches, stems and roots were linearly related to D^2H (after logarithmic transformation) in the tropical rain forest (D = DBH; H is height). Kira & Shidei 1967 have shown that the relation is exactly the same for Japanese evergreen forest.

Fig. 3 shows total D^2H of all surviving trees per area at the restoration project site in Malaysia and in Japan. Two remarkable differences occur in this figure. First, growth rates accelerate more quickly in the tropics (at 300 - 500 days vs. 1500 - 2000 days at Tokyo Bay). Second, the slope of the line is steeper for the tropics than the warm temperate forest. The slope of the lines in this figure gives the productivity in a unit area per time. The productivity in Malaysia and Japan as calculated from the slope of the lines was 27.3 and 16.6 ton/ha/yr, respectively.

Most of the tree tissue consists of cellulose, hemicellulose and lignin. Assuming that cellulose $(C_6H_{10}O_5)_n$ is the main product of photosynthesis, we calculated the rate of fixation of carbon dioxide. Restored forests in Malaysia fix carbon dioxide at a rate of 44.4 ton/ha/yr, which is 1.64 × as fast as in the warm temperate forest in Japan with 27.0 ton/ha/yr. The time required to reach stable growth rates in Malaysia was also much shorter than in Japan. Therefore restoration in the tropics is very effective in terms of carbon dioxide fixation. Further clarification for these phenomena will require a numerical relationship between total D^2H and plant densities before and after canopy become closed, and data for sites with different species combinations.

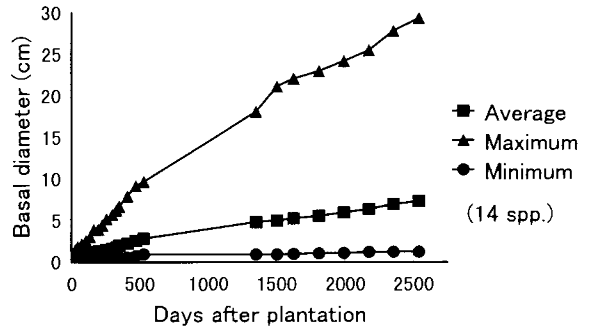

Fig. 2. Growth curve in basal diameter at Sarawak/Borneo.

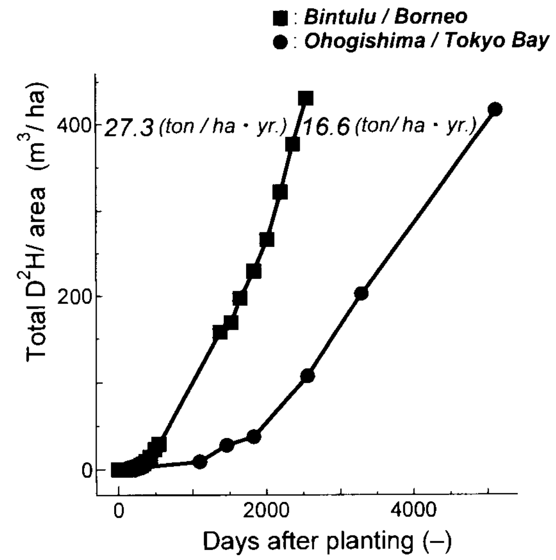

Fig. 3. Volume indicator D2H in Malaysia (tropical rain forest zone) and Japan (laurel forest zone).

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Regrowth assessment in Negeri Sembilan, Malaysia based on vegetation studies

Mohd Zaki, Hamzah[1,2]
& Fujiwara, Kazue[1]

[1]*Department of Vegetation Science, Institute of Environmental Science and Technology, Yokohama National University, 79-7 Tokiwadai, Hodogaya-ku, Yokohama 240-8501, Japan;*
[2]*Present address: Faculty of Forestry, Universiti Putra Malaysia, 43400 Serdang, Selangor, Malaysia;*
Fax +60394325l4; E-mail mzaki@forr.upm.edu.my

Abstract. A recovery assessment based on phytosociological studies in the state of Negeri Sembilan, Malaysia showed that the natural recovery (succession) is very slow for areas that were heavily logged and compacted, such as the sites formerly used as logging roads and timber landings during forest harvesting. Only early-succession species such as *Melastoma, Eupatorium* and *Paspalum* inhabited these sites. Such sites have harsh environmental conditions, namely low nutrient levels, shallow and heavily compacted soil, and an unfavourable microclimate, and it will take decades to recover to the original state. These sites and similar ones require intensive rehabilitation efforts. The sites that were harvested from 1963 to 1973 with conventional harvesting techniques (under the Malayan Uniform System) have also shown a relatively slow recovery rate. The sites have small average coverage by emergent (super tree – ST) trees, ranging from 7% to 13%, and only a few dipterocarps occupy this layer. On the other hand, the sites harvested in 1984 under the Selective Management System recorded an average ST-layer coverage of 14% and fairly even coverage in the tree (dominant), tree understorey (co-dominant), shrub and herb layers. Due to the lack of dipterocarp species in these forests, the forests require replanting of dipterocarp species to enrich them.

Keywords: Mixed dipterocarp forest; Natural recovery.

Introduction

Over the years, the tropical forests in Peninsular Malaysia have declined from 73% of the land area in 1966 to ca. 61% in 1970-1972 and to 49% in 1981-1982 (Nik Muhamad 1995). According to Ahmad Zainal (1992), deforestation in Peninsular Malaysia increased from about 0.25 million ha per annum between 1981-1985 to 0.48 million ha in 1989. The major cause of deforestation has been the expansion of crop-tree plantations such as rubber and oil palm.

Besides total deforestation (conversion), the remaining forest areas in Peninsular Malaysia are under constant pressure from commercial and illegal harvesting. According to estimates produced by the Ministry of Primary Industries Malaysia (1989), an average of 233 800 ha of forest land in Peninsular Malaysia was harvested annually from 1981-1987.

With all deforestation, either total or in the form of commercial harvesting, the deforested areas require some kind of assessment as to their natural recovery and succession. The Forestry Department in particular has put a lot of effort into this. One of the strategies implemented by the department is to carry out post-felling inventories one or two years after harvesting in all harvested forest areas.

Another approach towards this objective that can complement the post-felling inventories is the regrowth assessment via the use of phytosociological vegetation studies. A regrowth assessment study was carried out in the state of Negeri Sembilan, Malaysia to assess the rate of natural recovery (succession) of the logged-over forest land.

Material and Methods

Description of the study area

The study was conducted in Negeri Sembilan, Malaysia (Fig. 1), which has 184 844 ha of forest area, of which 169 202 ha are located in forest reserves (Anon. 1994). The majorities of these forests are classified as lowland and hill forests. Ever since independence (1957), the forests in the state have been managed firstly by the Malayan Uniform System (MUS) and currently by the Selective Management System (SMS). According to the MUS system, all mature trees of all species above 45 cm DBH are removed in a single operation. On the other hand, the SMS system was introduced to allow for more flexible forest harvesting regimes which are consistent with the need to safeguard the environment. Only a few trees above the diameter cutting limit (50 cm for dipterocarp and 45 cm for non-dipterocarp trees) will be harvested, leaving the residual for the future.

According to the Drainage and Irrigation Department of Malaysia, the state of Negeri Sembilan generally receives an average annual rainfall of 2517 mm (1986 to 1992). The highest precipitation normally occurs during the months of March-May and September-January. The mean monthly temperature in the state ranges from 24.5 °C to 27 °C.

Research method

Vegetation studies based on the method of Braun-Blanquet (Fujiwara 1987) were carried out over a period of two years (1997 to 1998) and covered several forests of different ages: primary forest, secondary and regenerating forest and severely degraded logged over areas. The studies will provide detailed information on:

1. Percentage of vegetation cover in different layers: emergent trees (super trees = ST), dominant trees (T1), co-dominant and intermediate trees (T2), shrubs (S) and herbs;
2. Current status or rate of natural recovery (succession) of the forests harvested at different periods of time;
3. Rehabilitation requirements for the logged-over areas

35 phytosociological relevés of different sizes (ranging from 120 m^2 to 3000 m^2) were made in several forest areas of different ages in Negeri Sembilan (Table 1).

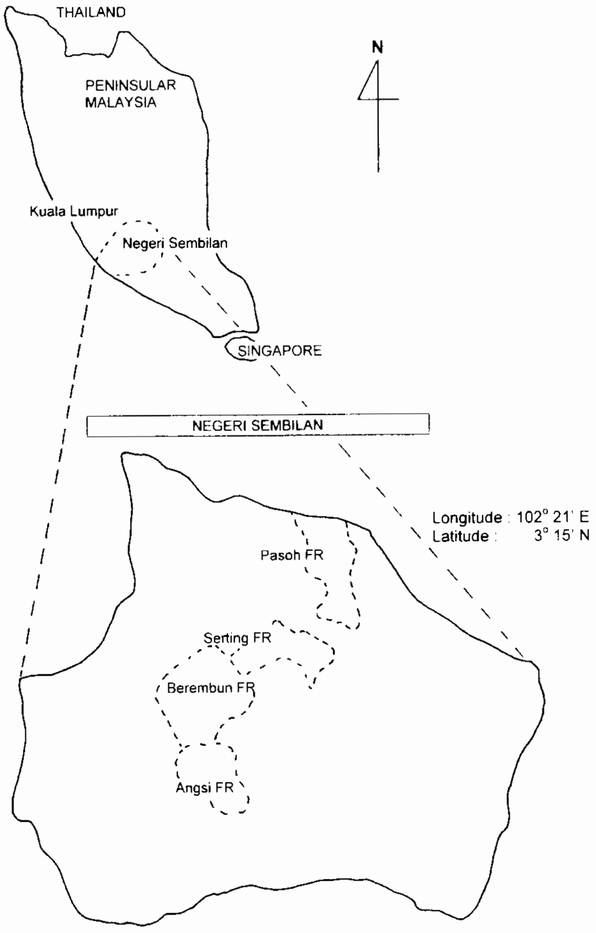

Fig. 1. Location of the study sites.

Results and Discussion

Forest coverage recovery

Forest areas that were used as logging roads and timber landings during forest harvesting recorded the lowest recovery of forest cover. The sites have not recovered any of the top layers, ST, T1 and T2. The sites only recovered the S- and H-layers, with a percent coverage of 67 to 90% and 20 to 56%, respectively (Table 2). Table 2 also shows that the sites which were harvested in 1984-1986 and not used as road or landing attained a moderate ST-layer coverage of 14%.

Table 1. Location of the relevés. FR = Forest Reserve.

Forest area	No. of relevés	Location
Primary forest	6	Berembun FR, Pasoh FR and Serting FR
Forest harvested in 1958	6	Pasoh FR
Forest harvested in 1963-1964	5	Angsi FR and Pasoh FR
Forest harvested in 1970-1974	4	Pasoh FR
Forest harvested in 1984-1986 (normal)	8	Pasoh FR
Forest harvested in 1984 (deck)	3	Pasoh FR
Forest harvested in 1996 (normal and logging road)	2	Pasoh FR

The sites that were harvested from 1963 to 1973 showed a relatively slow recovery rate. The sites exhibited an average coverage of ST of 7% - 13%, which could be considered as low to moderate. However, the recovery for T1- and T2-layers was good. By far, the best recovery was recorded by the forests that were harvested in 1958-1959. The sites reported an average ST coverage of 24% which is comparable to that of the primary forests. The sites also recorded high coverage percentage of T1- and T2-layers; in fact the cover of 57% for T1-layer exceeded that of the primary forests.

According to the statistical analysis, there were significant differences between the coverage percentages of ST- and T1-layers of the 35 relevés. On the other hand, there was no significant difference for the T2-, S- and H-layers.

Species recovery

As indicated by Table 3, the species recovery (succession) is very slow for sites that were heavily logged and compacted, such as the sites previously used as logging roads and timber landings during forest harvesting. Only early-successional species of genera such as *Melastoma, Eupatorium, Paspalum, Trema, Musa* and *Mallotus* are able to establish themselves on the sites. Such sites and similar ones with harsh environmental conditions will take decades to recover to the original state unless intensive rehabilitation approaches such as replanting of tree species are carried out to hasten their recovery. The approach taken must ensure the high survival rate of the planted seedlings on such sites.

As mentioned earlier, the sites harvested from 1963 to 1973 (under MUS) showed a relatively slow recovery rate.

Table 2. Summary of regeneration and succession. MUS = Malaysian Uniform System; SMS = Selective Management System.

Average coverage at different forest layers:	Forest harvested in							
	1958	1963-1964	1970-1974	1984/1986 (normal)	1984 (deck)	1996 (normal)	1996 (road)	Primary forest
ST	24	7	13	14	0	0	0	25
T1	57	50	32	54	0	10	0	39
T2	52	48	60	50	0	20	0	54
S	45	54	61	59	67	50	90	68
H	42	26	20	32	56	60	20	28
Recovery rate	good	low	medium	medium	very low	low	very low	
Management system	MUS	MUS	MUS	SMS	SMS	SMS	SMS	

Table 3. Summary of natural recovery and rehabilitation requirement. For layer symbols, see Text.

	Forest harvested in				Primary forest	
	1958		1963-1964			
Dominant species - ST- and T1-layers	*Shorea leprosula* *Shorea pauciflora* *Shorea laevis* *Shorea parvifolia* *Shorea macroptera*	*Dipterocarpus cornutus* *Mangifera* sp. *Dyera costulata* *Parkia speciosa*	*Parashorea densiflora* *Shorea leavis* *Shorea macroptera* *Shorea multiflora*	*Swintonia* sp. *Monocarpia marginalis* *Atrocarpus lowii* *Santiria tomentosa*	*Dipterocarpus cornutus* *Hopea dryobalanoides* *Parashorea lucida* *Shorea roxburghii*	*Intsia palembanica* *Cynometra malaccensis* *Scaphium macropodon* *Diospyros sumatrana*
Dipterocarps in S- and H-layers:	*Shorea macroptera* *Shorea leprosula* *Hopea pubescens*	*Shorea parvifolia* *Shorea multiflora* *Hopea beccariana*	*Shorea multiflora* *Shorea glauca* *Shorea leprosula*	*Shorea curtisii* *Shorea macroptera* *Parashorea densiflora*	*Shorea pauciflora* *Parashorea lucida* *Hopea dryobalanoides*	*Vatica odorata* *Shorea leprosula* *Shorea bracteolata*
Rehabilitation requirement:	Recovery acceptable: No need for rehabilitation		More time for T1- and T2-layers to become ST			

	Forest harvested in					
	1970-1974		1984-1986 (normal)		1984 and 1996 (deck & road)	1996 (normal)
Dominant species in ST- and T1-layers	*Dipterocarpus grandiflorus* *Shorea curtisii* *Shorea mulltiflora* *Vatica* sp.	*Scaphium macropodon*	*Shorea laevis* *Shorea leprosula* *Shorea maxwelliana* *Shorea macroptera* *Hopea pubescens* *Strombosia maingayi* *Baccaurea reticulata*	*Millettia atropurpurea* *Mangifera indica* *Macaranga gigantea* *Shorea macropodon* *Anthocephalus chinensis* *Sapium baccatum*	S- and H-layers only *Melastoma* sp. *Trema* sp. *Mallotus* sp. *Paspalum* sp. *Eupatorium* sp. *Musa* sp.	*Eugenia grandis* *Shorea macropodon* *Shorea baccatum* *Endospermum malaccense*
Dipterocarps in S- and H-layers:	*Shorea curtisii* *Shorea multiflora*	*Vatica* sp.	*Dipterocarpus oblongifolia* *Dipterocarpus cornutus* *Shorea pauciflora*	*Hopea pubescens* *Shorea macroptera* *Shorea multiflora*	none	*Shorea bracteolata* *Shorea pauciflora*
Rehabilitation requirement:	More time for T1- and T2-layers to become ST		Replanting of dipterocarp species		Very intensive replanting	Replanting of dipterocarp species

This phenomenon might have been caused by the management technique (MUS), which encouraged the harvesting of all timber above a minimum cutting limit. Usually most of these sites were stocked with trees bigger than the minimum diameter cutting limit, resulting in most of the trees being cut leaving behind only smaller trees and saplings. Since the emergent is sparse (canopy cover of 7% to 13%) in the stands harvested from 1963 to 1973, only a few dipterocarps, such as *Dipterocarpus grandiflorus, Parashorea densiflora* and *Shorea leavis* are found occupying the layer. These stands require a few more years for the dipterocarps from the lower canopy layers to reach the dominant and emergent sizes.

The sites harvested ca. 38 yr before the studies (harvested in 1958 and 1959), have recovered towards their natural states before the harvest. The ST- and T1-layers of these stands are dominated mainly by dipterocarps, such as *Dipterocarpus cornutus, Shorea acuminata, S. laevis, S. leprosula* and *S. macroptera*. The other species are *Dyera costulata, Mangifera* spec. and *Parkia speciosa*. The dominant cover of dipterocarps in the upper layers resembles that of the primary forests in Negeri Sembilan. These stands are also relatively rich in dipterocarp saplings and seedlings (S- and H-layers).

The sites harvested from 1981 to 1984 have recovered fairly well, with a moderate average coverage of ST layer of 14 %. The selective felling (under SMS) that was practised during the harvest could have contributed to the fast recovery of the sites. SMS advocates a choice between different management options based on the pre-harvesting inventory of stocking levels to determine the minimum diameter cutting limits and species selection for harvesting. Only a selected portion of the stand was harvested leaving the residue for future harvest (Anon. 1997). Due to the smaller number of trees harvested, the harvesting damage on the stand is also minimal, allowing the stand to recover fairly fast.

Even though these stands have a fair coverage of the ST- and T1-layers, the number of dipterocarps in these layers is few. The two layers are mainly dominated by non-dipterocarps, such as *Millettia atropurpurea, Mangifera indica, Sapium baccatum, Strombosia maingayi, Scaphium macropodon* and *Baccaurea reticulata*. The presence of *Macaranga gigantea* and *Anthocephalus chinensis* in these stands is indicative that these stands are at the early phase of a middle-succession period. Since the number and coverage of dipterocarps is relatively small, these stands could be planted with some dipterocarps to enrich them.

The stand harvested in 1996 under SMS has an average coverage of the T1-layer of 10% and the T2-layer of 20%. The non-dipterocarps such as *Eugenia grandis, Endospermum malaccense, Scaphium macropodon* and *Sapium baccatum* dominate these two layers. The presence of dipterocarps is small with only *Shorea leprosula, S. bracteolata* and *S. pauciflora* present in the T2-, S- and H-layers. As in the sites harvested from 1981 to 1984, this stand requires replanting of dipterocarp species to hasten its recovery.

Conclusions and Recommendations

The following conclusions and recommendations can be stated from this study:

1. Phytosociological vegetation studies are useful to elucidate the actual status of the natural recovery (succession) of deforested areas.
2. The forest which was managed under the old system (Malayan Uniform System) requires more time for its natural recovery. On the other hand, the forest managed under the Selective Management System has recovered fairly well in a short period of time.
3. The stands which were heavily logged and compacted require intensive replanting to hasten their recovery to the natural state.
4. Some stands, especially the ones harvested from 1980 to 1996, still require some replanting of some species from the dipterocarp family to enrich these stands.
5. It is recommended that further analyses be made on the data from the vegetation studies, previous logging and pre-felling inventories to elucidate the degree of closeness or difference of the recovering forests from the natural state.

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Effects of burning and grazing on grasslands in southern Brazil

Quadros, Fernando L. F. De[1] &
Pillar, Valério De Patta[2]

[1]*Departamento de Zootecnia, Universidade Federal de Santa Maria, Santa Maria, RS, 97105-900, Brazil; Fax +55552208692; E-mail fquadros@ ccr.ufsm.br;* [2]*Departamento de Ecologia, Universidade Federal do Rio Grande do Sul, Porto Alegre, RS, 91540-000, Brazil; Fax +55513166936; E-mail vpillar@ecologia.ufrgs.br*

Abstract. The natural grassland vegetation type in South America known as *campos* has most likely evolved under a disturbance regime that always included fire and grazing. Fire has occurred with a decreasing intensity and increasing frequency for the last 13 thousand years, while grazing increased intensity and frequency mainly in the last 400 yr. We conducted a field trial to evaluate the effects of fire and grazing disturbances on a grassland area at Santa Maria in the state of Rio Grande do Sul. Transects of contiguous quadrats were arranged in a factorial design (burned or not burned in late winter, grazed or excluded). Data on visual estimates of species aboveground biomass were subjected to ordination. In the first two years, vegetation trajectories on ordination space were similar in direction and magnitude for burned and unburned relevés within the same grazing regime. Most variation in species composition was due to grazing regime and landscape position. We used randomization testing to evaluate differences on vegetation state and on vegetation change (magnitude and direction or only magnitude of change). The tests indicated no significant short-term effects of fire and grazing and their interaction. This could be indicating an apparent resilience of the species composition, supporting the hypothesis that the campos vegetation is in a steady-state dependent on grazing and fire disturbances.

Keywords: Campos; Clustering; Fire; Natural pasture; Principal Coordinate Analysis; Randomization test; Succession.

Introduction

Campos vegetation, a type of natural grassland, covers at present ca. 120 000 km^2 in the state of Rio Grande do Sul, Southern Brazil, which corresponds to about half of the state's area. In the 17th century, during the establishment of the Jesuit missions on the eastern side of the Uruguai river, cattle and horses were introduced (Kern et al. 1991) and large ranches ('vacarias') were run by local farmers. Since then campos vegetation has been the major support for a cattle ranching economy. Fire is regularly used in late winter when ranch management is such that excessive biomass accumulates during the growing season, and gets senescent by the next spring. In the last three decades a large proportion of areas with campos vegetation has been allocated to cropland. Sometimes crops are cultivated on a rotational basis in which the natural grassland recovers during the few years the land is left fallow but grazed (Pillar & Quadros 1997).

An interesting question is whether fire has always been an element of the natural campos ecosystem, and intensified after the arrival of humans in the region around 12 000 -13 000 B.P. (Kern et al. 1991). The fire history in southern Brazil is not well known, but recent findings in the mixed *Araucaria*-broadleaved forest region in Paraná (Behling 1996), which shows a similar mosaic of forest and campos as in Rio Grande do Sul, indicate that the frequency of fires increased at the beginning of the Holocene, and that they were likely anthropogenic. This finding further supports the idea that the pre-Colombian anthropogenic influence on the vegetation, including dissemination of naturally occurring plants, should not be overlooked (Schüle 1990; Dean 1995).

However, there is no indication that natural fires in grassland were rare in South America before the arrival of man. A high frequency of fires was detected since 35 000 B.P. in a mountain region in São Paulo, which was dominated by campos until the end of the Pleistocene (Behling 1997). It is quite obvious that the grazing intensity of grassland areas increased after the introduction of domestic cattle, resulting in a reduction of the number of areas with enough fuel accumulation for extended naturally ignited fires. Furthermore, when grassland is left ungrazed for a long time fuel accumulates and any fire tends to be much more intense, being capable of burning plant types that would not burn under a low intensity fire, such as forest trees invading grassland (Pillar & Quadros 1997).

The campos, even the areas dominated by shrubs, are fire prone if sufficient senescent biomass has accumulated. The rate of senescence of older leaves in grasses increases during dry spells. Furthermore, senescent leaves of tall tussock grasses in general remain attached to the plants, increasing flammability of the whole plant (Bond & van Wilgen 1996). Accumulation of biomass, and therefore flammability levels, are related to grazing regimes (Bond & van Wilgen 1996). Ranchers usually adjust the stocking rate of pastures on the campos on the basis of the carrying capacity during the winter. The consequence is more accumulation of ungrazed biomass during the main growing season in the spring and summer.

From these facts we hypothesize first that vegetation dynamics in campos subjected to fire and grazing should follow non-directional trends, reflecting a disturbance-dependent steady-state. Secondly, exclusion of grazing and fire should produce clearly directional vegetation change.

Methods

The experiment was set on the Animal Science Department experimental area at the Universidade Federal de Santa Maria campus, at 29°45'S and 53°45'W, 95 m above sea level. The climate is wet subtropical (Cfa) with a mean temperature of 19.2 °C and a mean annual precipitation of 1769 mm. Frosts occur from April to October. The soil is a hapludult, in the convex slope, and a albaqualf, in the concave slope (Anon. 1994).

The disturbance factors fire and grazing were combined in four treatments: (1) burned, grazing exclosure; (2) burned and grazed; (3) not burned, grazing exclosure; (4) not burned but grazed. These were replicated in two landscape positions (convex slope, concave slope) in transects of 30 contiguous quadrats (0.5 m × 0.5 m). Treatments (1) and (2) were burned on August 1995.

Aboveground biomass by species was estimated via double-sampling field procedures of BOTANAL (Tothill et al. 1992). The available biomass was visually estimated with a rank-assignment to the species, according to the program's multipliers algorithm which was calibrated by cutting quadrats with similar biomass. Exploratory data analysis used sum of squares clustering and principal coordinates analysis (see, i.a., Podani 1994). Randomization testing compared treatments on the basis of species composition (Pillar & Orlóci 1996). All analyses were performed by MULTIV software (Pillar 1997). The data included the period from August 1995 (prior to burning) to December 1996.

Results and Discussion

Prior to the application of the treatments, we observed low variance between the sampling units within each landscape position, except for one of the transects in the concave slope, that was closer to gallery forest. Trajectories on vegetation composition from the first until the last evaluation of the same sampling unit can be observed in the ordination diagram (Fig. 1), which comprises 83.6 % of the total variation. The grazed quadrats, regardless of the burning treatment, follow similar directions and have the longest trajectories.

Based on the species with the highest correlation with the two axes, we can say that grazed units started from a state with dominance of *Andropogon lateralis*, *Erianthus asper* and *Aristida laevis*, three tussock grasses, and arrive at a state characterized by the dominance of prostrate species such as *Paspalum notatum*, *Dichondra sericea* and *Desmodium incanum*. Exclosure units showed a more irregular behaviour and had shorter trajectories in ordination space. This did not agree with observations of directional changes in the community composition after grazing exclusion in campos vegetation as in Boldrini & Eggers (1997) and Facelli & D'Angela (1990).

The explanation of these features may be found in the behaviour of the grazing animals and in the measures that were taken. The paddock where the experiment was arranged had a low grazing pressure before the beginning of the evaluations, leading to fuel accumulation that allowed a successful burning treatment. The burned area comprises ca. 4 ha surrounding the grazing-excluded and unburned areas. This leads to a higher grazing frequency and intensity in this area due to larger availability of the regrowth leaves after burning. We evaluate aboveground biomass by species, and as the grazing pressure rises the prostrate species increase their share, notwithstanding the tussock grasses still being present. albeit with a lower contribution.

Fire and grazing removes herbage and both can be seen as 'herbivores', opening gaps at the start of the growing season, but the last does it selectively and more frequently. Plants resprouting or emerging in burnt or grazed areas receive higher light intensity and red/far-red ratio, that promotes tiller formation in grasses and branching in dicots, with shorter internodes and more horizontal angles (Noy-Meir 1995). This favours the prostrate species mentioned above, in contrast with lower radiation in the undisturbed sites, where tall erect shoots of tussock grasses were enhanced.

We compared the species composition of the treatments in the last survey by randomization testing. The analysis used all 100 species that were detected. The test indicated that the effects of fire ($P < 0.76$), grazing ($P < 0.09$) and its interaction ($P < 0.7$) were not statistically significant, but the lower probability of the grazing effect was indicative of the relevance of this disturbance factor. These findings agree with those of Castilhos & Jacques (1984), Damé et al. (1996) and Kersting (1994), who found no significant effect of fire on similar vegetation in the same region, and those of Coutinho (1994) regarding fire on Brazilian rangelands.

An expected interaction between fire and grazing – as

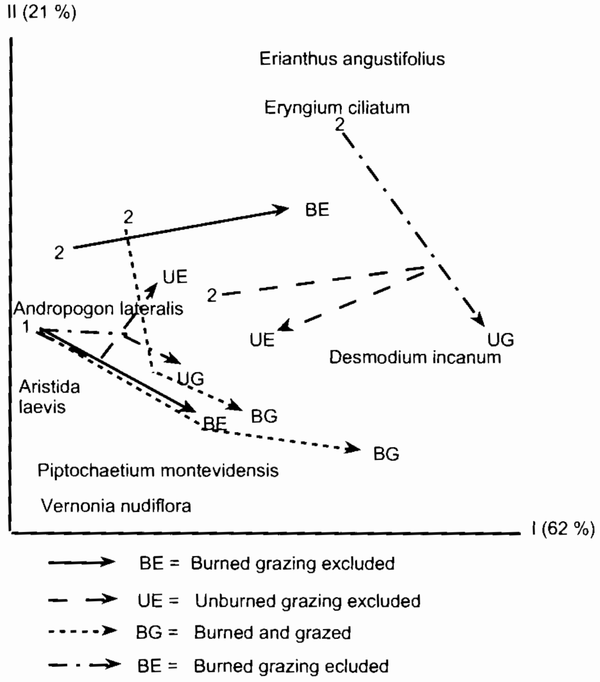

Fig. 1. Grassland vegetation composition trajectories in the ordination plane (Principal Coordinates Analysis). The resemblance measure was Euclidean distance, standardized by the transection totals. The numbers indicate initial relevés (August 1995), before the treatments were applied, and two relief positions (1= convex slope; 2 = concave slope). The letters point to the final relevés (December 1996). The treatments are explained in the legend. The species are placed in the diagram according to their correlation $r > | 0.5|$) rescaled with the axes. Numbers in brackets indicate % of total variation for each axis.

was found in tall-grass prairie (Collins 1990) and Mediterranean grasslands (Noy-Meir 1995) – may not be detected in the short term because the relevés have a similar management history before the treatments were applied.

Our study could have shown that campos vegetation developed resilience strategies to these disturbance factors, or the results may be attributed only to the short term of the trial, limiting any conclusion about succession.

The latter observation showed us that more study in this area is needed and indicated the necessity of testing prediction models of vegetation dynamics. One possibility is the use of Markov chains as evaluated by Orlóci et al. (1993) and Quadros & Pillar (1999).

Preliminary conclusions

As we conjectured, the campos vegetation in the short-term appears to be in a steady-state, with a chaotic dynamics. However, a resilient behavior to this disturbance elements in the long term could not be proved yet.

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Defining a legend for the future vegetation map of Tropical Arabia

Scholte, Paul

Centre of Environmental Science, P.O. Box 9518, 2300 RA Leiden, The Netherlands;
Fax +31 71 5277496; E-mail scholkerst@cs.com

Abstract. Ecologically, tropical Arabia is closely related to NE Africa, but lack of information necessitated White to exclude it from his Vegetation Map of Africa. White's map has frequently been used as a basis for environmental planning. During the last decade various floristic and vegetation studies have been carried out in Arabia, resulting in, *i.a.* our 1:500 000 vegetation map of Yemen (western part). This map contains 32 legend units based on physiography, altitude, vegetation structure and floristic composition. In an accompanying booklet, climate, geology and land use have been described. In the north, these mapping units have been matched with units of the 1:1M vegetation map of SW Saudi-Arabia whereas flora and vegetation analyses of Oman and E. Yemen have guided their extrapolation into the east. A discussion is presented on the phytogeographical position of tropical Arabia. The resulting preliminary legend of the future 1: 5M vegetation map of tropical Arabia has been standardized to White's map with the help of more detailed vegetation maps of NE African countries. Additional satellite image interpretation and field checks in E. Yemen and Oman should complement this legend to finalize the vegetation map of tropical Arabia.

Introduction

Ecologically, tropical Arabia is closely related to NE Africa (Schweinfurth 1891; White & Léonard 1991). With the completion of the 1:5M vegetation map of Africa (White 1983), the Arabian peninsula was omitted, however, because of lack of sufficient information (White & Léonard 1991). Recently, a 1:5M vegetation map of tropical mainland Asia was published (Blasco et al. 1996) and with similar maps available of tropical America and SE Asia (Anon 1981; Whitmore 1984), Arabia fills a conspicuous gap on the global tropical vegetation map. Danin et al. (1992) intended to prepare a phytogeographic map of SW Asia, including Arabia, but have ceased their efforts (Danin, in litt. 1997). The need for a map of tropical Arabia is shown by the frequent use of White's vegetation map as instrument for conservation planning (e.g. MacKinnon & MacKinnon 1987). To cite only one example of this neglect of tropical Arabia ecosystems, in a recent study on succulents and their habitat conservation (Oldfield 1997), White's map was used as a basic map, resulting in the omission of SW Arabia, one of the main centres of succulent distribution (Ellenberg 1981; Newton 1980). Since the appearance of the vegetation map of Africa in 1983, vegetation maps were produced of SW Saudi Arabia (König 1987) and western Yemen (Scholte et al. 1991). For the eastern part of tropical Arabia, vegetation descriptions of Dhofar and the Hadramaut appeared (Radcliffe-Smith 1980; Sale 1980; Gabali & Gifri 1991), as well as a map of the vegetation zones of Oman (Ghazanfar 1991). The study of the Arabian flora was further boosted by the ongoing production of the Flora of Arabia resulting in, amongst other things, a series of phytogeographical analyses (Miller & Nyberg 1991; White & Léonard 1991; Ghazanfar 1992). Based on this new information, I would like to present a compilation of map legends as well as vegetation and landscape descriptions, in preparation of a 1:5M vegetation map of tropical Arabia.

Material and Methods

König (1987) indicated, without further details on the methods applied that his 1:1M map is based on Landsat images (1972-1973). He described the distinguished plant communities, but not the mapping units in which they occur. The 1:500000 map of Scholte et al. (1991) is based on a combination of Landsat (1972-1973) images and more detailed and recent SPOT images (1983-1986). It followed a physiographical approach (Zonneveld 1988) and is based on detailed studies in each of the eight main landscapes with additional field checks elsewhere. The legend of 32 units is hierarchically composed, with physiography as first, altitude as second and vegetation structure and composition as third entry. In an accompanying booklet, climate, geology and land use was described for each unit. Because of the wide variety of vegetation types occurring in Yemen, more than in any other part of the Arabian Peninsula, this map has been used as starting point for the comparison with the other maps and vegetation descriptions.

To interpret the mapping units of White (1983) and their relevance for the Arabian situation, I included a comparison with vegetation maps from the African Red Sea shore. Limited details for Djibouti and Somalia were given on the vegetation map of Africa (White 1983), that is based on the more, detailed 1:5M scale map of Pichi-Sermolli (1957). More recently, detailed information has become available for Djibouti (Audru et al. 1987), whereas Hemming (1998) compiled studies on Somalia. Unfortunately, Hemming's descriptions did not match the accompanying map; therefore it was excluded from the overall legend comparison to be presented below.

Discussion was raised on the classification of African vegetation, for which the physiognomic concepts used by White (1983, 1993) do not provide sufficient clarity (e.g. Lawesson 1994). For the vegetation map of Yemen, Scholte et al. (1991) developed a structural typification, based on van Gils & Wijngaarden (1984). Tree and shrub cover determined the physiognomy and in case they did not reach 1%, dwarf-shrub and grass cover determined the units. When the cover of the latter categories was lower than 1% as well, the area was called 'bare land' (Fig. 1). Woody plants are divided into trees (> 3m), shrubs (1 - 3 m) and dwarf-shrubs (< 1 m), in order to differentiate the rare units where trees are present. This classification will be followed in the present study, although reference will be made to White's concepts given its wide application.

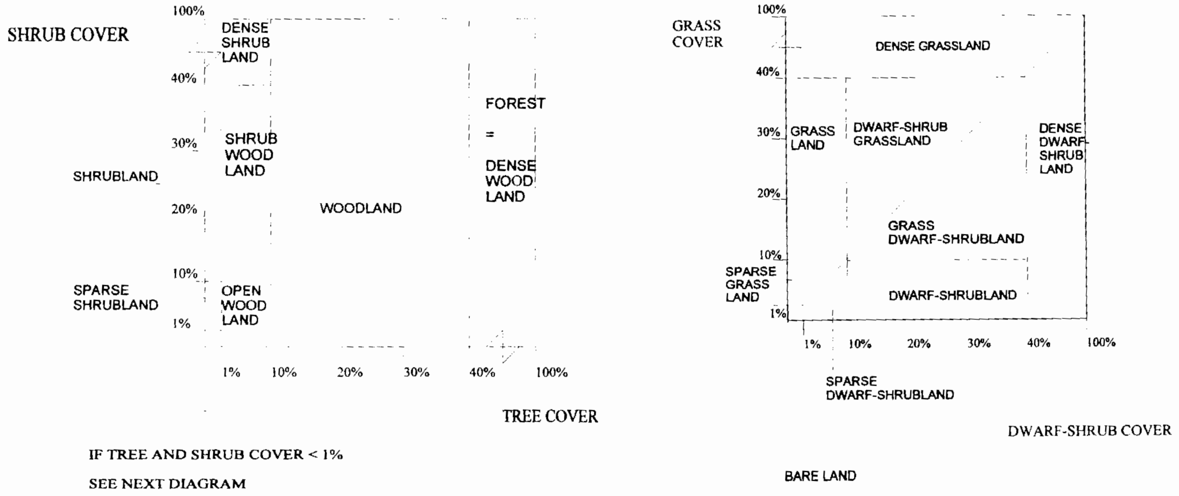

Fig. 1. Vegetation structure diagram (after Scholte et al. 1991).

Results and Discussion

General

In Table 1, presented at the end of the contribution, legends of the studied maps are presented in order of correspondence. In a few cases no corresponding units were found, which is indicated by 'no equivalent'. For the proposed legend for tropical Arabia the comparison results in four physiographic/altitude units subdivided into eight units based on vegetation structure. This should be compared with 10 corresponding units of the African vegetation map, based on chorology and physiognomy (White 1983). Neighbouring units, in the interior of the desert outside tropical Arabia, correspond with the 'psammophilous' unit of White (1983). Future fieldwork may bring the number of legend units for tropical Arabia to 10 when areas not yet well surveyed in the Jol/Hadramaut and Dhofar justify this.

Phytogeography of tropical Arabia

Limits of the study area. Arabia is widely considered as a crossroad of phytogeographical regions of the African and Asian continent and the Mediterranean Basin and has intrigued botanists since the first explorations (Engler 1925; Lavranos 1975). According to Zohary (1966) the northern limit of the Sudanian region should be drawn somewhat north of the Tropic of Cancer, with latitudinal zigzags and interdentations ranging from the 24-30° N. I have taken a somewhat more restricted interpretation of 'tropical', excluding the Saharo-Sindian zone of White & Léonard (1991), or the Nubio-Sindian equivalent of Zohary (1966), to which the majority of the inland Arabian vegetation communities belong. Tropical Arabia is therefore considered to be limited in the north by the line Jeddah -Medina, i.e. the northern part of the area in SW Saudi-Arabia covered by König (1987).

Kürschner (1986) and Ghazanfar (1991) showed the close resemblance of the Omani vegetation with extratropical mainland Asia, i.e. Iran and Baluchistan. The Nubo-Sindian local centre of endemism is, according to Ghazanfar (1992), restricted in Oman to the northeastern region that excludes its occurrence further west in Arabia, as suggested by White & Léonard (1991). I follow Ghazanfar (1992) with the designation of the inner parts of Oman and Yemen, implying that the remaining part of Yemen belongs to either the Arabian/Saharan regional subzone of the Saharo-Sindian regional zone, the Somali-Masai regional centre of endemism, or to the Afro-montane regional centre of endemism.

A point of discussion is the inclusion of the Medium altitude Eastern Mountains of Scholte et al. (1991) into the Somali-Masai regional centre of endemism, or, alternatively, into the Saharan regional subzone (Ghazanfar 1992). The presence of several typical Somali-Masai species (e.g. *Acacia caupoptila, A. etbaica, A. orfota, Commiphora habessinica, Dracaena serrulata*) and its strong resemblance to the Medium Altitude Western Mountains justifies the inclusion of the Medium altitude Eastern Mountains in the Somali-Masai regional centre. Wood (1997) also suggested that the tropical African element dominates in the Eastern Mountain range. White & Léonard (1991), however, indicated on their maps the Medium Altitude Mountains as well as the northern Hadramaut area in Southern Yemen as belonging to the Nubo-Sindian local centre of endemism (or, as I indicated above, in the Saharan regional subzone of Ghazanfar 1992). As such it is comparable to the drier parts of the Tihama coastal plain and Tihama foothills, which none of these authors have indicated as belonging to this zone. Nevertheless it is clearly a transition zone towards the easterly located Arabian regional subzone (Ghazanfar 1992), and their equivalents on the African mainland (coastal desert and hammadas and regs) have been clearly distinguished.

I propose, for pragmatic reasons, to omit the Saharan regional subzone of Ghazanfar (1992) as zone as such, and only to use the distinction between the Somali-Masai regional centre of endemism and the Arabian regional subzone

(Ghazanfar 1992) of the Sahara-Sindian regional zone (White & Léonard 1991). Instead, floristic elements of the Saharan regional subzone can be distinguished in many vegetation types throughout the area with species such as *Acacia tortilis, Aerva javanica, Calotropis procera, Cassia italica, Occharadenus baccatus* and *Ziziphus spina-christii*.

White & Léonard (1991) included the Central Oman coastal area, indicated as Saharan regional subzone by Ghazanfar (1991), into the Somalia-Masai regional centre of endemism. This contradicts Ghazanfar (1992) and Zohary (1966) who considered the strip of desert between the Dhofar Mountains and the Oman Mountains an effective plant barrier of plant distribution into the east. I consider the Dhofar mountain range as the most easterly boundary of the Somali-Masai regional centre of endemism, and as such the most eastern part of tropical Arabia.

Distinction of Afromontane archipelago-like regional centre of endemism with the Somali-Masai regional centre of endemism

Our surveys in the Western Mountains of Yemen showed the major changes in vegetation composition and structure which take place at a surprisingly constant altitude of 1800 m. Predominantly annual grasses and *Acacia* and *Commiphora* shrubs disappear and perennial grasses and dwarf-shrubs take over. In the subhumid areas around Ibb and Mahwit, with an average rainfall of > 800 mm/yr, this boundary was found at an altitude of ca. 1600 m (Scholte et al. 1991). According to White (1983), most Afromontane communities are found only above 2000 m, but where the climate is more oceanic they can occur as low as at 1200 m. Across the Red Sea, the *Juniperus excelsa* Day forest in Djibouti, at an altitude of 1200-1600 m, close to the sea, is situated in a typical Afromontane zone (see also Audru et al. 1987).

The distinct Dhofar mountains, despite their proximity to the ocean, are too low (< 1000 m) to be part of the Afromontane region. Only Jabal Semhan reaches more than 2000 m, but because of its aridity, Afromontane elements are expected to be restricted, as was observed in the Eastern Mountains of Western Yemen (Scholte et al. 1991). The same can probably be said of the Jol plateau that reaches an altitude of 2000 m, but future fieldwork should confirm these assumptions. No Afroalpine zone can be distinguished as the highest mountain on the Arabian Peninsula, Jabal Shu'ayb in western Yemen is lower than the lower limit of ca. 3800 m (White 1983).

Links with NE Africa

Since the first botanists visited SW Arabia, the similarity in flora between NE Africa and SW Arabia was expressed (Schweinfurth 1891; Engler 1925; Newton 1980; White & Léonard 1991). Engler (1925) stressed, however, also a number of differences in climate and geology between both sides of the Red Sea. The lower mountains in Eritrea are subject to winter rains, which are absent from Yemen. Engler (1925) argued that granite mountains dominate the African part whereas volcanic dominates the Arabian part (note however the conspicuous presence of granite mountains such as J. Bura and J. Milhan in the Yemen Western Mountains). This contradicts the conclusion of Beydoun (1972) who just stressed the similarity in geology, more in the Western part (Western Yemen and Eritrea/Tigray) than in the part he examined (northern Somalia and Eastern Yemen).

Conclusions

The present study aims at preparing an extension of the vegetation map of Africa, of which the methodology was followed as much as possible. It also fits in the recent initiative of a Russian team that is presently preparing a 1:4M vegetation map of Asia (Safronova et al. 1997). In their classification, tropical vegetation is distinguished from extra-tropical vegetation, on the highest hierarchical level. Secondly, high mountains are distinguished from plains and low plateaux, which despite a higher boundary (3000 m, Safronova pers. comm. 1998), corresponds to the proposed legend for tropical Arabia. On a lower hierarchical level, major differences occur, which should be the subject of future discussions.

As insufficient information was available for the Hadramaut and Mahra areas in the eastern part of Yemen, an exploratory survey, based on additional satellite image interpretation, is planned for 2000 which may result in some changes in the legend proposed. Subsequent contacts with Arabian vegetation scientists will be exploited in preparing the 1: 5M vegetation map of tropical Arabia.

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Table 1. Legend comparison and proposed legend for a map of tropical Arabia scale 1:5M. The first rows in the Table indicate the authors, map scale and legend entry in hierarchic sequence. Units marked * only partly correspond.

W. Yemen	**SW Saudi-Arabia**	**Dhofar**	**Arabia proposed**	**Africa**	**Djihouti**
Scholte et al. 1991 1:500 000 Physiography Altitude Vegetation structure and comp.	König 1987 1:1 M Physiognomy Vegetation structure and comp.	Ghazanfar 1991 1:5M Physiography	Scholte in prep. 1:5M Physiography Altitude ('chorology') Vegetation structure	White 1983 1:5M Chorology Physiognomy	Audru et al. 1987 1:250 000 Physiography Vegetation structure Floristic composition
Tihama coastal plain (< 400m)			**Coastal desert plain**		
T1 Mangrove	Mangrove (39)		Mangrove: *Avicennia* woodland	77 Mangrove	19. Mangrove
T2 Sabkha, *Suaeda* sparse dwarf-shrubland and bare land	Halophyte vegetation (40		Bare land to (halophytic) dwarf-shrubland	68 Coastal desert	17 Succulent *Suaeda* steppe + 18 Littoral *Limonium* steppe + 12 Littoral meadow
T3 Palm groves, *Phoenix-Salvadora* woodland	Tihama wadi-woody comm. (8) *Tamarix* woodland (9)		*Hyphaene/Tamarix* (open) woodland	71 Reg, hamada, wadi*	15. Wet ligneous formation with *Hyphaene thebaica** P2. *Salvadora persica* shrubland
T4 Salt-bush lands, *Salsola-Odyssea* dwarf-shrubland	*Panicum turgidum* grassland*	Semi-desert grassland	Bare land to (halophytic) dwarf-shrubland	68 Coastal desert	H1. Herb steppe with *Lasiurus scindicus*
T5 *Panicum* sparse grassland and bare land	*P. turgidum* grassland (33) *P. turgidum* grassland on coastal dunes (34) Inland dunes of the Tihama (36)		Ibid.	Ibid.	H2. Herb steppe with *Panicum turgidum*
T6 *Dactyloctenium* cultivated land (irrigated)	Tihama wadi-woody comm. (8)		Bare land to (halophytic) dwarf-shrubland+ cult. land	Ibid.	P4. Anthropogeneous formation with *Prosopis chilensis**
T7 *Ziziphus-Dobera* cultivated land (mainly rainfed)	*Acacia* thorny savanna*		*Acacia-Comm.* (sparse) shrubland	Ibid.	
T8 *Acacia-Commiphora* open woodland and bare land	*A. tortilis-Commiphora* -thorny savanna (13)	Ibid.	Ibid.	42 SM *A-C* deciduous bushland and thicket	P3.Woody steppe with *A. tortilis* and *A. asak*
Tihama Foothills and lower Western Mountains (< 1000 m)			**Low mountains**		
W11 *Adenium* sparse dwarf-shrubland	*A. tortilis-Commiphora* & *Euphorbia cuneata* comm. dry woodland (12)*		(sparse) shrubland	*Acacia-Comm.* bushland and thicket	42 SM A comm.: Deciduous
W12 *Dobera-Delonix* sparse shrubland	*A. asak* comm.: Dry woodland (14)*	Deciduous bushland*	Ibid.	Ibid.	C2 Steppe with *A. tortilis*
W13 *Acacia tortilis* sparse dwarf-shrubland	Ibid.		Ibid.	Ibid.	
W14 *Combretum-Anisotes* (shrub) woodland	Ibid. Sclerophyllous wood (5)?	Semi-evergreen woodland*	Evergreen shrubwoodland	38 (semi-) evergreen bushland and thicket 19 undiff. Afromontane veg.	
W15 *Acacia mellifera* sparse shrubland	*A. tortilis-Commiphora*; *E. cuneata-Commiphora* Dry woodland (12)*		*Acacia-Comm.* (sparse) shrubland	42 SM *A-C* deciduous bushland and thicket	C1.Steppe with *A. mellifera*
Medium Alt. Western Mountains (1000-1800 m)			**Low mountains**		
Wm1 *Euphorbia* dwarf-shrubland	No equiv.		*Acacia-Comm.* (sparse) shrubland	42 SM *A-C* deciduous bushland and thicket	
Wm2 *Acacia asak-Grewia* shrubland	*A. asak* comm. Dry woodland (14)* *A. etbaica* Dry woodland (15) Sclerophyllous wood (5)		Ibid.	Ibid.	
High Altitude Western Mountains (> 1800 m)			**High mountains**	17 Cultivation and secondary grassland	
Wh1 *Themeda* dwarf-shrub grassland	No equiv.		Dwarfshrub grassland	land and montane forest	
Wh2 *Euphorbia ammak* cultivated land	Succulent wood (25)		Ibid.	Ibid.	
Wh3 *Hyparrhenia-Psiadia* grassland	Evergreen open xeromorphic shrubland (26)		Ibid.	Ibid.	M6 Steppe with *Aizoon canariense* M7 Plateau succulent steppe
Wh4 *Juniperus-Cichorium* dwarf-shrubland	*Juniperus excelsa* open wood (3) *J. excelsa* open wood + Sclerophyllous wood Evergreen open xeromorphic shrubland		Ibid. + *J. procera* (open) woodland *J. procera* (open) woodland	Ibid.	
No equiv.	*J. excelsa-Olea europaea* forest (1)		Ibid.	19a *J. procera* forest	M1 *J. procera* forest
Highland plains			**Highland plains**		
H1 *Ziziphus* open woodland (1000-1800 m)	*A. asak* comm. Dry woodland (14)		*Acacia-Comm.* (sparse) shrubland	42 SM *A-C* deciduous bushland and thicket 29b Undiff. woodland	
H2 *Acacia origena* open woodland (2000-2200 m)	*A. origena* or *A. gerrardii* Dry woodland (21)		Dwarf-shrub grassland	17 Cultivation and secondary grassland	
H3 *Microchloa* grassland (> 2200 m)			Ibid.		
High Eastern Mountains and Highlands (>1800 m)			**High Mountains**		
Eh1 *Lavandula* dwarf-shrubland	Evergreen open xeromorphic shrubland (26)		Dwarf-shrub grassland	17 Cultivation and secondary grassland	

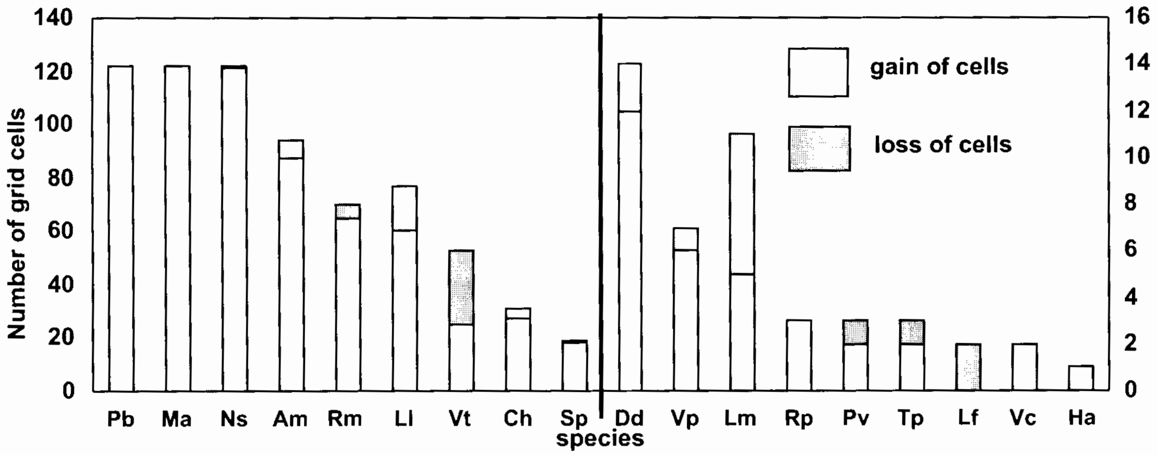

Fig. 2. Total number of settled grid cells for all species monitored. Gains and losses refer to the change in number of settled grid cells between 1992 and 1996. Pb = *Polygonum bistorta*, Ma = *Meum athamanticum*, Ns = *Nardus stricta*, Am = *Arnica montana*, Rm = *Rhinanthus minor*, Ll = *Lathyrus linifolius*, Vt = *Viola tricolor*, Ch = *Cardaminopsis halleri*, Sp = *Succisa pratensis*, Dd = *Dianthus deltoides*, Vp = *Viola palustris*, Lm = *Lilium martagon*, Rp = *Ranunculus platanifolius*, Pv = *Polygala vulgaris*, Tp = *Thesium pyrenaicum*, Lf = *Lychnis flos-cuculi*, Vc = *Viola canina*, Ha = *Hieracium aurantiacum*.

Harz project, neither an invasion of disturbance indicators was encountered, nor of weeds or of intruders from the edges. This favourable result was mainly due to the careful transplantation technique which transferred the sods piece by piece and reduced disturbance to a minimum. However, even with this immense expenditure of time and money, the technique may not be successful with other vegetation types. The conditions in the Harz project have also been very favourable with respect to climate. High precipitation during the transplantation period, which is the rule at 600 m a.s.l. in this part of the Harz mountains, provided optimal conditions for the meadows to continue growth after being transferred to the target area. On the other hand, water was not too abundant. Montane meadows are comparably easy to transplant because they are not dependent on ground-water. Transplantation projects of communities which are influenced by ground-water have been far less successful (cf. Klötzli 1975; Klötzli & Keel 1976).

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Field boundary effects on the composition of a species-rich weed community in southeastern France

Dutoit, T.[1*], Gerbaud, E.[1], Ourcival, J.M.[2], Hill, B.[3] & Roche, Ph.[3]

[1]*Institut Méditerranéen d'Ecologie et de Paléoécologie, Université de Provence, UPRESA/CNRS 6116 IMEP, FST Saint-Jérôme, case 421 bis, F-13397 Marseilles Cedex 20, France;* [2]*CNRS-CEFE, 1919, route de Mende, F-34293 Montpellier Cedex 05, France;* [3]*Institut Méditerranéen d'Ecologie et de Paléoécologie, Université d'Aix-Marseilles III, UPRESA/CNRS 6116 IMEP, FST Saint-Jérôme, case 461, F-13397 Marseilles Cedex 20, France;*
**Fax+33491288707; E-mail thierry.dutoit@bioeco.u-3mrs.fr*

Abstract. Plant composition and seed bank of a species-rich arable weed community were sampled in an arable wheat field in the Vaucluse (southeastern France). The results showed that seed bank distribution and plant composition are primarily influenced by distance from the field boundary rather than soil characteristics or wheat density. These patterns were true for the boundary species but not for the typical segetal species in Mediterranean fields.

Keywords: Arable field; Distribution; Vaucluse.

Nomenclature: Tutin et al. (1964-1980).

Introduction

In the last few decades, species diversity of arable fields in Western Europe has decreased substantially (Aymonin 1962; Holzner 1978; Olivereau 1996; Dalmas 1997). The main reasons for this decrease are likely to be herbicide treatments for weed control and the increased use of fertilisers in recent decades (Dekker 1997). The field boundaries are commonly perceived by land owners to be a haven for weeds, pests and disease (Marshall & Smith 1987). However, informal observations suggest that crop hedges (headlands and corners of arable fields) tend to be areas with high botanical diversity and previous surveys have also supported this view (Marshall 1989; Wilson & Aebischer 1995).

In this study, arable weed distribution in relation to distance from the field boundary was monitored in an arable field which is located in southeastern France. The aims of this survey were primarily to examine the relationship between the distribution of arable weeds and distance from the field boundary as well as to understand the importance of soil conditions and seed banks in the spatial variability of aboveground vegetation in a region where traditional extensive arable management still exists.

Methods

An arable field was chosen which had been planted with a winter wheat crop in October 1997 but which had not received any herbicide treatments. This field was located near a farm in the Luberon regional park, Vaucluse (5° 26' E, 43° 55' N), southeastern France. The soil was calcareous with a large amount of clay. The field was previously cultivated with cereals (winter wheat in 1995 and barley in 1996) and has never received any herbicide treatments since the first ploughing of an old field several years ago. This management is not a special case and could be compared with the management of most of the arable fields in this study area (Dutoit et al. 1999).

Analysis of the aboveground vegetation

Five transects were laid out perpendicularly from the field boundary to the middle of the crop (25 m), in an arable field of 50 m × 50 m with sampling points located at 1-m intervals along each transect (125 quadrats). The transects are starting just near the stripe bordering the arable field at the beginning of the crop edge. The direction of ploughing was parallel to the field boundary and the crop edge investigated was not a headland. The transects were positioned away from the corner of the field to avoid any possible variation when compared with the other sides of the field. In May 1998, all dicotyledons and grass weed species seedlings were identified at each point in a 1-m^2 quadrat and counted in a 400-cm^2 subquadrat positioned in a corner of the 1-m^2 quadrat. Wheat density in the 400-cm^2 quadrats was estimated by counting the individuals.

Analysis of the soil seed bank

The soil seed bank was sampled in January 1998. Soil cores were taken using a cylindrical steel tube with a 2-cm radius (cross-sectional area 12.5 cm^2) to a depth of 30 cm, representing approximate ploughing depth. A total of 125 (5 × 25) soil samples and quadrats was examined.

The number of seeds in the soil samples was determined by allowing viable seeds to germinate (Roberts 1981). Each soil core was broken down, placed on a 2-cm layer of sterile coarse sand in separate trays (45 cm × 30 cm × 8 cm), kept in an unheated greenhouse for six months and watered if necessary. Each tray was stirred at two week intervals and emerging seedlings were counted and removed or replanted for later identification.

Environmental variables

Spatial variability in the weed seed bank was related to the following physical and chemical characteristics of the soil: 1. Porosity; 2. pH (H_2O) Soil pH was determined in a slurry with water using a glass electrode. 3. Nitrogen and carbon were analysed using respectively Kjeldahl and Anne Methods. For K, P, Mg, and Ca three soil samples were taken in January 1998 for each of the five transects. Analysis of extractable K_2O, P_2O_5, MgO and CaO was performed by atomic absorption spectrophotometry after extraction with ammonium acetate and EDTA (pH = 4,65).

Statistical analysis

Using ADE software, (1) Principal Component Analysis (PCA) was performed on a [8 variables × 15 samples] matrix to identify the main soil gradients involved in the distribution of arable weed communities. (2) Two Correspondence Analyses (CA) were performed on the [25 quadrats × 62 species] matrix of the above ground vegetation and the [25 quadrats × 40 species] matrix of the soil seed bank to compare the composition and structure of the arable weed community according to distance from the field margin. A pair co-structure analysis was also used to compare the differences between the distribution of soil seed banks and the aboveground vegetation (Torre & Chessel 1995). Species richness, density, diversity (Shannon index) and evenness for the seed bank and above ground vegetation were analysed according to distance from the arable field margin using the ANOVA test. Comparison of these dependent variables with the environmental variables was made using simple linear regressions (STATVIEW software).

Results

76 species were identified, 62 in aboveground vegetation, 40 in the soil seed bank and 26 species in both. In the Luberon Regional Park 16 species could be considered to have segetal characteristics based on Guende & Olivier (1997). Sørensens index value ($Cs = 0.46$) and the pair co-structure analysis (similarity : 3.2%) revealed that composition and distribution of the soil seed bank was significantly different from the above ground vegetation.

The PCA performed on the environmental matrix revealed which soil characteristics influence soil fertility from the field boundary to the middle of the field and between the five transects (Fig. 1). The first three axes accounted for almost 78 % of total variation, with 41.7% for axis 1 (variance = 3.33). Axis 1 is strongly related to pH (contribution 22.6) and soil samples with a high pH (5a, b, c, see legends of Fig. 1 and Table 1). However, axis 1 is also influenced by K (23,3), C (17,95) and Mg (14,9) concentrations and soil samples 1b, 1c are characterised by high contents of these elements. Axis 1 represents a fertility gradient for soil samples from the first transect, taken from the left-hand side of the crop, to the fifth transect, taken from the right-hand side of the crop. However, no fertility gradient could be identified from the field margin to the middle of the crop (Fig. 1). These results were confirmed by ANOVA tests which showed significant differences only for Phosphorus, whose values increased from the field boundary to the middle of the crop (Table 1). Significant differences were also found for pH and porosity between the five transects (Table 1).

The first axis for the two CAs performed respectively on aboveground vegetation (Fig. 2a) and soil seed bank (Fig. 2b) accounted for 23% and 13.3 % of the total variation, respectively. Axis 1 was strongly influenced by species which occurred only in the samples located at 1 m and 2 m from the field boundary. Particularly, *Agrimonia officinalis*, *Geranium dissectum*, *Lolium rigidum*, *Medicago lupulina*, *Lathyrus hirsutus*, *Picris echioides* and *Eringyum campestre* for aboveground vegetation (Fig. 2a) and *Phleum pratense*, *Dipsacus fullonum*, *Carex flacca* and *Hypericum perforatum* for soil seed bank (Fig. 2b).

Species richness, diversity (Shannon index) and evenness of the seed bank and aboveground vegetation showed no significant differences between the plots located near the field boundary (1 and 2) and the others plots (3 to 25). Only the above ground vegetation density of plot 1 was significantly lower than the others.

Simple linear regression analyses were performed for species richness, diversity, density and evenness of the seed bank, above ground vegetation and environmental variables (soil characteristics, PAR Values). Only wheat density showed a significant relationship to above ground vegetation diversity and evenness (Fig. 3a, b), with an error probability of $p < 0.0001$.

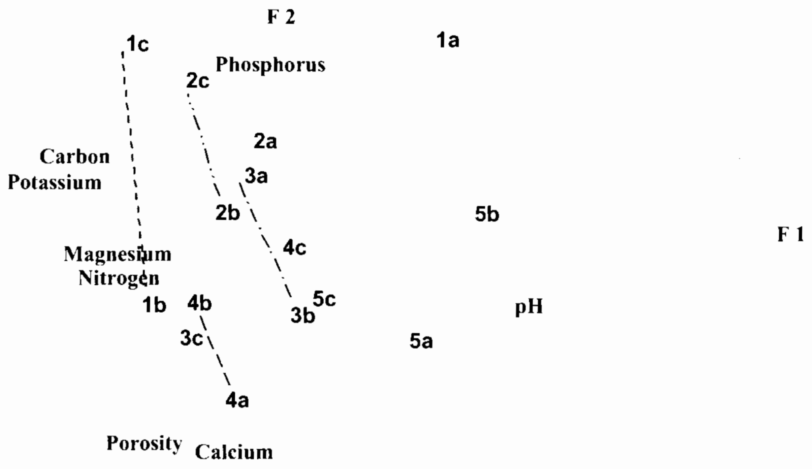

Fig. 1. PCA performed on the soil data sampled at the beginning (**a**, 0 m), middle (**b**, 13 m) and end (**c**, 25 m) of the five transects (1-5).

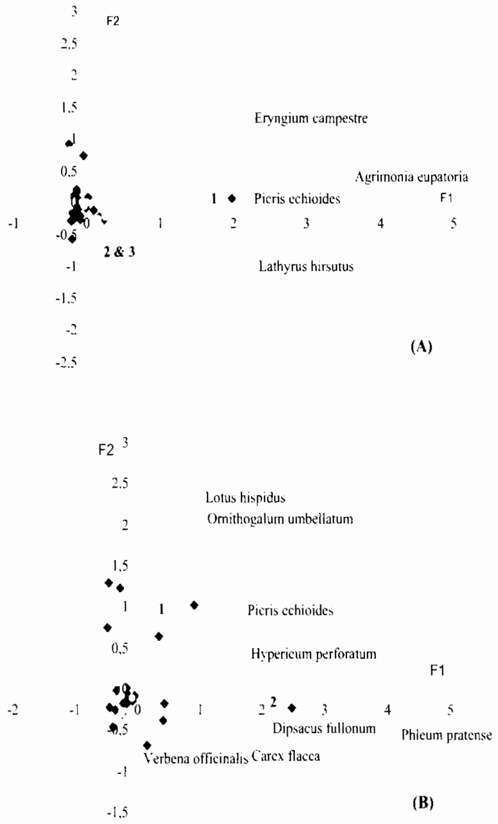

Fig. 2. (**A**) CA on the main composition of aboveground vegetation plots and (**B**) on the main composition of soil seed bank data. ○ = species, ◆ = plots. Only species and samples showing a significant correlation with axis 1 have been named. In (A), coordinates of *Geranium dissectum*, *Medicago lupulina* and *Prunus spinosa* are the same as for *Agrimonia eupatoria*.

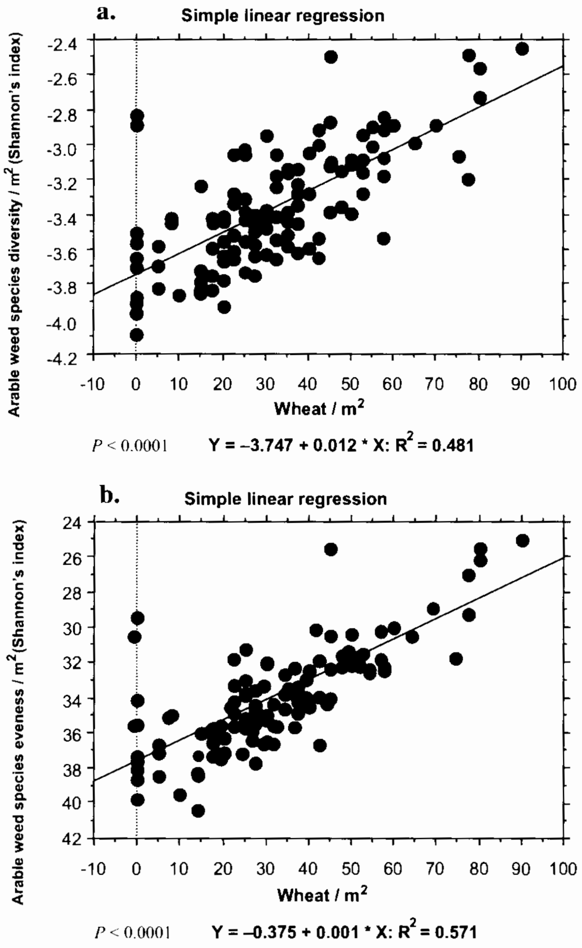

Fig. 3. Simple linear regression between diversity (**a**), evenness (**b**) of the above ground vegetation and wheat density.

Table 1. Soil characteristics of samples taken at three points: in the beginning (a, 0 m), middle (b, 13 m) and end (c, 25 m) of the transects ($n = 5$). (Standard error in brackets; significance : * $p < 0.05$, Numbers in exponents indicate the sample (I) or transect (II) which showed significant differences).

	pH	Porosity	C ‰	N ‰	P ‰	K ‰	Ca ‰	Mg ‰
I ($n = 5$)								
a	8.25	0.550	28.16	0.838	0.004*	0.406	10.52	0.220
	(0.040)	*(0.019)*	*(2.142)*	*(0.053)*	*(0.001)*^{b,c}	*(0.018)*	*(0.129)*	*(0.016)*
b	8.23	0.544	31.97	0.878	0.007	0.440	10.71	0.180
	(0.032)	*(0.019)*	*(2.792)*	*(0.026)*	*(0.001)*	*(0.009)*	*(0.112)*	*(0.009)*
c	8.27	0.536	27.18	0.816	0.006	0.400	10.61	0.156
	(0.031)	*(0.017)*	*(3.858)*	*(0.042)*	*(0.001)*	*(0.017)*	*(0.151)*	*(0.020)*
II ($n = 3$)								
1	8.14*	0.550*	35.25*	0.847	0.007	0.433	10.59	0.200
	(0.028)$^{2\text{-}5}$	*(0.021)*^{5}	*(2.519)*^{5}	*(0.058)*	*(0.001)*	*(0.018)*	*(0.182)*	*(0.021)*
2	8.23*	0.533	34.84*	0.867	0.006	0.437	10.42	0.210
	(0.009)5	*(0.003)*	*(2.365)*^{4,5}	*(0.041)*	*(0.001)*	*(0.012)*	*(0.046)*	*(0.020)*
3	8.26*	0.580*	27.46	0.840	0.005	0.427	10.87	0.203
	(0.018)	*(0.021)*^{4}	*(2.365)*	*(0.056)*	*(0.001)*	*(0.013)*	*(0.136)*	*(0.009)*
4	8.29*	0.560*	26.64*	0.907	0.006	0.393	10.70	0.160
	(0.032)	*(0.017)*^{5}	*(1.751)*	*(0.055)*	*(0.001)*	*(0.027)*	*(0.127)*	*(0.044)*
5	8.33*	0.493*	21.31*	0.760	0.006	0.387	10.48	0.153
	(0.012)	*(0.015)*	*(3.299)*	*(0.047)*	*(0.002)*	*(0.024)*	*(0.229)*	*(0.003)*

Discussion

Multivariate analysis (AFC) showed that some species were restricted to the outer 3 m of the field margin for aboveground vegetation and 2 m for the soil seed bank. These species included mostly those typical of calcareous grasslands situated near the crop, e.g. *Agrimonia officinalis*, *Carex flacca*, *Dipsacus fullonum*, *Eryngium campestre*, *Lathyrus hirsutus* and *Picris echioides*. It is possible that seedlings of grassland species may originate from parent plants in the field boundary. Nevertheless, a previous study of seed spread from a weedy area into an adjacent cultivated field indicated that seed dispersal for most species was limited (Hume & Archibold 1986).

Other reasons must therefore be found to account for the distribution of arable weeds. Farming machinery often turns on the headland, resulting in lower crop yields. The presence of typical grassland species and high seedling density in the headland could also be explained by the effects of crop competition, which increase across the arable field, creating more opportunities for these species to develop near the field boundary than in sites located further away (Firbank 1991).

Our study showed that there was no significant increase in species richness, diversity and evenness in the seed banks and the above ground vegetation in plots sampled near the field boundary. No distinct differences between the environmental relationships in the soil seed bank and the above ground vegetation could be observed using the pair co-structure analysis and the Sørensen index. In arable soils, the spatial pattern that exists immediately after seed rain is modified by agricultural practices and because farm machinery can transport weed seeds.

An EEC project for the conservation of species-rich headland in the Vaucluse has recently been initiated. This project includes reducing wheat seedling density on crop edges to increase arable weed richness. However, our results showed that this type of action could be more beneficial to the typical species of calcareous grasslands or field boundaries than to the typical segetal species of southeastern France. Consequently, it is essential that the effects of such practices on arable weed populations are understood before they are applied on a large scale.

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On the seed banks of grazed and ungrazed Baltic coastal grasslands

Jutila b. Erkkilä, Heli M.

Honkalankatu 2B9, FIN-13210 Hämeenlinna, Finland;
Fax +35836521500; heli.jutila@utu.fi

Abstract. Four grazed and four ungrazed coastal grasslands, two of them in the delta of the river Kokemäenjoki and the others by the sea, were studied in SW Finland. A total of 13463 seedlings and 104 species germinated from cold-treated samples (n=636; depth = 10 cm), which makes an average of 13 669 seeds/m^2 in the seashore and 22005 seeds/m^2 in the delta. The seed bank was significantly larger and richer in the delta than in the seashore both in grazed and ungrazed samples. Most seedlings and species were monocots and perennials. The most abundant species in the seed bank of both seashore and delta were *Carex nigra* and *Juncus gerardii*. The highest density and species richness of seed bank were found at middle elevations i.e. at the intermediate level of water level fluctuation stress. The seed bank was larger and richer in ungrazed than grazed samples. Grazing reduced the seed bank of 29 species in these coastal grasslands. An exception from the trend was that the number of hydrophyte species and seedlings in the seed bank was increased by grazing in the whole data set and all elevation classes.

Keywords: Grazing, Water level.

Nomenclature: Hämet-Ahti et al. (1998).

Introduction

In Baltic coastal areas the typical vegetation zonation of shore communities is in a continuous movement to the sea due to land-uplift creating new land for primary succession. In a Baltic river delta the process is even quicker due to sedimentation of the material transported by the river. After the 1940s the cessation of grazing and mowing lead to changes in shore landscape and expansion of common reed (*Phragmites australis*). Recently there has been attempts to restore especially the bird fauna of these coastal grasslands by reintroducing grazing. I have studied the effect of grazing on vegetation of these coastal grasslands (Jutila 1997, 1999a). In this paper I describe the germinable seed bank of Baltic coastal grasslands considering the differences between the delta and seashore grasslands, the water level fluctuation and the effects of grazing and bearing in mind the possible implications of the use of seed bank in restoration.

Material and Methods

The study area is situated on the western coast of Finland, near the town of Pori (61°30'-61°33'N / 21°28'-21°41'E). Four grazed and four ungrazed coastal grasslands, two of them in the delta (transects G4 and UG4) of the river Kokemäenjoki and the rest by the sea, were investigated in 1993 and 1994 (Jutila 1997, 1999a). The annual mean temperature, precipitation and the average duration of snow cover of the study area is +4.3°C (−6.5°C in January, +16.0 °C in July), 536 mm (22mm February, 75mm August), and 94 days, respectively (Finnish Meteorological Station Service). The sea is frozen for ca. 95 days (Seinä & 1991). During the growing season, the water level usually fluctuates within 20 cm limits, but changes of up to 1 m can occur.

Altogether 636 seed bank samples were taken with a corer of 4.8 cm in diameter to the depth of 10 cm along transects running from the waterline to the woods: in the seashore 343 samples (number of samples by transects: G1: 30, UG1: 50, G2: 53, UG2: 70, G3: 85, UG3a: 55, (Jutila 1998a) and in the delta 125 samples (G4: 65, UG4: 60, (Jutila 1998b). The vegetation plots (1 m × 1 m) located beside every second seed bank sampling point were studied. Transects were levelled.

Seed bank samples were treated five months at 5°C, two weeks at − 1 °C and two weeks at 5 °C before germination. Samples were spread out in a 0.5 cm layer on a mixture of fertilised peat and sand (1:1) and grown at a photoperiod of 16 hours of light (20°C) and 8 h of dark (15°C). Samples were germinated for ca. 3 months, then all plants were removed and germinated again for 3 months.

Statistical analyses were performed using the Statistical Analysis System, SAS. The data were log-transformed, ln(x+1), if necessary. ANOVA (procedure GLM in SAS), Mann-Whitney U-test and a pairwise t-test were used.

Results

Altogether 13463 seedlings germinated, 8486 from the seashore samples and 4977 from the delta samples. This results in a calculated average of 13669 seeds/m^2 in the seashore and 22005 seeds/m^2 in the delta. On average, 24.7 (0-227) seedlings and four species per sample germinated in the seashore and 39.8 (1-218) seedlings and six species per sample in the delta, respectively. The seed bank was significantly larger and richer in the delta than in the seashore both in grazed and ungrazed samples (Fig. 1).

The total number of species found in the seed bank of the coastal grasslands was 104 (82 seashore and 48 delta). Most seedlings and species were monocotyledons and perennials. The most abundant species in the seed bank were *Carex nigra* and *Juncus gerardii* both at the seashore and in the delta, *Schoenoplectus tabernaemontani*, *Eleocharis uniglumis*, *Agrostis stolonifera*, *Juncus bufonius* at the seashore and *Carex aquatilis*, *Calla palustris* and *Potentilla palustris* in the delta.

The highest densities of seed bank were found at middle elevations (at 20-50 cm at the seashore and at 10-20 cm in the delta). Also the highest species richness of the seed bank occurred at middle elevations, at slightly higher position (at 50-70 cm at the seashore and at 10-20 cm in the delta). These results were significant, except regarding the seedling densities of the delta samples. Several species had

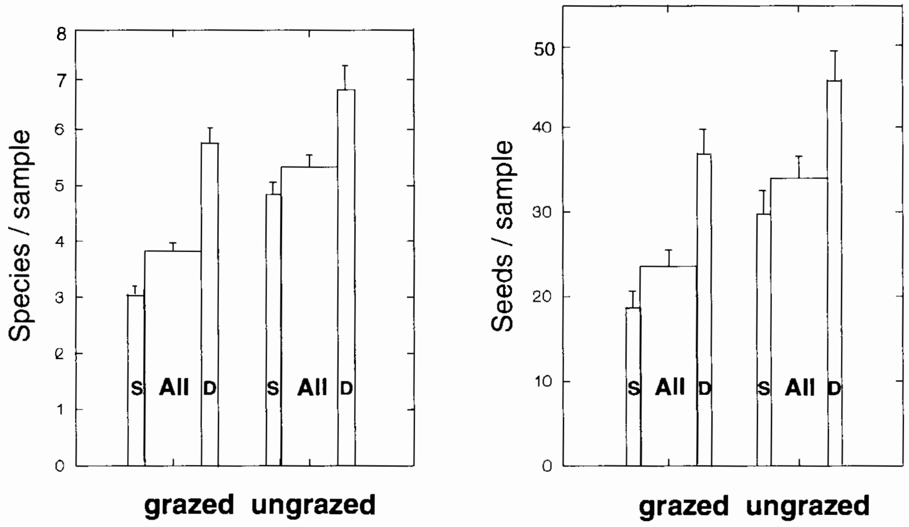

Fig. 1. The effect of grazing on the mean number of germinated species and seedlings per sample (+SE). All samples (All), seashore samples (S) and delta samples (D) are shown with separate bars. Results of the Mann-Whitney *U*-test indicate significant differences ($P<0.05$) between grazed and ungrazed samples. The mean number of germinated species and seedlings per sample (+SE) is significantly ($P<0.05$) higher in delta samples than in seashore samples.

an epilittoral seed bank (meaning that more seeds germinated above 20 cm in delta sites and above 50 cm at seashore sites than below it, respectively). *Agrostis canina* and *Juncus alpinoarticulatus* had an epilittoral seed bank both at the seashore and the delta sites. In the delta *Agrostis stolonifera, Carex panicea, Eleocharis palustris, Juncus bufonius* and *Potentilla anserina* had an epilittoral seed bank. On the seashore the seed banks of the following species were concentrated at the epilittoral for:

Agrostis capillaris, Alnus glutinosa, Artemisia vulgaris, Carex nigra, Centaurium littorale, Cerastium fontanum, Elymus repens, Epilobium angustifolium, E. palustre, Filipendula ulmaria, Galium uliginosum, Potentilla argentea, Ranunculus acris, R. cymbalaria, Rumex acetosella, Sagina procumbens, Stellaria graminea, Veronica chamaedrys, Viola canina and *V. tricolor*.

However, significantly more seeds germinating below 50 cm than above it on the seashore were found for:

Agrostis stolonifera, Betula pubescens, Calamagrostis stricta, Eleocharis uniglumis, Juncus bufonius and *Schoenoplectus tabernaemontani*

The seed bank of ungrazed samples was larger and richer than the one of grazed samples at the seashore and in the delta when the whole data set was used (Fig. 1). The density of the seed bank was decreased by grazing in two transect pairs (G2-UG2 and G4-UG4) and the trend was similar in one more transect pair. The negative effect of grazing on species and seedlings was most evident at the highest elevation. An exception from the trend was that the number of hydrophyte species and seedlings of the seed bank was increased by grazing for the whole data set and in all elevation classes.

The total number of species in the seed bank of grazed samples (49) was clearly smaller than that of ungrazed samples (70) on the seashore, but in the delta the total number of species was somewhat higher in grazed (37) than in ungrazed samples (33). Grazing reduced significantly the size of the seed bank of 29 species, 21 species on the seashore (26% of the species) and 10 species in the delta (20% of the species). On the other hand it increased the density of the seed bank for seven species in the delta (14% of the species), but only three species on the seashore (4% of species). Both on the seashore and in the delta grazing reduced the seed bank of *Galium palustre* and *Juncus alpinoarticulatus* and increased that of *J. gerardii.* There was a lack of resemblance between seed bank and vegetation in seashore and in delta. Species present solely in the seed bank were mainly annuals or biennials and those solely in adult vegetation were mainly perennials.

Discussion

The seed densities found in the delta and in the seashore were higher than those found in several other freshwater wetlands and brackish or saline marshes (see references in Jutila 1998a,b, 1999b). Jerling (1983) found much higher seed density in the Baltic seashore, but his samples were not cold-treated. It is interesting that the coastal areas, which are in the beginning of succession, have a large seed bank. This might indicate that seeds are not restricting factors in the succession of these environments.

The higher seed densities in the seed bank in the delta compared with the seashore, can be explained by the negative influence of the saline water (Jutila 1998b) and the frequent fluctuation of the water level on the seashore. Freshwater seed banks have commonly been found to be larger than the ones influenced by saline water (Leck et al. 1989a). Seeds transported by river water from a large catchment area may spread on grasslands during flooding or they may sediment and accumulate in the soil until they are uncovered by water.

The high dominance of perennials was evident both in seashore and in delta similarly as found in some other studies (Kirkman & Sharitz 1994). The contribution of *Juncus gerardii* (33.8% of seedlings in the seashore samples) was not nearly as great as in my earlier study with immediately germinated samples of G3 and $UG3_a$ (73%; Jutila 1998b) or in the studies of Jerling (1983: *Juncus gerardii* 86.7%) and Shumway & Bertness (1992: *Juncus gerardii* 99.9%). My present and earlier results (1997b) indicate that a large part of the seed bank and especially that of *J. gerardii* is transient. In spite of that, after spring germination an extensive permanent seed bank of *J. gerardii* is left in the field as Jerling (1983) also described. Most species had only a small seed bank or none at all, indicating that vegetative propagation is likely to be more important than propagation from seeds for many species. The large seed bank of coastal grasslands plays an important role in the succession of these communities and it can be used in restoration to some extent.

The total number of species found in the seed bank of the coastal grasslands (altogether 104 species) in Pori was higher than found in several other studies (e.g. Milton 1939; Jerling 1983; Leck et al. 1989b). There were 14 species in the seed bank (3 delta and 14 seashore) that have not been found earlier in persistent seed banks according to Thompson et. al. (1997).

The water level fluctuation is an important stress factor in coastal areas. Its influence is most prominent at the waterline and decreases at higher elevations. I found that the highest density and species richness of seed bank was at middle elevations i.e. at intermediate stress levels (similar results in Jerling 1983; Wisheu & Keddy 1991; Navie et al. 1996). In seashore the highest species richness of seed bank peaked at a somewhat higher elevation i.e. lower level of stress than the maximum density of seed bank. Based on these results I have made *a model* (Jutila 1998b). A flooding stress restricts the species adapted to the lowest elevations and even though the seed production is high (e.g. in reed stand), the persistence of seeds can be low. Furthermore, the most important reason for small seed banks at low elevations is the washing off by waves and floods, which push unattached plant material to higher elevations. Still, many hydro- and geolittoral species, especially on the seashore, have most of their seeds at low elevations where they have been produced.

Grazing reduced the density of the seed bank of the Baltic coastal grasslands. Bertiller (1992) observed that the seed bank was reduced as grazing intensity increased and plant cover decreased. The decrease of seeds in the seed bank after grazing is also evident in the studies by Granström (1988), Russi et al. (1992), McDonald et al. (1996) and Bakker et al. (1996). Animals eat flowers and seeds! One reason for the bigger seed bank in the ungrazed sites is also that taller geolittoral vegetation collects more sediment and litter including seeds compared to the shorter vegetation in the grazed sites (Grumblat 1987; Andresen et al. 1990; Jutila 1997). Hydrophytes are an exceptional species group, in which the seed bank was increased by grazing. This is probably due to the fact that cattle trampling creates wet bare spots in which hydrophytes can invade and when the amount of hydrophytes increases the seed production increases. Also Russi et al. (1992) reported on some species whose numbers in the seed bank increased with grazing. *Juncus gerardii* clearly benefited from grazing: the seed bank was increased both in the seashore and in the delta, and the aboveground cover was increased in the seashore (Jutila 1999b). In the delta both the seed bank and the aboveground cover of *Potentilla anserina* was increased by grazing (Jutila 1998e). Interestingly, the vegetation cover of *Agrostis stolonifera* (seashore) and *Elymus repens* (both seashore and delta) increased with grazing (Jutila 1997b), but the seed bank decreased with it (see also Ungar & Woodell 1993). This might be a general phenomenon for many grass species, which can effectively adapt to grazing by vegetative growth and dispersal.

Grazing decreased the seed bank of 29 species in these coastal grasslands. The clearly severe effect of grazing in the seashore (more species suffering and less species benefiting from grazing) than in the delta was obvious also on the vegetation (Jutila 1997). Actually, in the delta the aboveground species richness in grazed plots was higher than that in ungrazed ones. Grazing reduced both the aboveground cover (Jutila 1998e) and the seed bank of the following species: *Galium palustre* (both on the seashore and in the delta), *Viola canina* (in the seashore), *Cicuta virosa, Lythrum salicaria, Potentilla palustris* and *Stellaria palustris* (in the delta). The reduction of the seed bank by grazing was not evident in the upper elevations and closest to the open sea. This might indicate that grazing in connection to water level stress reduces the seed bank, but grazing alone would not necessarily do so.

Wisheu & Keddy (1991) observed that shoreline seed banks are not deeply buried (unpublished data on the coastal grasslands of Pori also indicates that) and so may be particularly sensitive to disturbance. This seems to fit my study area, where the disturbance is grazing. It reduced the species richness in the seed bank (mean number of species / sample and the total number of species in grazed transects), although Gibson & Brown (1991) have claimed that grazing is known to increase the species diversity of germinable seed banks (see also Donelan & Thompson 1980). According to the intermediate disturbance hypothesis (Connell 1978) a disturbance, such as grazing, probably has an optimum, which is different for every vegetation and seed bank type (Levassor et al. 1990). Grazing reduced most consistently the number of annuals and biennials in the seed bank and also in the established vegetation (Jutila 1997b). This is in disagreement with Kinucan & Smeins (1992), who pointed out that grazing increases the proportion of annual dicots in the seed bank.

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Changes in plant cover and net primary production in the forest-steppe zone of West Siberia

Titlyanova, Argenta A. & Kosykh, Natalia P.

Laboratory of Biogeocoenology, Institute of Soil Sciences and Agrochemistry, Siberian Branch of the Russian Academy of Sciences, Novosibirsk 630099, Russia;
Fax +73832227652; E-mail argenta@issa.nsk.su

Abstract. Three centuries ago, the Siberian forest-steppe zone was covered by conifer and mixed forests. Grasslands appeared gradually as result of forest clearing by man. Forest-steppe landscapes arose which were built up of meadow steppes and insular groves of aspen and birch. Intensive use of land began 150 yr ago. At present, 76% of the total area of the forest-steppe zone has changed due to forest clearing, steppe ploughing and haymaking and grazing of meadows. The total net primary production, NPP, of the past plant cover is estimated as 515 million t dw/yr. The high NPP of the grasslands, i.e. 15 - 25 t dw/ha/yr, is due to intensive root growth. The share of the aboveground production is not more than 30% of the NPP. Substitution of natural grasslands with agroecosystems (with NPP-values varying from 6 to 11 t/ha/yr), intensive use of forest and a degradation of pastures resulted in a large decrease in NPP of the forest-steppe zone to 304 million t dw/yr.

Keywords: Agroecosystem; Forest; Grassland; Plant cover; Primary production; Steppe.

Nomenclature: Cherepanov (1981).

Introduction

The part of West Siberia that is at present covered by forest-steppe, was covered by coniferous and mixed forests three centuries ago. Grasslands appeared later as a result of forest clearing by man. Massive forest cutting started in 1760 due to the development of iron and copper melting in West Siberia. Further important factors stimulating changes in the landscape were the migration of people from Central Russia to Siberia in 1850 and the construction of the Trans-Siberian Railway at the beginning of the 20th century. All these factors resulted in new clearings and ploughing of clearings and grasslands. 150 yr ago small-leaved forest occupied about 50% of the forest-steppe zone, whereas meadow steppes – dominated by bunch grasses – and dry meadows appeared after forest clearing, occupying 45% and 5% of the whole area, respectively. At present 45% of the total area are ploughed, 39% are covered by insular groves of aspen and birch, and 23% are used as hay-meadows and rangeland (Laschinsky & Sedelnikov 1992).

In the past, the forest-steppe zone used to have a very high net primary production (NPP). In meadow steppes and steppe meadows the NPP value may be assumed to be not less than 15 to 25 t/ha/yr, i.e. not less than NPP value estimated in the present day meadow steppes and stepped meadows (Bazilevich 1993; Titlyanova 1991).

Several factors determine the high productivity of grasslands. These grasslands are situated on chernozems and chernozem-like soils that are very rich in nitrogen and other nutrients. Most of the annual precipitation (65- 85%) falls during the warm half of the year. Plant species common in steppes and meadows are very productive and allocate the main part of their photosynthesized organic matter to below-ground organs. The carbon cost of below-ground organs is lower since the respiration rate of steppe species roots is half that of the shoots. Thus, the larger the contribution of the belowground organs to the total plant phytomass, the less respiration expenditures are, and, as a result, the higher the net production of plants is. The belowground production contributes no less than 70% to total NPP (Titlyanova 1991). The high belowground production results in a large input of organic matter into the soil and accounts in part for the great accumulation of soil organic carbon in grassland chernozemic soils.

Study area

The total area investigated in Southwest Siberia includes ca. 104 million ha with the following landscape regions: taiga zone (49 million ha), forest steppe zone (30 million ha), steppe zone (12 million ha), mountain landscapes and river valleys (6 million ha).

The forest-steppe zone is located from 53° N to 55° N and it is the most favourable zone in West Siberia for agriculture. The climate is continental, with moderate warm summers and cold winters. The mean yearly temperature changes southward from – 0.5°C to – 0.3°C with a mean July temperature from 18.4°C to 18.7°C, and a mean January temperature from –20.5°C to –19.4°C. The average precipitation changes southward from 450 mm to 350 mm, from which 60 - 70% falls between May and September.

The main ecosystems in the past there were aspen- birch forests, meadows and meadow steppes. Forests are linked to grey forest soils, meadows to meadow soils, meadow steppes to chernosems. As it was mentioned before now 45% of the forest-steppe total area are ploughed.

Results

Through the anthropogenic impacts the types of plant communities and their parameters were changed. Forest clearing in the forest-steppe zone led to the formation of tallgrass meadows, which are very rich in species (Table 1). Green phytomass, aboveground production, ANP, and belowground production, BNP, increase also as compared to forest. Regular haymaking changes species composition, increases species number, decreases ANP and increases BNP a little. The next stage of grassland transformation under moderate grazing is bluegrass meadow which is characterized by lower levels of these parameters. The last stage forms under heavy and long-term grazing and is represented by degraded forb meadows with a very low NPP value.

Table 1. Community and production characteristics of anthropogenic communities in former virgin Birch forest habitats.

Community*	Impact *	Main plant species*	No.* of species per 100 m^2	Degree* of cover	Green phytomass g/m^2	ANP g/m^2/yr	BNP g/m^2/yr	NPP g/m^2/yr
Birch grove	Virgin	*Betula fruticosa, Populus tremula, Calamagrostis arundinacea, Poa angustifolia, Fragaria viridis*	25 - 30	-	360	780	220	1000
Secondary tall-grass meadow	After clearing	*Calamagrostis arundinacea, Brachypodium pinnatum, Aegopodium podagraria, Crepis sibirica*	50 - 70	90 - 100	500 - 600	800	800	1600
Forb-grass meadow	Regular haying	*Dactylis glomerata, Phleum pratense, Festuca pratensis, Lathyrus pratensis*	60 - 75	95 - 100	300 - 400	500	1200	1700
Bluegrass meadow	Moderate grazing	*Poa pratensis, Festuca pratensis, Trifolium repens, Taraxacum officinale*	25 - 30	60 - 80	200 - 250	300	550	850
Forb meadow degraded	Heavy and long-term grazing	*Achillea millefolium, Potentilla argentea, Polygonum aviculare*	15 - 20	50 - 80	150 - 200	250	400	750

* After Malzeva & Parshutina (1992).

Haymaking and grazing in meadow steppes lead to the replacement of *Stipa pennata* (large bunch grass) by *Stipa capillata* (large bunch grass) (Table 2). At this stage of succession small bunch grasses (*Festuca valesiaca, Koeleria cristata*) appear in the sward. The species richness, degree of coverage, phytomass and ANP value decrease. Belowground production does not change markedly, sometimes increasing a little. Moderate grazing (next stage of pasture succession) results in transformation of large bunch grass secondary steppe into small bunch grass secondary steppe, with further decrease in richness, green phytomass, ANP and pronounced decrease in BNP. Heavy grazing leads to a formation of sedge-forb community with very low richness, degree of coverage and NPP value.

Substitution of natural grasslands with agroecosystems with lower NPP (11 - 13 t dw/ha/yr, Table 2) also decreased the production of the region (Kiryushin et al 1993).

Total net primary production of plant cover of the forest-steppe zone in the past is estimated as 515·10^6 t dw /yr. Substitution of natural grasslands with agroecosystems, intensive use of forest and degradation of pastures resulted in great decrease in total primary production of forest-steppe zone to 304·10^6 t dw/yr. For the total Southwest Siberian region net primary production in the undisturbed ecosystems is estimated as 1236·10^6 dw/yr. The present-day plant cover produces 886·10^6 t dw/yr.

The distribution of areas with different levels of NPP also changed (Fig. 1). Where a considerable part of the area had a production of more than 16 t/ha/yr in the past, up to 30 t/ha/yr, at the moment there is little area left with a productivity of more than 11 t/ha/yr!

Table 2. Community and production characteristics of anthropogenic communities on former virgin bunchgrass steppe.

Community*	Impact*	Main plant species*	No* of species per 100m^2	Degree* of cover	Green phytomass g/m^2	ANP g/m^2/yr	BNP g/m^2/yr	NPP g/m^2/yr
Large-hunchgrass steppe with forbs	Virgin	*Stipa pennata, Poa stepposa, Phleum phleoides, Galium verum, Medicago falcata*	55 - 60	90 - 100	300 - 350	430	1640	2070
Large-bunchgrass secondary steppe	Haying or light grazing	*Stipa capillata, Festuca valesiaca, Koeleria cristata, Galium verum, Medicago falcata*	45 - 50	70 - 80	180 - 210	300	1650	1950
Small - bunchgrass secondary steppe	Moderate grazing	*Festuca valesiaca, Koeleria cristata Carex duriuscula, Medicago falcata*	25 - 30	65 - 75	120 - 160	250	1000	1250
Sedge-forb degraded steppe	Heavy grazing	*Carex duriuscula, Artemisia frigida, Artemisia glauca*	12 - 15	30 - 45	40 - 50	100	800	900
Wheat agroecosystem	Ploughing and cultivation	*Triticum aestivum*	-	-	530	630	190	820
Maize agroecosystem	Ploughing and cultivation	*Zea mays*	-	-	580	650	250	900
Potato agroecosystem	Ploughing and cultivation	*Solanum tuberosum*	-	-	150	180	180	360

* After Malzeva & Parshutina (1992).

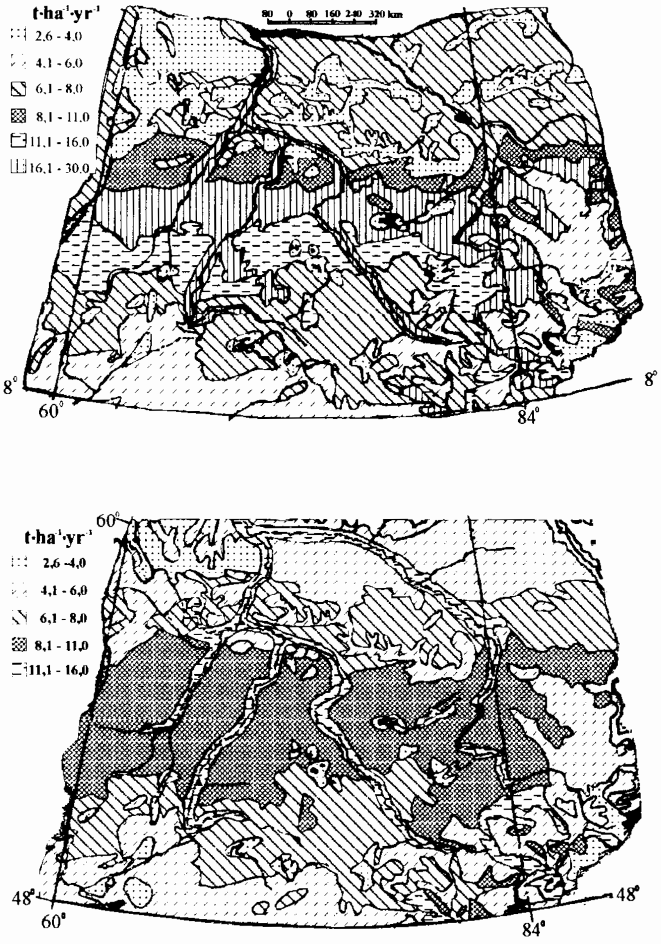

Fig. 1. Net primary production of the plant cover in West-South Siberia. **a.** Past (after Bazilevich 1993). **b.** Present. (after Titlyanova & Kosykh 1997).

Discussion

Changes in land use are the dominant factor affecting the carbon budget. Because of the difference in biomass, net primary production and input of organic matter into the soil, the balance between carbon source and sink in virgin and human-used ecosystems is different. Expansion of arable land into forest and grass lands results not only in the loss of the large pool of carbon stored in the biota, but also in the loss over a few years of the carbon stored in forest and grassland soils (Woodwell 1984).

In natural ecosystems the annual plant material input to the soil is equal to the annual net primary production. In agroecosystems the input of carbon with plant residues to soils decreases owing to the reduction of NPP and the output of carbon with the crop. A decrease of organic substance input to the soil leads to a decrease of humus formation which became less than soil organic matter mineralization. The imbalance of carbon results in a decrease of soil carbon pool and an increase of CO_2 emission from the soil (Titlyanova 1985).

A heavy grazing impact also leads to a decrease of NPP and a reduced input of organic substance to the soil. In response to a decrease of carbon input the soil organic matter decreases and CO_2 emission increases. In this way used lands in West Siberia transformed into carbon sources.

At the same time West Siberia has a sink for carbon since the latter may accumulate in peatlands. The increase in the peat layer is ca. 0.5 mm to 1.0 mm/yr (Buringh 1984).

Global carbon losses from terrestrial plants as a consequence of land use conversion to regular cropping were estimated to be $39.3 \cdot 10^{15}$ g (Richards et al. 1983). Estimations of the cumulative world transfer of carbon from the soil to the atmosphere since prehistoric time varies from $40 \cdot 10^{15}$ g C (Schlesinger 1984) up to $537 \cdot 10^{15}$ g C (Buringh 1984). A gap between estimations is due to difficulties associated with the measurement of changes in the vegetation of the earth, especially changes in the areas of forests and grasslands.

The short and documented period of historical change in the plant cover of West Siberia has made it possible to evaluate the carbon budget trend in the last 150 years. Carbon losses from terrestrial biomass associated with forest and grassland conversion to regular cropping were estimated to be $0.44 \cdot 10^{15}$ g. The losses of organic carbon from soils of West Siberia during the last two centuries reached $1.12 \cdot 10^{15}$ g. As mentioned above peatlands serve as a sink for carbon. The area covered by peatlands in West Siberia is ca. $30 \cdot 10^6$ ha. During this century peatlands gained ca. $1.5 \cdot 10^{15}$ g carbon. So gaseous carbon output from destroyed plant cover and used soils of West Siberia is balanced by carbon input to peatlands.

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Vegetation patterns on degraded raised bogs: a contribution towards restoration

Goodyear, Joanne[1] & Sliva, Jan[2*]

[1]*Institute for Grassland and Environmental Research, North Wyke, Okehampton, Devon, EX20 2BS, United Kingdom;*
Fax +44 1837 82139; E-mail joanne.goodyear@bbsrc.ac.uk;
[2]*Technical University of Munich, Dept. of Vegetation Ecology, Am Hochanger 6, D-85350 Freising, Germany;*
[*]*Fax +498161714143; E-mail sliva@pollux.weihenstephan.de*

Abstract. Raised bogs are unique ecosystems that are being rapidly destroyed by human activities. Attempts to restore these ecologically and economically important landscapes are often frustrated by the hostile environmental conditions left after peat harvesting. Hochrunstfilze is a harvested raised bog in Bavaria, abandoned since 1967. The site has re-vegetated naturally with a mix of species typical of natural and disturbed bogs, including *Sphagnum* spp. This study investigates the abiotic conditions facilitating recolonization and explores the relationship with species distributions on site. Measurements included water level, water and peat chemistry and stratigraphical studies. Vegetation was surveyed by relevé and biotic-abiotic correlations were analysed using Canonical Correspondence Analysis (CCA). Water table level was the most important variable in explaining the distribution of species in the heterogeneous vegetation ($p < 0.01$). The site has achieved 100% vegetation cover within 30 yr of abandonment, due to a large remnant seed bank and maintenance of uncut baulks as refugia. The implications for restoration techniques on cut-over bogs is discussed.

Keywords: Ombrotrophic bog; Ordination; Restoration, Southern Germany.

Nomenclature: Fitter et al. (1996) for vascular plants; Andrus (1980) for *Sphagnum* species.

Introduction

Regeneration of cut-over raised bogs with the aim of rehabilitating ecological function has proved to be difficult. Vegetation removal and extensive drainage are the main factors that inhibit a fast rehabilitation of such sites (Sliva et al. 1997). Despite harsh conditions, within decades the natural processes of recolonization and succession produce a vegetation cover typical of nutrient-poor mires on some of these areas, especially those cut by hand or digger which leave a more heterogenous peat surface (Poschlod 1988; Lavoie & Rochefort 1996). This project aims to investigate the relationship between the environmental conditions present on a cut-over and abandoned raised bog and the vegetation able to colonize under these conditions. The investigation of an area previously disturbed by humans and re-vegetated solely through natural processes demonstrates the extent of possible recovery and suggests how human restoration can work with these processes.

Site

Hochrunstfilze is an area of previously cut-over raised bog (ca. 300 ha) lying within the Rosenheim basin in the Alpine foothills of southern Germany (47°48' N, 12°05' E). The climate is cool and humid - average annual air temperature 8.3 °C; average annual precipitation 1225 mm. The peat deposit is (was) ca. 5m deep.

By the 1920s, the original mire surface had already been removed by small-scale peat cutting (Paul & Ruoff 1927). The current surface structure of the study area was created by progressive hand-cutting of north-south strips roughly 50 - 100 m wide and 300 m long, leaving raised baulks and lower cutting floors. Between 1967 and 1969 peat cutting stopped and the site abandoned without any restoration measures.

Methods

A 420-m long transect running east-west across the harvested area was established. The present surface topography of the site was surveyed along the transect. 32 dipwells (4cm diameter slotted PVC tubing) were inserted along the transect, to a depth of 1.5 m. A more detailed secondary dipwell transect was set up between dipwells 17 and 22, comprising 13 wells set a few metres apart to monitor water table fluctuations across a single raised baulk. Water table depth, pH and conductivity were measured fortnightly. Water was sampled from each dipwell and analysed for calcium and potassium using a flame photometer.

The carbon:nitrogen (C:N) ratios of peat at three different depths (0 - 25 cm, 50 - 75 cm, 100 - 125 cm) were determined at each dipwell site using a Russian sampler. Additionally, traditional stratigraphical investigation of the peat profile at selected points allowed estimation of the von Post humification class and characterization of the peat layers using macrofossils.

Vegetation cover was investigated using 16-m^2 relevés close to each dipwell. The % cover of vegetation layers and species were estimated using an adapted form of Braun-Blanquet's scale (Pfadenhauer et al. 1986). These were converted into their appropriate average cover value for analysis.

Species and environmental data were collated. The correlation between abiotic and biotic factors was tested using CANOCO (ter Braak 1988). Two analyses were run. The first included all 12 environmental variables and all species (log-transformed). The second did not use transformed data and investigated the effect of five selected environmental variables (maximum water table, pH, minimum conductivity, [P^+] and [Ca^{2+}]) on all species. A Monte Carlo test was run to test the significance of the second analysis.

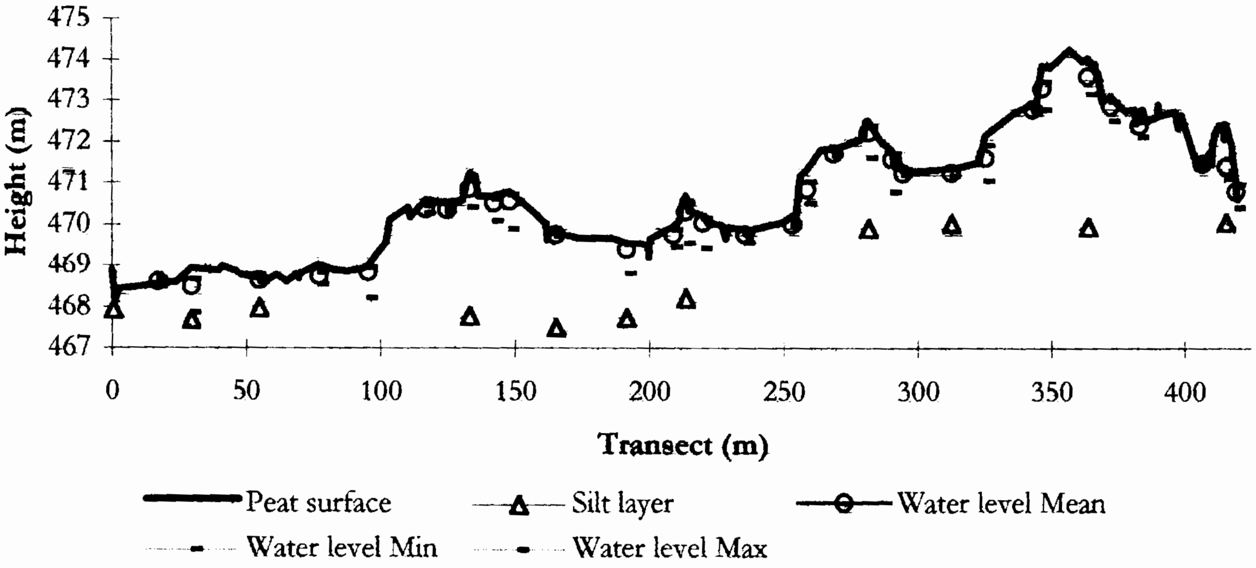

Fig. 1. Topographical profile of transect across Hochrunstfilze showing water levels (max, mean and min) at each dipwell (numbered from left). The silt layer indicates the depth of mineral ground under the remaining peat.

Results

Topography and hydrology

The heterogenous nature of the surface is evident, comprising a series of raised baulks, separated by cutting floors, and drainage ditches (Fig. 1). The water table levels show great variability both in the spatial variation of mean levels between wells, and in the degree of temporal fluctuation. The least variation is found on flat surfaces, or those that are low relative to the land surrounding them. The secondary dipwell transect revealed that the water table pattern within a baulk can vary significantly. Over a horizontal distance of 40 m, the water level can rise by 2 m to within 0.3 m of the peat surface, providing a significant water store within the peat.

Water chemistry

No clear trend in the values of pH (4.1; range 3.6-5.0), conductivity (44 µS/cm; range 17-150) calcium concentration (mg/l; range 1.5-5.5) and potassium concentration (range 0.1-9.8) are shown. These values are comparable to other ombrotrophic bogs in the region (Sliva 1997 Waughman 1980), showing that, despite peat extraction, the site has not been influenced by the circumneutral groundwater. Conductivity is significantly correlated with Ca^{2+} concentration ($p < 0.01$), but not water level ($p > 0.1$).

Peat quality

The depth of peat remaining is shown in Fig. 1. No significant differences in the peat stratigraphy were encountered across the study area. On cutting floors, roughly 1.3 m of well-decomposed peat remains (Von Post value H 4-8). On the baulks, the peat is up to 3.5 m deep. The upper few cm are highly decomposed, suggesting that decomposition rates have increased recently, perhaps as a result of draining or cutting. The C:N analysis shows that the surface layers (C:N ratio of 25-38) are more mineralized than deeper layers (50 - 125 cm deep; C:N 29 - 62). There is no significant change in C:N ratio along the transect

Current vegetation cover

The vegetation cover across the site is nearly 100 %, suggesting that colonization in the 30 yr since abandonment has been rapid. Separation of plant communities using traditional phytosociological methods was not possible despite the apparent visual differences between the *Molinia caerulea*-dominated cutting floors and the *Calluna vulgaris*-dominated baulks. This is attributable to the young successional stage of the stands, a small number of relevés (37) and heterogeneous species distribution. Species present across the transect included those typical of natural and disturbed bogs, notably six *Sphagnum* spp. While *S. cuspidatum* was confined to seven sites where the water table approaches the peat surface, *S. magellanicum* and *S. capillifolium* are more widespread, occurring in *Molinia* hummock fields and beneath *Calluna vulgaris* on baulks in 23 quadrats. The near-ubiquitous presence of many species does not aid separation of sub-units, although such a widespread occurrence of *Sphagnum* species across the site is encouraging in terms of regeneration processes.

Statistics

In the first CANOCO-analysis, the water table level explains one third of the variance across the site, being the only significant variable ($p < 0.01$, F ratio > 2.28). Other abiotic variables showed no significant influence on vegetation pattern, even when water level was taken as a covariable ($p > 0.15$). More variables achieved significance when the data were not log-transformed, thus lowering the influence of 'rare' species (Fig. 2). Maximum water table

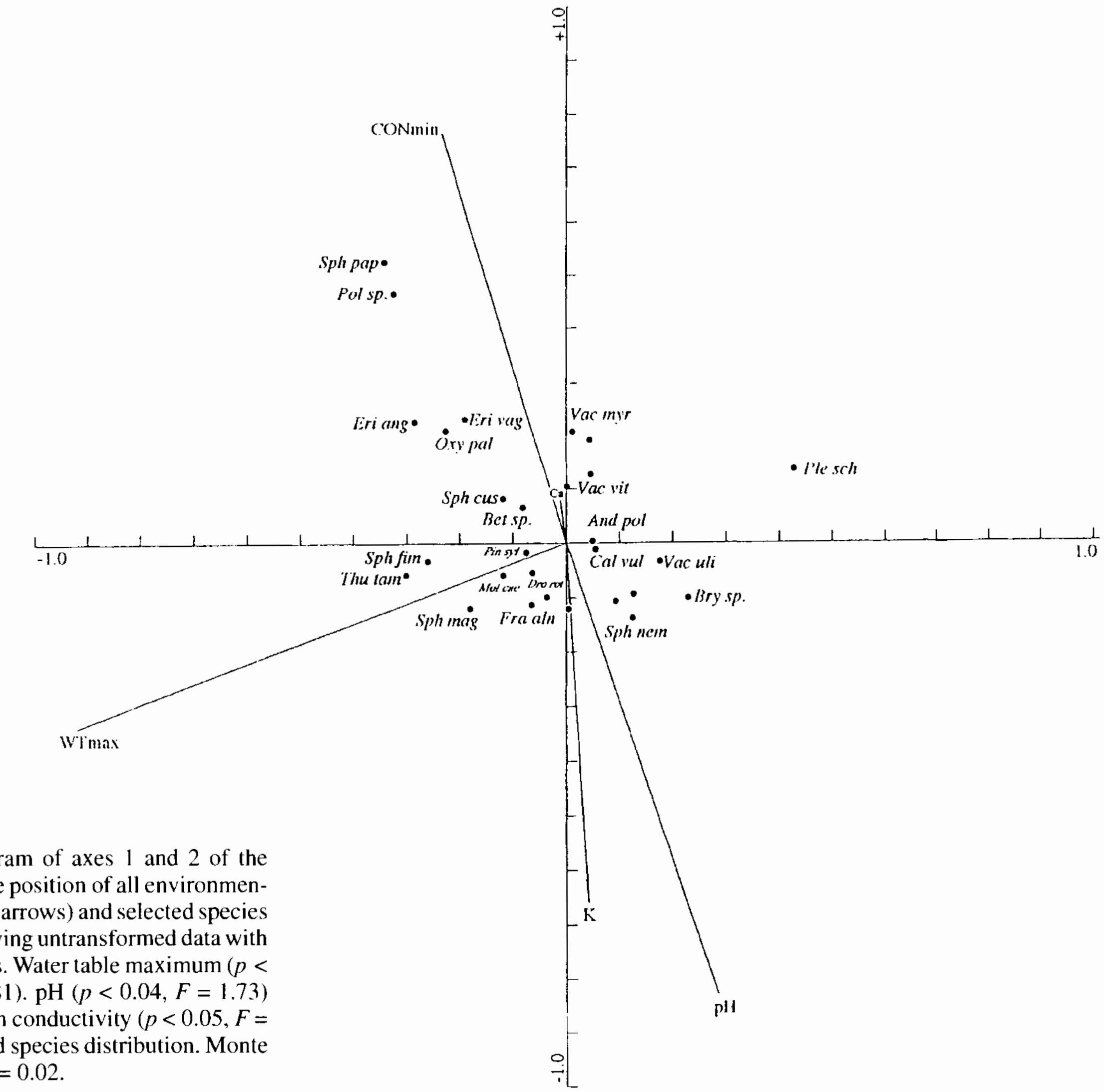

Fig. 2. Diagram of axes 1 and 2 of the CCA with the position of all environmental variables (arrows) and selected species (points) showing untransformed data with five variables. Water table maximum ($p < 0.04$, $F = 2.81$). pH ($p < 0.04$, $F = 1.73$) and minimum conductivity ($p < 0.05$, $F = 1.65$) affected species distribution. Monte Carlo test; $p = 0.02$.

($p = 0.04$), pH ($p = 0.04$) and minimum conductivity ($p = 0.05$) accounted for 74% of the variation observed (Monte Carlo test; $p = 0.02$). While most species cluster around the mean, *Sphagnum papillosum*, *Eriophorum* spec., *Polytrichum* sp. and some of the ericaceous shrubs are distributed along the positive conductivity axis, favouring sites with higher minimum conductivity values. *Picea abies* and *Pleurozium schreberi* are positioned on the negative WTmax axis, showing that they occupy dry sites. Ericaceous shrubs (*Calluna*, *Vaccinium*, *Andromeda*) are also positioned in sites with a lower than average maximum water level, together with *Sphagnum capillifolium*.

Discussion

This study has found that the present environmental conditions on Hochrunstfilze (particularly water chemistry) do not vary significantly from those of undisturbed ombrotrophic bogs (Waughman 1980), nor do they vary greatly across the site. There is no evidence that circumneutral groundwater is affecting the site. The CCA-ordinations show that, of the variables measured, water table level is the only factor significantly influencing vegetation distribution across the site. In contrast, Hesse (1971) found that the wet-dry gradient across baulks influences the pH, conductivity and C:N ratios at the surface through relative water levels and fluctuations.

Hochrunstfilze has almost totally re-vegetated within 30 yr of abandonment with a variety of species typical of ombrotrophic bogs, disturbed bogs and drier heaths. This is more rapid than records for other block-cut peatlands (e.g. Lavoie & Rochefort 1996). Previous studies suggest that parts of the site were vegetated less than 10 yr after abandonment (Kaule 1974). Species distribution is typically interpreted as variations along a simple environmental gradient according to habitat preference, or to competition from other species. While water levels explained one-third of the variation in species distribution across the site (Fig. 2), the variables measured during this study could not explain the remaining species distribution. Other unrecorded factors, such as the previous exploitation history of the site, may explain more of the observed species distribution. The hand-cutting of peat blocks on cutting floors between baulks created Hochrunstfilze's heterogeneous topography. Much of the upper vegetation and peat layer was kept on the site by laying turves onto previously cut surfaces. Knowledge of the peat cutting methods provides insight into the re-vegetation of Hochrunstfilze. There are two main issues - the maintenance of a diaspore bank for bog species and the effect of baulks on the hydrology of the bog.

The relatively fast colonization of Hochrunstfilze by vegetation predominantly indicative of ombrotrophic mire conditions is easily explained by the presence of a seed-source on-site. This provides a surer source of typical bog vegetation than diaspore rain from the surrounding areas, enabling more rapid colonization (cf. Salonen 1987) and probably also prevented species of disturbed bogs or dry heaths becoming more dominant. The uncut baulks remained vegetated, so that colonization of any 'window of opportunity' would be rapid, while the heterogeneous topography provided a wide range of niches. The transference of the top layer from one area of the site to another, and from baulk to cutting floor, explains the heterogeneous nature of the vegetation as the whole area shares a common seed bank.

The rate of secondary succession on Hochrunstfilze is difficult to quantify, particularly as there is evidence showing site was vegetated in part before the end of exploitation (Kaule 1974). As the vegetation has not been monitored, the rate of successional change is not known. Similarly, rates of *Sphagnum* expansion on the site cannot be estimated from the current data set. However, in one relevé, roughly 50 cm of neogenous peat has formed within the last fifty years. Such results suggest that Hochrunstfilze has suitable environmental conditions to support *Sphagnum* populations in some areas, but establishing such a beneficial state over the entire site presents huge problems.

Following the groundwater mound theory, the large incisions caused by block-cutting peat should have lowered the perched water mound in the vicinity. Detailed investigation of water table levels across a single baulk revealed that it was able to retain much of the incident precipitation, maintaining a water table up to 2 m above that of neighbouring cutting floors. The narrow baulk at well 31 does not demonstrate this (Fig. 1, Transect 410 m), suggesting that a certain volume (or quality) of peat is necessary to exert sufficient capillary force on the water. The water table within the baulk is lower and less stable than that of the cutting floors, suggesting that it may act as a water storage area which gradually loses water to the cutting floors in dry weather, ensuring that the cutting floors remain permanently wet.

The results presented here show that block-cut peat retains water well and may help maintain the stable water table of the cutting floors. Block-cutting can maintain the seed bank and add heterogeneity to the bog environment, suggesting that the removal of the baulks to create shallow lagoons on large flat areas of peat (e.g. Eggelsman 1987) may not always be the most effective way of restoring bog vegetation to the site. While it is not safe to make generalizations from site-specific studies, our results suggest that retention of baulks, perhaps coupled with the creation of slightly concave surfaces on the tops to increase water storage capacity, is preferable to maintain water table stability.

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Species dynamics in wet heathland restoration

Kesel, Raimund & Urban, Katharina

Department of Vegetation Science and Nature Conservation, Institute for Ecology and Evolutionary Biology, University of Bremen, PB 330440, DE-28334 Bremen, Germany;
Fax +494212187052; E-mail raimund.kesel@uni-bremen.de

Abstract. The dynamics of two rare wet heathland species, *Gentiana pneumonanthe* and *Rhynchospora fusca* as well as some common heathland species such as *Calluna vulgaris, Erica tetralix, Agrostis canina* and *Molinia caerulea* were studied in experimental permanent plots in a wet heathland near Bremen, NW Germany. The objective was to assess the effectiveness of sod cutting and mowing in promoting species-rich wet heathland. All plots were influenced by changing water tables with periods of inundation and drought.

Sod cutting was most successful in promoting characteristic species of wet heathland and in inhibiting *Molinia*, whereas mowing was only effective at the beginning of the experiment and after inundation. *Gentiana* seedlings and adult shoots slowly became more and more abundant after sod cutting. In contrast, *Rhynchospora fusca* soon formed closed stands first through seed germination and later through fast clonal growth. Hydrology and microclimate determined the distribution and dominance of the wet heathland species as well as the speed of canopy development.

For both disturbance-dependent rare species, the availability of appropriate gaps within the vegetation is of crucial importance. To promote existing populations of *Gentiana pneumonanthe*, small-scale sod cuttings are suggested which create gaps without disturbing existing individuals too much. In order to promote *Rhynchospora fusca*, large-scale sod cuttings are recommended. On degenerated stands the seed bank will be activated and the development of a wet heathland with its characteristic floristic composition and dynamics is initiated.

Keywords: *Agrostis canina*; *Calluna vulgaris*; *Erica tetralix*; Gap; *Gentiana pneumonanthe*; *Molinia caerulea*; Mowing; Permanent plot; *Rhynchospora fusca*; Sod cutting.

Nomenclature: Oberdorfer (1994).

Introduction

The main aim of wet heathland restoration is to promote original wet heathland vegetation and to protect and stimulate rare species by management. These rare species can serve as target species, because first they characterize a fitting context of ecological conditions, and secondly they contribute to a local gene pool of ecologically adapted plants. These are the two foci of restoration ecology (van Andel 1998). It is necessary to understand the ecology and life properties of the rare species in their successional context (Klötzli 1991; Müller 1996). And above all it is necessary to protect and promote even the smallest population in order to have the material available for restorations in the future.

The objective of the work presented here is to study the regeneration and succession of wet heathland by permanent plot field experiments. According to the target species concept, two rare and endangered species within their community were especially taken into account: *Gentiana pneumonanthe* and *Rhynchospora fusca*. Both species are known to have a very weak ability to disperse, *Gentiana* exclusively by seeds and *Rhynchospora* also by clonal growth (Kaplan 1990; Oostermeijer et al. 1994; Křenová & Lepš 1996). Therefore maintaining existing populations should have a higher priority than trying to create new stands.

In wet heathland restoration, practices like mowing, grazing, and sod cutting are the methods of choice (Bakker 1989; Wittig 1996). In our work the success of mowing and sod cutting in a wet heathland is compared with respect to the promotion of *Gentiana pneumonanthe* and *Rhynchospora fusca* and the avoidance of the promotion of *Molinia caerulea*. From the results, measures of maintenance and management for restoration have been derived.

Material and Methods

Study area

The study area is part of a pleistocene inland sand dune landscape formed by wind and interspersed with many blowouts which are permanently or occasionally filled with water. The area is situated near Bremen, Northwest Germany. It is a 3 ha remainder of a former extended heath landscape of ca. 20 km^2, which was spotted with many ponds (Urban & Drengemann 1996). Today, it is included in a 12.5 ha nature reserve, which is surrounded by urban and military areas. The study sites 'Katzenpohl' (KP) and 'Eispohl' (EP) support a large population of *Gentiana pneumonanthe* (20 000 - 25 000 shoots). The soil is a nutrient-poor sandy substrate with pH of 3.3, the pond water is oligotrophic and well buffered (pH 6-7.5). The vegetation is a mixture of different wet and dry heathland communities including pond and shore vegetation determined by the height and the duration of inundations.

Hydrology

The groundwater level is a backwater horizon which follows the terrain features. It is exclusively fed with rain water. The surface water level curves (Fig. 1) display a permanently filled pond at EP with a variation of almost 2 m. In contrast, KP is an occasionally filled pond and the water level showed a variation of ca. 4 m. It had water in 1988/ 1989 and 1994/1995, but in between the pool was dried up. The water levels have been recorded by above- and belowground water-gauges.

Experimental design

Two experiments were conducted to study species development after sod cutting and mowing. One experiment consisted of small plots (0.25 m^2) at KP, and one consisted of a large scale sod-cut plot (1500 m^2) at EP.

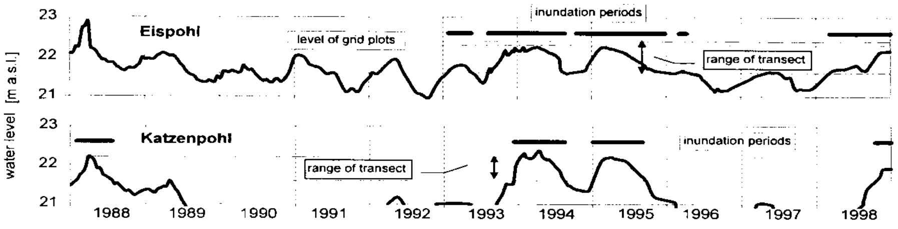

Fig. 1. Surface water level curves and inundation periods affecting at least parts of the transects at EP and KP between 1988 and 1998 and level of the experimental plots (transect and grid plots on the EP island and transect plots at KP).

Experiment 1. At KP, a set of 20 permanent plots of 50 cm × 50 cm was established in 1989 along a transect through the wet *Erica* heathland: four were sod-cut, four mown and cleared from litter (every year), and 12 were controls. These transect plots were flooded for about 7 months from January to July in 1988, 1994 and 1995 (see Fig. 1).

Experiment 2. At EP, an island which used to be a stand of wet heathland the vegetation consisted in 1992 predominantly of *Molinia caerulea.* The vegetation layer of the 1500-m^2 island and also the upper soil layer of about 10-15 cm was removed. Some spots still inhabited by wet heathland species were left untouched. After cutting, the hay harvested from a wet heathland mowing on KP was introduced to stimulate a better development of the proper initial floristic composition. The vegetation records of KP suggest, that the hay mainly contained seeds of *Calluna vulgaris*, *Erica tetralix*, *Molinia caerulea*, *Agrostis canina*, *Lysimachia vulgaris* and *Gentiana pneumonanthe*, but no *Rhynchsopora fusca* or other rare species.

Sampling methods

The vegetation of the plots at KP was recorded once a year in September or October. Dominance by outer (shape) and inner (within-shape) cover (real cover = outer × inner), group structure, abundance, growth height, and phenology were noticed according to Barkman et al. (1964).

In each plot at KP, the numbers of seedlings and juveniles as well as the numbers of adult vegetative and flowering shoots of *Gentiana* (following the age stage drawings of Oostermeijer et al. 1994b) were counted separately. Dormant stages were not estimated. We counted shoots of adult plants instead of individuals, because the reproductive capacity is well correlated with shoot number since the number of flowering shoots of one individual can vary between one and thirty. Counting shoots leads to a higher estimate of population size, compared to counting individuals, but allows a more realistic estimation of the success of management practices in relation to the vitality and reproduction capacity of *Gentiana pneumonanthe*.

The vegetation recovery at EP was studied between 1996 and 1998 on two permanent grid-plots of 5 m × 5 m and 4m × 4 m, and in 25-m^2 plots arranged along a 46-m transect. Cover percentage and abundance of the species were recorded within every grid m^2 and transect plot. At least parts of the transect were inundated between 1993 and 1995, the grid plots were not inundated (see Fig. 1).

Results

Vegetation development at Katzenpohl

The 10-yr permanent plot studies on KP between 1989 and 1998 show a different response of wet heathland species (a) to naturally changing conditions like changes of the pond water table and (b) to the different measures of sod cutting and mowing.

The two heather species *Erica tetralix* (Fig. 2a) and *Calluna vulgaris* (Fig. 2b) developed similarly. Both were able to expand during the drier years at the beginning of the study. The flooding event in 1994/1995 led to a total breakdown of both the populations. Both started to regenerate gradually after inundation. The heather species were neither

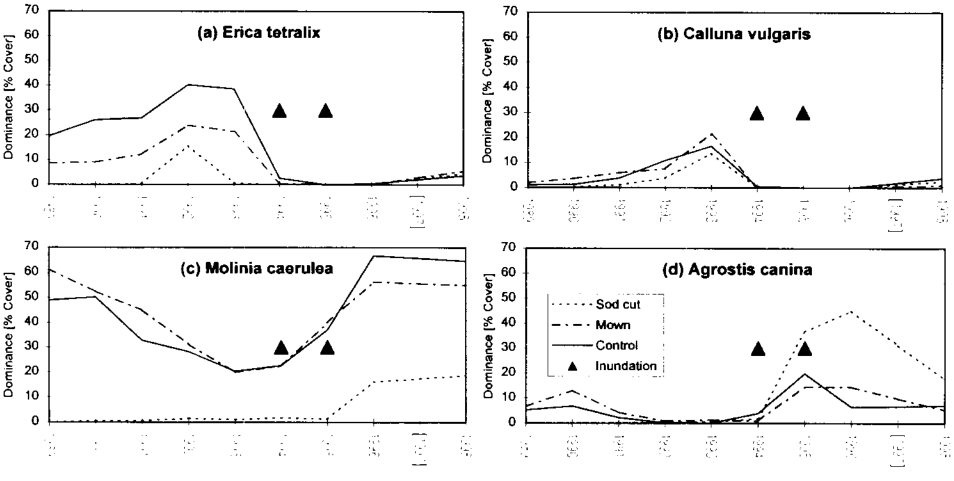

Fig. 2. Dominance development of *Erica tetralix* (**a**), *Calluna vulgaris* (**b**), *Molinia caerulea* (**c**) and *Agrostis canina* (**d**) after different measures in the transect plots at KP. In 1997 the plots were not analysed.

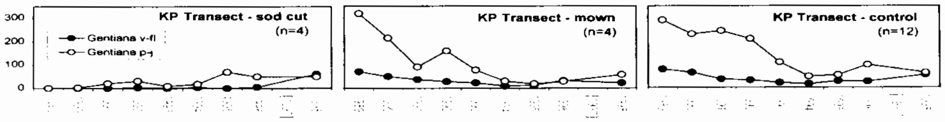

Fig. 3. Development of *Gentiana pneumonanthe* [shoots/m^2] in the transect plots at Katzenpohl.

promoted significantly by sod cutting nor by mowing.

The two grasses *Molinia caerulea* (Fig. 2c) and *Agrostis canina* (Fig. 2d) showed the opposite development. After a slight increase in the first year they decreased constantly in the mown and the control plots during the dry years, and they showed hardly any regeneration in the sod-cut plots. The high water levels in 1994 and 1995, however, encouraged the growth of both species in all three plot variants, but after two years *Agrostis* began to decline again. *Agrostis canina* was most stimulated on the sod-cut plots, *Molinia caerulea* was significantly inhibited by sod cutting.

Development of Gentiana pneumonanthe

In the control and the mown plots of the transect *Gentiana pneumonanthe* declined during the time the pool did not contain any water (Fig. 3). During this period, large amounts of seedlings were recorded, but the conditions were not favourable for the establishment of *Gentiana*. Subsequently, the high water level in 1994 and 1995 led to a short-term increase in abundance.

In contrast, the abundance of *Gentiana* in the sod cut plots showed a low but constant increase after sod cutting in 1989, which was enhanced after the flooding event in 1994-1995. 10 yr after sod cutting, *Gentiana* had reached the same numbers as in the control plots.

Development on the Eispohl island

The recolonization on the EP island after sod cutting in 1992 developed very gradually. After 6 yr the vegetation cover was still rather low in the largest part: 40 - 80% (Fig. 4). Similarly, the establishment of plant species occurred very slowly. Frequent inundations resulted in high species numbers, high species dynamics and a comparatively low total cover. The non-inundated part of the study site inhabited less species, showed a much more stable species composition and a closer canopy. Here, most of the wet heathland species occurred.

All of the wet heathland species which had still been present on the island enlarged their populations through the spreading of seeds: *Trichophorum cespitosum, Gentiana pneumonanthe, Drosera intermedia, D. rotundifolia, Erica tetralix, Calluna vulgaris* and *Molinia caerulea.* The spreading of seeds was enhanced through the import of heathland hay from Katzenpohl. Additionally the seeds of *Rhynchospora alba* and the very rare *Ranunculus ololeucos* had been activated from the soil seed bank. The success of sod cutting is clearly reflected in the fact that now almost all *Littorelletea* and wet heathland species occurring in the area (Drengemann et al. 1995) can (also) be found on the sod-cut island.

Species distribution was mainly determined by soil humidity. In the wettest and frequently inundated parts *Agrostis canina* established and also seedlings of *Gentiana pneumonanthe* occurred. The sites just above the highest water table were optimal for the development of *Erica tetralix* which was also dominant in the depression at the beginning of the transect. Also *Gentiana* could best establish in this depression. *Rhynchospora fusca* dominated at an intermediate level, whereas *Calluna vulgaris* developed best on the highest level.

Rhynchospora fusca on Eispohl island

Among all the species occurring on the island, special attention was paid to *Rhynchospora fusca* which was previously observed at a nearby stand. It appeared in the third year after the impact and had already gained some dominance in the next year (Fig. 5). In 1998, 6 yr after the impact, it was the most prominent plant on the whole island. It exceeded by far the growing speed of any other species.

The 5 m × 5 m grid represents an optimal stand for *Rhynchospora* whereas the higher situated 4 m × 4 m grid was more suitable for *Calluna vulgaris* (Fig. 6). Germination played a major role only in the first year of settlement. In the second year the established plants enlarged by clonal growth and only few new groups originated from seeds. In the third and fourth year the former separated groups grew even more together, forming almost one continuous large

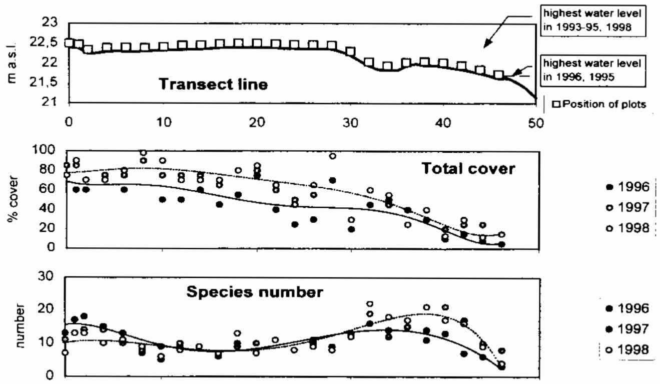

Fig. 4. Dominance and species number distribution of wet heathland species in the EP island transect.

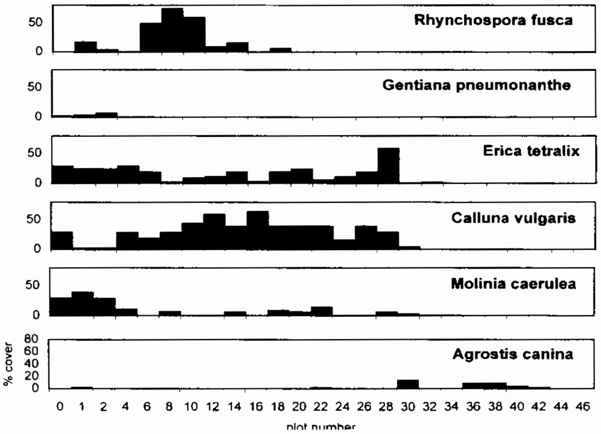

Fig. 5. Dominance distribution of wet heathland species in the EP island transect in 1998.

patch in 1998. Even though the seed production of *Rhynchopora fusca* was enormous and open spaces were available, no germination could be detected after the second year. Seemingly, the safe sites for germination had already been occupied in the first and second year. Then clonal growth was of major importance. The density of shoots was usually between 1500 and 1800/m^2 and increased with aging to 2200. However, where *Calluna*, *Erica* or *Molinia* grew within the group, the density decreased to about 1200/m^2.

Discussion

Gentiana pneumonanthe

Gentiana pneumonanthe germinates only on bare soils with full light conditions. The species has a short living seed bank; seeds probably survive only three years at the most, but the plants can reach an age of 10-20 yr (Chapman et al. 1989; Oostermeijer et al. 1992, 1994). *Gentiana pneumonanthe* does not expand vegetatively, but it is able to survive unfavourable seasons (even years) subterraneously in a dormant state (Oostermeijer et al. 1994). As a gap species it requires moist microclimatic conditions in order to germinate and to establish properly. We agree with Křenová & Lepš (1996), that *Gentiana* has its highest recruitment and seedling survival in sod-cut sites, which present suitable conditions over a longer period of time. But the seedling to adult establishment phase is critical as well. This risk can be minimised by creating small scale cuttings of a few dm^2.

We observed that with the development of small moss cushions (preferably *Sphagnum* species), but also litter layers and small and low *Erica* bushes within such small cuttings, safe sites for a successful establishment of juveniles and adults are provided at the edges of this structures. This mechanism is working for 10 and more years, as our results indicate. That observation coincides with the positive correlations Oostermeijer et al. (1994) found between moss and litter cover and proportion of adult plants and between bare soil surface and seedlings and juveniles.

The hydrological conditions have a great influence on the population development of *Gentiana pneumonanthe*. On sites affected by drought, population density and vitality decreased, while episodical short-term flooding on these sites caused an increase of seedlings and shoot numbers. In contrast, the moister sites provided optimal conditions for the shoot growth of *Gentiana pneumonanthe*. The highest recruitment rate of seedlings was observed after long inundations which opened up many gaps within the vegetation through the die-back of other species such as *Erica tetralix* and *Calluna vulgaris*.

Consequently, to promote and to stimulate existing *Gentiana pneumonanthe* populations, the best maintenance is to create as many small gaps and edges as possible by small-scale cutting or ploughing or moderate cattle grazing of the wet heathland within or in the neighbourhood of prevailing *Gentiana* populations. The advantage is that one does not disturb existing populations as a whole. This maintenance should be done every 10 - 15 yr depending on vegetation development, especially *Molinia* dominance.

Rhynchospora fusca

The sod-cut Eispohl island was a young stand on oligotrophic sand, where *Rhynchospora fusca* clearly is a pioneer plant. It was best in rapidly closing up the stand. Once established, the species expanded vegetatively and

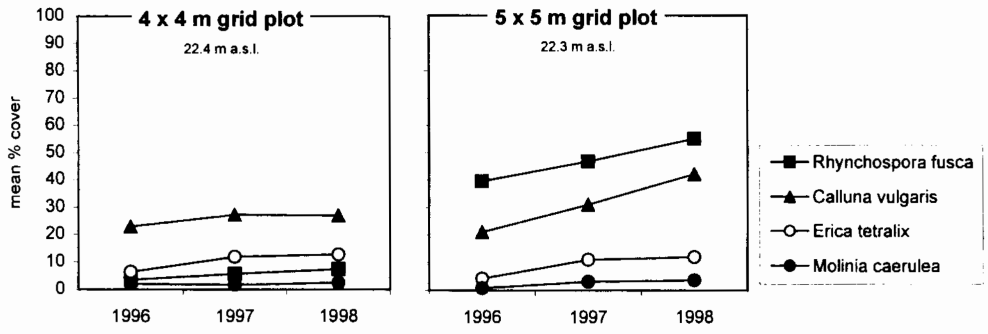

Fig. 6. Development of species cover in the 4 m × 4 m and 5 m × 5 m grid plot on EP island between 1996 and 1998. Cover is estimated as mean cover of 16 and 25 grid squares.

resisted temporary drought. *Rhynchospora* appeared in an early stage of succession which is characterized by a high light availability because of a rather open canopy and a mineral soil where the formation of an organic top soil has not yet begun.

Rhynchospora was growing best on the higher sites of the island (e.g. the 5 m × 5 m grid), which accordingly represents its most favoured habitat. In this stand the species almost reached its saturation within four years. Its further extension though will be limited by *Calluna vulgaris* and *Molinia caerulea*.

In established communities, *Rhynchospora* occurs only on sites where plants growth is limited by a very low nutrient availability and where a fluctuating water table causes disturbances. For a further development of *Rhynchospora*, it will be of crucial importance that larger blank gaps exist. In small gaps its appearance is only episodical. As the results from the experimental plots on Katzenpohl indicate, a breakdown of the *Calluna* and *Erica* heathland can be expected after a high water table event. A die-back of the heather vegetation would than open suitable habitats for *Rhynchospora*. Therefore it is to be expected that *Rhynchospora* is more likely to survive close to the mean water table.

Restoration of species-rich wet heathland

The success of restoration depends on several interacting conditions like seed availability from seed rain or soil seed bank, favourable conditions for germination, establishment within suitable vegetation structures, and successful development of mature, seed producing individuals (Willems & Bik 1998). In many cases introduction of seeds and of organic materials including seeds is necessary to provide better initial floristic conditions. Hay material also offers suitable micro-sites for the germination and the survival of heathland species and acts as a mulch, conserving moisture on skeletal mineral wastes and suppressing weed growth (Pywell et al. 1996).

Comparing the two measures mowing and sod cutting with respect to wet heathland regeneration, our permanent plot study shows that sod cutting was the most successful. Mowing enhanced the growth of *Erica tetralix* and *Calluna vulgaris* and also of *Gentiana pneumonanthe* only for a short period after the first mowing of an old stand. *Molinia caerulea* however, the unwelcome species with its ability to dominate wet heathland stands and to withstand inundations if once formed tussocks, had most difficulties to regenerate after sod cutting. Other wet heathland species may profit from this inhibition which was not observed in mown stands. The best development of species-rich heathland was observed on sod-cut stands with frequent but shallow inundations.

Our study also shows, that sod cutting advantages predominate for 10 and more years, but also depend on unpredictable events like water table variations. These may either lead to a promotion or to a total breakdown of the populations. If it is possible to maintain the same water table, breakdowns could be avoided and dynamics can be directed.

Thus, to encourage a new succession and restoration of species-rich wet heathland with *Rhynchospora fusca* and *Gentiana pneumonanthe* as the target species, the best maintenance is sod cutting. In species-poor stands dominated by *Molinia caerulea* or other grasses, larger areas should get sod cut whereas in existing species-rich stands only small-scale sod cutting or episodical grazing is needed.

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Monitoring fen vegetation in southern Germany using airborne scanner data

Kuhn, Gisbert & Pfadenhauer, Joerg

Chair of Vegetation Ecology, Technical University of Munich, D-85350 Freising-Weihenstephan, Germany; Fax +498161714143; E-mail kuhn@pollux.edv.agrar.tu-muenchen.de

Abstract. In order to test the usefulness of airborne scanner data for monitoring fen vegetation scanner data of the Wurzacher Ried site in southern Germany were acquired in 1995. The data were recorded in six wavebands (visible, near infrared, thermal infrared) with a pixel size of 1 m × 1 m. For automatical supervised classification the Maximum-Likelihood algorithm was used. Thus a number of vegetation elements, i.e. species and vegetation types, can be distinguished. The accuracy of class assignment differs: some classes are distinguished with high reliability whereas others are not. This is due to continuous transitions and fine-scale heterogeneity in fen vegetation, which does not meet the requirements of remote sensing. As a compromise, 15 classes where chosen to be useful in a monitoring programme because their assignment is highly reliable. In a random verification process 88% of the tested points were classified appropriately. In general, classes with less reliability can be avoided using classes on a lower level of detail.

Keywords: Automatical Classification; Mapping; Maximum Likelihood Algorithm; Mire; Remote Sensing; Wurzacher Ried.

Nomenclature: Oberdorfer (1990).

Introduction

For nature conservation and landscape planning data on vegetation are of critical importance. Such data can be acquired in several ways, each of which has specific advantages and shortcomings. One of them is remote sensing by means of an airborne multispectral scanner (Albertz 1991). This technique provides data, which are up-to-date, cost-efficient, already in a digital form and which allow a variety of analyses. Such systems have been investigated for natural vegetation (Weaver 1987; Treitz et al. 1992; Budd 1991; Kübler 1992; Ihse et al. 1992; Tucker 1980) but not yet for the special purpose of fine-scale monitoring of fen vegetation. The question to be answered in the present paper is: Which fen vegetation elements (species, communities) can be identified by using airborne scanner data?

The investigations were carried out in the Wurzacher Ried site (ca. 1715 ha, Southern Germany, near Lake Constance). In 1989 it was awarded the 'European Diploma' because of its international importance. Therefore some measures have been planned to restore the affected parts (e.g. by raising the groundwater table) and to protect the undisturbed areas. The effects of the measures should be controlled by monitoring fen and bog vegetation change. Because of the sensitivity of the vegetation it was aimed to realize monitoring by means of remote sensing.

For technical illustrations of scanning, digital image processing and automatical classification, see e.g. Jensen (1986), Lillesand & Kiefer (1987), Jähne (1989), Albertz (1991), Hildebrandt (1996).

Methods

The data were acquired on 29 June 1995 by the airborne DAEDALUS-MSS AA 3600 multispectral scanner, at a flying height of ca. 1000 m aboveground. The pixel size is 1 m × 1 m. Data were recorded in six wavebands:

0.45 - 0.52 µm blue	0.52 - 0.60 µm green
0.63 - 0.69 µm red	0.76 - 0.90 µm near infrared
0.91 - 1.05 µm near infrared	8.50 - 12.5 µm thermal infrared.

Due to a technical problem there was no waveband in middle infrared (3.0 - 5.5 µm) available. Geometrical rectification and mosaic checking was carried out by the air flight company. The resulting file has a size of 400 Megabytes. For data analysis (automatical classification) we used the Maximum-Likelihood-Algorithm (supervised, i.e. the program used reference sites as examples) and the ISODATA-Algorithm (non-supervised, i.e. the program divided the whole area in a given number of units without any additional information) in ERDAS 8.2 Imagine and TNT-MIPS 5.7.

Ground truthing data were taken from two existing vegetation maps (produced in 1989 and 1990), from 1:2.000 colour infrared air photographs and from own vegetation sampling on reference sites in the summer of 1995.

Results

In the Wurzacher Ried data of fen vegetation 15 classification units could be distinguished (Table 1).

- The list consists only of units with high separability (even if in the following figures it might seem different); the criterion for selecting units was the classification accuracy tested in a random process (see below).
- Tree species individuals can be identified if their diameter exceeds ca. 3 m. Herb species can only be identified if they cover an area of at least 10 m^2, i.e. as a local monodominant stand.
- The resulting classes are species, vegetation types and land-use types. It is not possible to restrict the choice to only one of these categories without renouncing valuable information. The property of a vegetation element to be detected by remote sensing data or not depends on several physical parameters. This property cannot be predicted and it is hardly comprehensible that one large and showy herb species can be detected and another one cannot, though it looks similar to our eyes. Thus the list of units achieved in automatical supervised classification (Table 1) seems to be built up quasi-randomly.

- The resulting list depends also in a special way on the

Table 1. Units achieved in automatical supervised classification (fen vegetation).

Automatically classified units	
1	Deciduous trees and bushes
2	*Picea abies*
3	*Pinus mugo*
4	*Phragmites communis/Phalaris arundinacea*
5	*Calluna vulgaris*
6	*Molinia caerulea*
7	*Cladium mariscus*
8	*Schoenus ferrugineus*
9	Dry meadows
10	Wet meadows
11	Mown meadows
12	Fallow meadows
13	Water
14	Roads
15	Shadow

properties of the site, e.g. species combinations, vegetation structure, vegetation complexity, geomorphology. Hence the list can be transferred to other sites only under certain restrictions.

Figs. 1 - 3 show three examples regarding the separability of classes. While some classes can be separated very well others are overlapping to a certain amount.

In order to verify the reliability of the classification, randomly chosen points were tested whether their classification meets that of the real vegetation (Gammon & Carter 1978, Kübler 1992). 130 points of an arbitrarily set grid on the resulting classification map were compared with 1:2.000 colour infrared air photographs and recent vegetation mapping (1995). For 88% of these points class assignment was matching the real vegetation class.

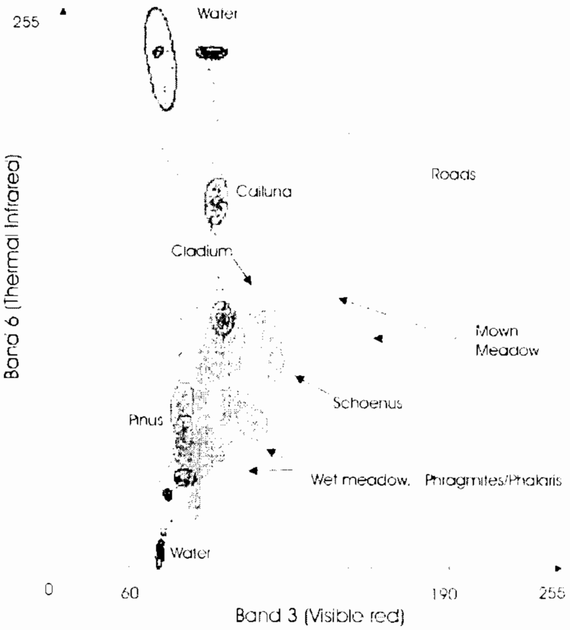

Fig. 1. Scatter plot of the supervised classification: grey tone distribution in band 3 and 6 of all reference sites are shown; as can be seen some classes are readily distinguishable whereas other classes (e.g. wet meadows, *Phragmites*) are not.

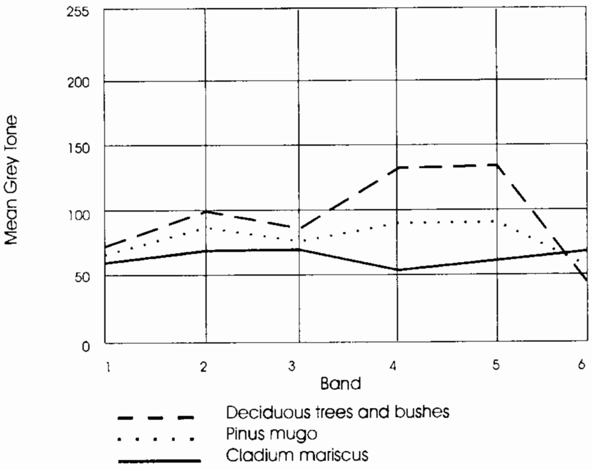

Fig. 2. Mean plot: mean grey tones of reference sites, which are readily distinguishable, are shown (for each band).

Discussion

Figs. 1 - 3 show problems arising from the classification method: continuous transitions and fine-scale heterogeneity in the natural vegetation cause overlapping in class assignment. Thus classification results are not absolutely reliable, though the verification result (88% appropriate) is quite good (Congalton 1991; Treitz et al. 1992; Maurer 1983). There are some factors which contribute variability to the data and leave the results therefore less reliable, e.g. weather and sensor technique (Kuhn 1998). However, one of the most important factors here is definition of reference sites. Although automatical classification is a tool which reduces interpreter bias on results, reference data still contribute variability and lessen the value of

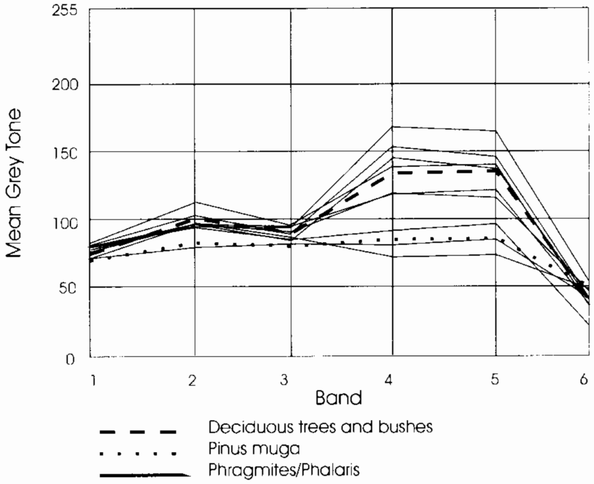

Fig. 3. Mean plot: mean grey tones of reference sites, which are hardly to distinguish, are shown (for each band); the class *Phragmites* is represented by several reference sites, which differ to some extent (therefore causing problems in assignment reliability, see Discussion).

automatical supervised classification for monitoring purposes (concerning natural vegetation). No matter if the same reference sites are used for two or more data acquisition events (which might be separated by several years) or if every time new sites are defined, it is not possible to find sites with absolutely constant (or identical) vegetation over several years.

One possibility to deal with that uncertainty is to restrict the classification to classes which can be identified with high accuracy, i.e. to diminish the level of detail. Technical developments might help compensating this loss of detail. New sensors are to be launched soon with improved spatial and spectral resolution (Mansberger 1998). Many multispectral scanners (in satellites or in aircrafts) collect data in 5 - 15 wavebands which cover 50 nm - 5000 nm (e.g. 0.45 µm - 0.52 µm, i.e. 70 nm) respectively. Newer generations of sensors can use up to several hundred wavebands at the same time which are very narrow (10 - 20 nm).

Nevertheless complex fen vegetation (high diversity in species composition and vegetation structure) is not a proper object for remote sensing, because it does not meet the requirements of remote sensing (large, homogeneous and well delimited areas).

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Conservation management modeling at En Afeq Nature Reserve, Israel

Olsvig-Whittaker, Linda*, Friedman, Doron, Magal, Yonat & Shurkey, Raia

Israel Nature and National Parks Protection Authority, 3 Am Ve Olamo, Jerusalem, Israel 95463;
**Fax 972256529232; Email linda.whittaker@nature-parks.org.il*

Abstract. The wetland nature reserve at En Afeq, Israel, was the site of a pilot study for applying Dutch methods for conservation management scenario modeling to Israeli conservation problems. Correlations derived from field data are used in scenario modeling to extrapolate changes in landscapes when given changes in driving environmental factors. The extrapolations are in turn projected as map images (scenarios) using GIS. The scenarios can be evaluated and compared in order to select an optimal management strategy. This paper outlines the conservation problems, theory and methodology employed in the project.

Keywords: Geographic Information System; Grazing; Hydrology; Scenario; Wetland.

Introduction

One of the most critical tasks of nature conservation managers is deciding upon optimal management practices in order to achieve desired conservation goals. Such decisions require (1) clear definition of conservation objectives, (2) clear understanding of the consequences of management, and (3) the ability to select an optimal policy from many possible management outcomes. This task is often made difficult by the complexity and stochasticity of ecological systems and ecological responses. Until recently, data analytical approaches have not been able to help conservation managers very well; ultimately the manager was left with some big leaps of intuitive guesswork. Among the more promising new approaches are those using computer-based decision support systems (DSS): interactive models of the system in question – for example, a nature reserve. One kind of DSS is the scenario: a model which uses both data analysis and expert opinion to project changes in landscapes through time on the basis of changes in driving environmental factors.

Scenarios are not always spatially explicit models, but the usefulness of visual projection has made GIS interfacing between data and model very widespread. Maps of scenario projections are a powerful way of presenting and comparing scenario outcomes (van den Berg et al. 1984; Knaapen et al. 1992; Harms et al. 1993; Schippers et al. 1996)

In conservation biology, different management regimes can be emulated on GIS, using different scenario options to predict whether a desired landscape condition can be reached, to search for an optimal management protocol, or to anticipate undesirable changes. This is already a practical management tool: scenarios are now being used generally in The Netherlands as an aid to conservation management (see Anon. 1990) to assist in giving management recommendations and timetables for management regimes. This approach is being adopted in other countries as well (see Ridgley & Heil 1997).

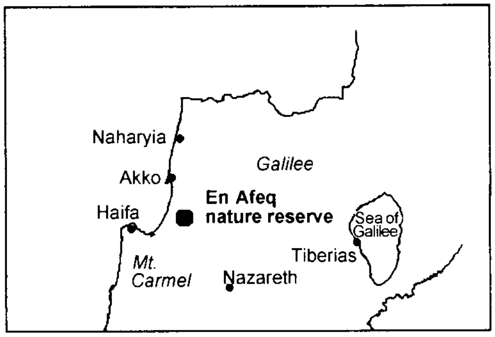
We are now conducting a pilot study of this approach in a selected Israeli nature reserve, the En Afeq Reserve in Western Galilee (Fig. 1).

The steps involve formulation of relevant management questions, decisions about data needed to answer these questions, data collection in the field, data bank management, data analysis, modeling and projection of trends, and GIS-based computerized projections (scenarios) for consequences from different management decisions.

Site description

En Afeq Nature Reserve is 66 ha in area, of which two-thirds are in wetlands and one third are dry, including the Tel Afeq archaeological site. The reserve has been roughly mapped into 11 habitat types (Fig. 1). En Afeq, only 4 km from the coastline, is the largest remaining freshwater

En Afeq in Northern Israel



Main habitats in En Afeq Nature reserve

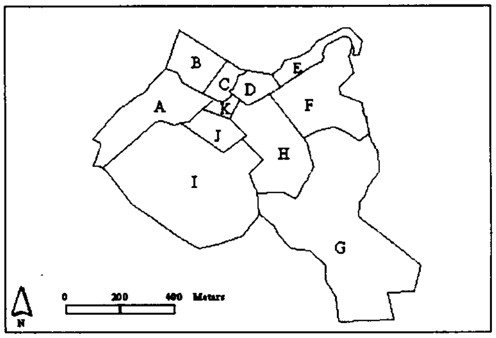


Fig. 1. Map of En Afeq. Habitats are marked by letter codes: A = Open woodland of pine and cypress; B = Western swamp with tamarisk; C = Two mill-pond pools; D = River terrace area; E = *Eucalyptus* woodland; F = Water meadow with buffalo grazing; G = Eastern swamp with freshwater springs; H = Lake; I = Tel Afeq dry grassland; J = Pine plantation; K = Office and other buildings.

wetland on the Israeli coast. The reserve is surrounded by agricultural fish ponds and fields, in the highly urbanized Zebulon Valley. En Afeq is quite small but very diverse. There is a Crusader fort/flour mill and mill pond system which still regulate the flow of water through the nature reserve, the ruins (*tel*) of a 4 000 year old Canaanite/ Israelite town (see Joshua 19:30 and Judges 1:31), and the freshwater springs which form the source of the Na'aman river.

En Afeq has a high conservation value because of its uniqueness, but is problematic because of its small area, heavy visitor pressure and vulnerability to extinctions, invasions, and pollution. Several management problems are recognized and dealt with actively (Table 1). The major problem in the reserve is loss of water flow during the last 50 years due to overpumping in surrounding areas. In the past, the discharge of springs on the Na'aman river was about 50-60 million cubic m/yr. Today only 10% of that is still discharged by the springs in the reserve. As a consequence, the wetlands and aquatic habitats have suffered from salinization. The average salinity of the Na'aman aquifer has doubled during the last 50 yr, and the salinity of the water in the nature reserve has increased correspondingly. Because of the salinization there has been an expansion of the halophytic *Tamarix* species and a loss of freshwater plant genera such as *Potamogeton* and *Nymphaea.*

Another major problem is related to grazing. The area has been grazed intensively over many decades, probably centuries, by Arab flocks and herds. When the reserve was established, grazing was initially excluded, but this resulted in severe encroachment by large annual thistles (*Notobasis syriaca* and *Silybum mariana)* which become dominant in the drier areas. Moderate cattle grazing under reserve management was quickly reintroduced to control these pest species in dry areas, and water buffalo were introduced experimentally as well to control these and other ruderal species in wetter areas. Although the grazing reduces the amount of thistles, other species become problematic. Hence a balanced grazing management has become important at En Afeq, and the appropriate type, level, and timing of management are problems to be studied in this project.

Methods

We have opted to use an analytical flow (Fig. 2) similar to that used in our Dutch field example at in the Drentse A (Schipper & Streefkerk 1993) with some modifications. We include one additional step: identification of goals.

Defining the problem

The first task in any conservation management problem is defining the goals. This has proven to be difficult since we often do not really know exactly what we want. We are sometimes exploring for options from which we can select the solution which 'looks' or 'feels' better, or the solution which is more pragmatic. In this case, goal definition may therefore work interactively with scenario projections which give us a 'picture' of our options.

En Afeq already has goals stated in a management plan, written in 1989, updated in 1996. In that document, the original goals were (1) 'preserving the structure and function of the habitats inside the declared reserve and the habitats along the Naaman river'. It gave tools to manage the reserve habitats but did not define the criteria to check whether the desired goals were achieved, nor did it define specific goals. It did state that one goal was (2) 'to determine the preferred character of the reserve, relying on past and present data' (but the original plan did not define what is 'past' and 'present' nor specify habitats). The original management plan also specified the need, (3) 'to prepare management and water monitoring procedures for the reserve' and the plan gave relatively specific instructions, but these were not updated in the last 10 yr and part of them are

Table 1. Management goals and tools for En Afeq.

Conservation goals
1. To represent the former extensive swamp landscape, species and dynamics as much as possible
2. To maximize biodiversity
3. To create and maintain high aesthetic value
4. To protect rare and valued species
5. To maintain low habitat fragmentation
6. To maintain ecosystem structure and function integrity
7. To restore and maintain naturalness of the landscape
8. To heighten environmental awareness in the public

Management tools and the goals they serve
1. Data collection (survey and monitoring, research projects): all goals
2. Reintroduction of former plant and animal species: goals 1, 2, 4 and 7
3. Creation of planted buffer zones: goals 3, 5 and 7
4. Water input from outside to reduce salinity: goals 1, 2, 3, 6 and 7
5. Stopping input of polluted water in order to reduce eutrophication: goals 1, 2, 3, 4, 6 and 7
6. Grazing management: use of cattle and water buffalo under regulated conditions: goals 1 and 2
7. Fire prevention: goal 3 (Note: The relevance for other goals must be tested.)
8. Population control of problematic species: tamarisk, fish, blackberry: goals 1, 2, 3, 4, 6 and 7
9. Improvement of public access: goal 8
10. Creation and maintenance of a public education center: goal 8

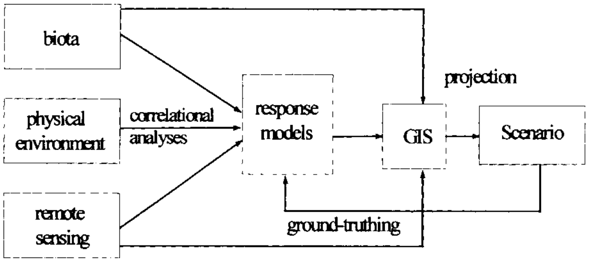


Fig. 2. Flow chart for creating scenarios.

no longer relevant. Also, the original plan did not address some current issues such as environmental awareness, public pressure and tourism, and development of public facilities.

In this study we are trying to be less vague than the existing management plan, and to adapt its goals to present conditions, needs and abilities. In En Afeq we have a particular problem in defining our goals since the landscape is anthropogenic (Forman 1995), pristine conditions are unknown, and restoration raises the question 'what past landscape do we want?' Rather than use the primeval condition as our goal, we must identify a set of conservation values which can be realized in a man-influenced environment.

In the process of our study, a small group of conservation biologists familiar with the reserve and its history attempted to itemize our goals via expert opinion. These first efforts are presented in Table 1. As we gain familiarity with modeling conservation management, and cooperation with our Dutch colleagues continues, the identification of quantifiable, useful conservation goals should improve.

Data collection

Initially we must rely heavily on expert opinion of staff members in the NNPPA and our associates to guide the definition of the ecosystems and their dynamics in En Afeq. So far we have been gathering expert opinion on vegetation and hydrological patterns and dynamics in a series of staff meetings and interviews with professionals in these fields. As data accumulate, the expert opinion on trends in vegetation in response to driving factors and management manipulations can be tested.

Nearly all the goals and management tools described in Table 1 involve manipulations of vegetation, which in turn drive the dynamics of animal populations and communities. Therefore, data collection for this study is currently oriented towards vegetation and factors affecting vegetation. Surveys were and are being done on topography, hydrology, and vegetation. Monitoring of weather and grazing are being done as well. Details of these studies are described in a companion article (see Olsvig-Whittaker et al. 1999).

Data analysis

Both statistical correlation analyses and deterministic models are being used as analytical tools in this study. Correlation of vegetation with the physical environment and grazing is currently being done by use of CANOCO's direct ordination methods (ter Braak 1987) and other forms of multivariate analysis.

The correlations determined by vegetation analyses are part of the information being used to develop a deterministic model for response of vegetation and selected plant species to grazing. This model is currently being developed by two of our Dutch graduate students using the Fortran Simulation Translator (C. Rappoldt and D.W.G. van Kraalingen, 1996). The model will be ground-truthed during the coming year. If successful, the predictions from the grazing model will also be used to drive the GIS-based scenarios.

Scenario modeling

Once adequate data bases are created and correlational analyses are completed, landscape responses to basic changes in environmental factors can be modeled. For mathematical projections, the polygons are converted to a raster system of cells with state variables. Changes in driving variables derived from the correlational studies will alter the status of raster cells in a stepwise fashion, mainly to conform with the needs of mapping (Star & Estes 1990; Chou 1997). The changes can then be uploaded to ARC-INFO (Anon. 1996) again for mapping the new status of the cells, the scenario.

The main environmental driving factors (salinization, periodic desiccation, *Tamarix* invasion, grazing intensity) will be modeled one by one. Landscape scenarios consequent on extreme values in these driving factors will be compared in an initial, exploratory stage.

Evaluation

Once extremes are estimated, combinations of more moderate management practices are compared. A set of scenarios are produced which can be evaluated (cf. Harms et al. 1993). We will develop semi-quantitative value scales for different states of the environment for conservation goals such as biodiversity, stability, connectivity of the landscape, ecosystem function, protection of rare species, etc. Once we have these scales, we will weight each scenario outcome according to the values assigned to it for each conservation goal.

We will begin by using the expert opinion-based conservation evaluation strategy used by the NNPPA, assigning qualitative values for different scenario outcomes (essentially an intuitive vote by experts). If the current evaluation system is not adequate for assigning values (as is likely), we must improve it in by consultation with other conservation organizations such as the Dutch State Forestry. Given several scenario 'pictures', we rank based on a semi-quantitative system (see Harms et al. 1993). For example, if we have 20 possible scenarios, we can 'score' them according to their contribution to our conservation values as 'good' or 'bad'.

Once a management plan is agreed upon and implemented, the scenario models can be compared to the actual consequences of the management. In The Netherlands, the situation on the ground is compared to the scenario approximately every five years. This kind of 'ground-truthing' for the model can be used to better guide the management as it becomes more refined.

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The impact of wetland restoration on the fen vegetation of Lake Hohn, northern Germany

Rixen, Christian & Trepel, Michael

Ecology Research Centre, University of Kiel, Schauenburger Strasse 112, D-24118 Kiel, Germany;
Fax +494318804083; E-mail rixen@fpsrv.slf.ch

Abstract. Essential factors in wetland restoration are water level and groundwater quality. To support and preserve the vegetation of a nutrient-poor fen (*Caricion nigrae*) in the Lake Hohn area, Northern Germany, the water level was increased so that floods occur in winter. Fertilization of surrounding farmland was stopped in 1991.

In seven years the vegetation developed from *Lolio-Potentillion* and *Cynosurion* to *Magnocaricion*, *Caricion nigrae* (a frame community) and *Calthion*. There is also a shift from former *Caricion nigrae* to *Magnocaricion* and *Phragmition* communities. The species composition of the newly established and the older *Caricetum nigrae* is different. Only the older stands include indicators of mesotrophic soils such as *Sphagnum* spp., *Pedicularis palustris* and *Succisa pratensis*.

According to an analysis of biomass, soil and groundwater composition the mire can be characterized as a poor fen. The low-productive vegetation is phosphorus-limited due to the influence of rain water. However, inundation of P-rich lake water may turn the poor fen into a fluviogenous fen with tall-growing *Magnocaricion* vegetation.

Nutrients have traditionally been removed by cutting, crop removal and grazing. High water levels prevent the use of machines and result partly in an undesired abandonment. Moderate rising of the water level and a consequent cutting and grazing regime are discussed as the optimal solution.

Keywords: *Caricetum nigrae*; Groundwater composition; Hydrology; Impoverishment, Nutrient; *Pedicularis palustris*; Phosphorus availability; Renaturation; Rewetting.

Introduction

Fens in central Europe have been damaged by drainage and fertilization in the last decades and centuries (e.g. Succow 1988; Pfadenhauer & Klötzli 1996). As a result, hydrology, chemical and physical soil properties are altered, sometimes irreversibly (Eggelsmann 1990).

In recent years much effort has been made to restore fens and their characteristic vegetation. The success depends on the level of peat degradation, water levels, the quality of ground- and surface water, seed banks and the utilization regime. Restoration measures can vary between discharge fens fed by calcium-rich groundwater and recharge fens influenced either by rainwater or by river water (Koerselman & Verhoeven 1995).

In this paper we focus on a fen receiving partly rain water and partly river water but actually not any calcium-rich groundwater. The hydrology causes a transition in plant cover from low-growing poor fen vegetation (*Caricetum nigrae*) to tall-growing rich fen vegetation with tall sedges like *Carex acuta* and reeds as *Phragmites australis* and *Glyceria maxima*. The aim of this study is to show the reaction of the vegetation to an altered water regime and to assess changes of water quality and soil properties.

The study area

The Lake Hohn area is a nature reserve situated in Schleswig-Holstein, Northern Germany, in the extensive wetland system of the rivers Eider, Treene and Sorge. The area displays characteristics of an oceanic climate with 847 mm mean annual rain fall and an average annual temperature of 8 °C. It is surrounded by bogs and moraines formed by the Saale glaciation.

The lake is shallow with a maximum depth of 1 m. The lake water is rich in nutrients, especially phosphorus, due to a former wastewater inlet from a nearby village and to P-leaching by peat mineralization from a neighbouring drained bog. The high nutrient content of the water effects a rapid terrestrialization of the lake. The water drains off through the small river Rinne.

The surrounding organic soils consist of mud deposits, fen peat and bog peat depending on the distance from the lake or the bog. The fens and wet meadows have been cultivated partly intensively and partly moderately by late mowing and grazing. Central parts of the fen have never been artificially fertilised.

Depending on soil, water level and cultivation intensity different vegetation types have developed: tall growing reeds and tall sedges under very wet conditions (*Phragmition* and *Magnocaricion*), stands with low sedges in moderately wet and cultivated sites (*Caricion nigrae*) and high productive *Lolio-Potentillion* and *Cynosurion* communities where utilization has been more intense.

The restoration project

From 1986 to 1991 restoration measures were conducted with the following aims:

- Conservation and improvement of the endangered flora and fauna of wetlands – rare fen plants, waders and water fowl;
- Creation of floodings similar to the natural regime before embankments and drainage at the beginning of the 20th century;
- Reduction of the nutrient content of the lake water in order to delay rapid terrestrialization.

To achieve the targets, fertilization of the meadows was stopped and the utilization was reduced to a moderate level with grazing and cutting, where it was possible. The water level was increased by a dam in the river about 50 cm in the summer and 80 cm in the winter. This leads to a water table little below the surface of the central fen part and to floods. The wastewater inlet into the lake from the village was ceased.

Methods

Vegetation survey

The plant communities of the nature reserve were mapped in 1987 (Koelbel 1995) and remapped in 1997. Additionally different types of the *Caricion nigrae* have been analysed regarding species composition and chemical characteristics (content of N and P). These types included stands with *Sphagnum*, *Molinietalia* and with *Magnocaricion* species.

Hydrology and soil

A transect with seven sample sites was established from the river through the central fen part up to the elevated margin (Fig. 1). Groundwater tubes (piezometers) were placed along this transect in the depth of 50 cm. Water was sampled in spring, summer and fall and analysed for the nutrients nitrogen, phosphorus and potassium. Soil samples were taken in late summer from each horizon to a depth of 2 m and analysed for pH and C:N ratio.

Results

Vegetation changes

The whole area has undergone vegetation changes with two major developments. Firstly, tall growing reeds, mainly *Glyceria maxima*, *Carex acuta*, *Phalaris arundinacea* and *Calamagrostis canescens*, could spread and establish due to higher water levels and a decreased utilization intensity. These species dispersed into former stands of *Caricion nigrae* and *Lolio-Potentillion*.

Secondly, *Caricion nigrae* stands have newly derived from former *Lolio-Potentillion* and *Cynosurion* vegetation, increasing the total covered area by twice as much as in 1987.

Analysis of the species composition of the *Caricion nigrae* stands that already existed before the rewetting and newly developed stands differed (Table 1). The older parts included types of the *Caricetum nigrae* with *Sphagnum* and *Molinietalia* species. Here, not only a reasonable number of stenoecious fen species can be found such as *Pedicularis palustris*, *Carex canescens* and *C. echinata*, but also *Molinietalia* species as indicators of nutrient-poor soils (e.g. *Succisa pratensis*).

The younger stands mainly consist of euryoecious fen species such as *Carex nigra*, *Carex* × *elythroides* and *Agrostis canina* and show floristic similarities to *Magnocaricion* communities. Due to a lack of species characteristic of the *Caricetum nigrae* this vegetation type represents a *Caricion nigrae* frame community.

Hydrological and pedological characteristics

The pH in soil and water along the transect indicates a lens of precipitation water in the upper horizons of the fen leading to acidic conditions (e.g. Grootjans 1985; van Diggelen et al. 1991), which is typical of the centre of an acid-poor fen. The C:N ratio of the soil in most horizons ranges between 10 and 15, pointing to a strongly humified peat in all parts of the fen.

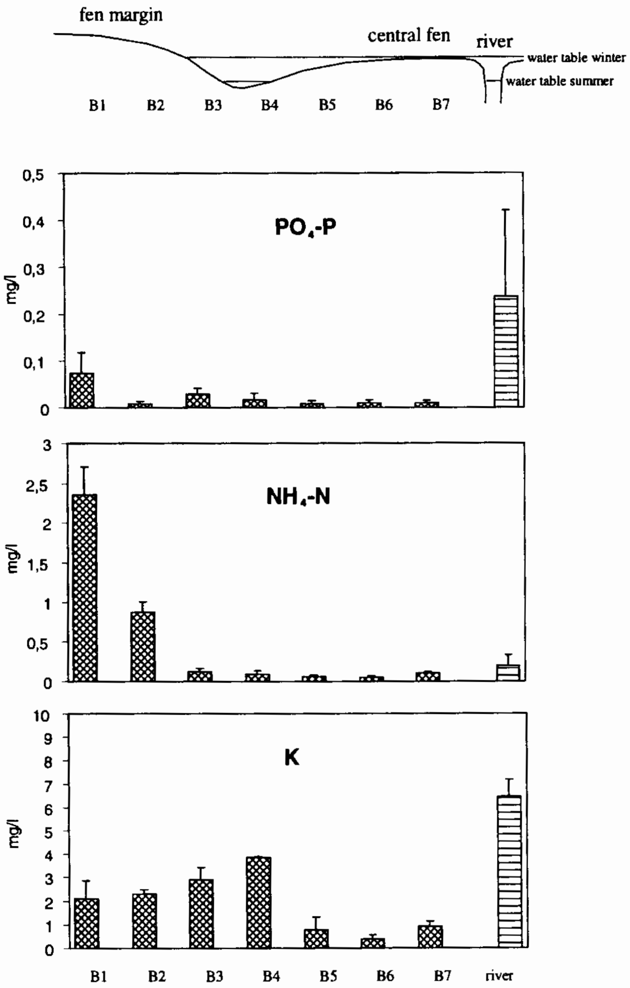

Fig. 1. Nutrient content in the groundwater (50 cm deep) and river water: transect from the fen margin through a wet depression along the central fen part to the river (average and standard deviation).

The major nutrients also show a characteristic pattern along the transect (Fig. 1). The phosphorus concentration in the river water is high with more than 0.2 mg PO_4-P/l. In the groundwater of most parts of the fen this concentration is relatively low, while it is slightly higher in the wet depression and high at the fen margin. The NH_4 content is lowest in the fen parts with the highest water levels and only high at the fen margin where the water table falls more than 50 cm below the surface. The K-concentration is very high in the river water, low in the central fen part and high again in the wet depression and at the fen margin.

These results indicate that the managed high water level can reduce mineralization of the peat but also that the floodings could have increased the input and solubility of P and K. The river and lake water quality has not yet im-

Table 1. Species composition of different types of the *Caricion nigrae*. Average species numbers from the communities *Scheuchzerio-Caricetea* (S-C), *Molinio-Arrhenateretea* (M-A) and *Phragmitetea* (Ph).

	S-C	M-A	Ph
Caricetum nigrae with *Sphagnum*	11	8	1
Caricetum nigrae with *Molinietalia* species	9	10	2
Caricion nigrae frame community	4	3	3

proved since the beginning of the restoration measures.

Chemical analysis of the biomass from *Caricion nigrae* communities points to different nutrient limitations (Table 2). Only the type with *Sphagnum* species shows an N:P ratio of more than 15, indicating a phosphorus limitation (Koerselman & Meuleman 1996). The N:P ratios of the other vegetation types are around 15 or below suggesting an NP co-limitation or an N-limitation.

Consequently the P-limitation of a main target vegetation type could be lifted by the floodwater. On the other hand an increased influence of precipitation water in the upper horizons could also result in nutrient impoverishment. Thus, two contradictory hydrological scenarios exist depending on the managed height of the water table.

Discussion and Conclusions

Consequences for the vegetation

The vegetation development in the Lake Hohn area is at the present time in a fragile state. In many places the drier fen parts have not yet been sufficiently impoverished by crop removal so that many of the endangered target species could not establish so far. In the wetter fen parts these species decreased.

Abandonment is probably a major factor for vegetation changes in many of the fen meadows. Although there has always been a nutrient input by floodings during the last centuries, biomass was harvested regularly which resulted in an impoverishment supporting *Caricetum nigrae* vegetation. Additionally disturbance by man and cattle could preserve gaps in the plant cover for low-competitive species (e.g. Grime 1979). In many years the very wet conditions prevent both the use of machines and the grazing of cattle. Thus tall-growing species with clonal growth absorb incoming nutrients without losing them through mowing. They replace low-growing species that depend on frequent germination in vegetation gaps.

A crucial point for the survival of the fen species is their dispersal towards the more elevated fen parts. All target species are still present in the actual vegetation until now, so there is a possibility for dispersal. In the case of *Pedicularis palustris* most individuals grow in wet localities that are hardly reached by cutting in wet years. So far, this species was not yet able to spread out effectively.

The challenge for the next years will be to impoverish the soil effectively and to spread diaspores to enhance establishment of the target species. Until that point the conservation of the plant populations has to be assured.

Table 2. Phosphorus and nitrogen content and N:P ratio in biomass of different types of the *Caricion nigrae*. Phosphorus and nitrogen concentrations are shown for 11 July (normal mowing time) and for four different sampling times from 21 May to 22 August (in brackets). The average N:P ratio and the standard deviation (in brackets) represent the sampling times.

	mg P/g drw	mg N/g drw	N:P ratio
Caricetum nigrae with *Sphagnum*	0.7 (1.4 – 0.7)	18.1 (26.6 – 21.8)	25.8 (6.5)
Caricetum nigrae with *Molinietalia* species	1.0 (1.5 – 0.7)	18.4 (47.7 – 17.8)	16.4 (2.9)
Caricion nigrae basic community	1.3 (3.2 – 1.2)	13.4 (29.4 – 11.2)	8.6 (1.8)

Consequences for the hydrological regime

As shown, poor fens can be sensitive to rewetting depending on the hydrology. In this case not only the direct nutrient input by the floodings is a problem to deal with but also the higher P-solubility in the soil. The decreasing redox potential can lead to an increase in pH and to an increased P-solubility as shown for the mostly inundated depressions (cf. Caraco et al. 1989; Vermeer & Joosten 1992; Koerselman & Verhoeven 1995). The hydrology in this fen is different from rich fens with Ca-rich groundwater, where the Ca-ions can bind P (Wassen & Barendregt 1992). Still, the acidification of fens can also have been caused by a lowering of the water table during the last centuries (Schot & Molenaar 1991). However, peat mineralization and N-release from the peat can be delayed with high water levels and a low redox potential as indicated with NH_4^+ contents within the transect (Grootjans et al. 1985). On the other hand also increased NH_4^+ concentrations have been observed after rewetting in the topsoil (Eschner & Liste 1995).

The specific hydrology results in a fragile balance between a poor fen fed by rain water and a fluviogenous fen dominated by lake water. Depending on the management, the fen can easily develop to one or the other side.

Implications for nature management

This project deals with an appropriately managed water level in order to reach the restoration targets. Besides the water chemistry, the utilization regime is crucial for vegetation development. Consequently the water level should be risen carefully. First of all an impoverishment by regular grazing and cutting should be achieved, which can take up to 10 yr before sufficient results are reached (Pfadenhauer & Klötzli 1996). Secondly, species should be dispersed and the water level has to be risen. In a fragile system as a cultivated poor fen, rewetting is easily overdone. Further time and research is needed to find out whether species like *Pedicularis palustris* and many other fen and wet meadow species (Schrautzer et al. 1996) manage to spread out from recent populations by themselves or if measures such as sowing or transplanting are necessary to preserve them from extinction.

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The quaking mire vegetation of Latvia

Salmina, Liene

University of Latvia, Department of Botany and Ecology
Kronvalda blvd. 4, LV-1586 Riga, Latvia;
Fax +371 7820113; E-mail lsalmina@com.latnet.lv

Abstract. Mire development due to lake terrestrialization is a common process occurring throughout Latvia. Mires of this kind of origin dominate in strongly hilly regions such as the Central Vidzeme and South Latvia geobotanical regions. The study lakes represent a group of small lakes, where, in the process of terrestrialization, mainly quaking mire vegetation has developed. The small size and depth, the lowering of the water table of the study lakes have favoured terrestrialization. The studied quaking mire vegetation includes the associations *Caricetum rostratae*, *Caricetum lasiocarpae*, *Caricetum limosae* and *Carici-Menianthetum*. The *Carex rostrata* community was the most common plant community in the filling-in lakes. The *Carex lasiocarpa* and *Carex- Menianthes trifoliata* communities were bordering open water, while the *Carex rostrata* plant community was found more landwards. The vegetation data was treated using the computer programme TURBO(VEG) (Hennekens 1995).

Keywords: Lake terrestrialization; Mire plant community; Synoptic table.

Nomenclature: Tabaka et al. (1988) for vascular plants; Smith (1993a, b) for bryophytes.

Introduction

Mire formation by terrestrialization of lakes is present throughout Latvia. Mires of this kind of origin dominate in the Central Vidzeme and in the South-East Latvia due to hilly relief with many lakes in these areas (Tabaka et al. 1990). Different mire communities can be distinguished in filling-in lakes. Mire vegetation of a number of filling-in lakes in Latvia was studied in 1995/1996 (Pakalne et al. 1996) and it was concluded that the filling-in lakes could support large species and plant communities diversity even if they were of small size. In areas where other mire types do not occur, these habitats are the only left for many rare mire plant species (Susko 1997). Still the quaking mire vegetation of Latvia is imperfectly known.

The aim of the study was to obtain information about the quaking mire vegetation in Latvia.

Study area

The study area is located in northeast Latvia, in the Central Vidzeme geobotanical region (Fig. 1), about 125 m a.s.l. (Kabucis 1995), 57° 30'N, 26° 00'E, on the northeast slope of the Vidzeme Upland. Geologically the study area is represented by morain hills and a morain plain formed by sandy fluvioglacial sediments. According to the FAO classification the dominating soil types in the study area are eutric gleysols and mollic gleysols in relief depressions and eutric podzoluvisols on relief elevations (Nikodemus 1998). The height above sea level causes special climatic features in the Vidzeme Upland. The climate is considered to be the coldest in Latvia. It is characterized by long and severe winters, a short frost-free period (less than 120 days) and a low effective temperature sum (1800 °C) (Tabaka et al. 1990; Laasimer et al. 1993; Aboltins 1995). The mean annual temperature is 4.0° - 4.5 °C and the mean annual precipitation 600 mm/yr. There are almost no raised bogs in the study area. Quaking mires of filling-in lakes dominate in this geobotanical region (Tabaka et al. 1990).

Methods

Quaking mire vegetation of filling-in lakes was studied in northeast Latvia, in the Central Vidzeme geobotanical region (Tabaka et al. 1990), in the Vidzeme District of Spruce Forests according to Laasimer (Laasimer et al. 1993) (Fig. 1). To describe mire vegetation of filling-in lakes relevés of 1 m × 1 m size were made in floristically homogeneous plots. The Central European mire classification approach (Dierssen 1982) was used to distinguish and classify mire vegetation of filling-in lakes. For mire vegetation analysis computer programme TURBO(VEG) (Hennekens 1995) was used. Altogether 199 relevés were analysed.

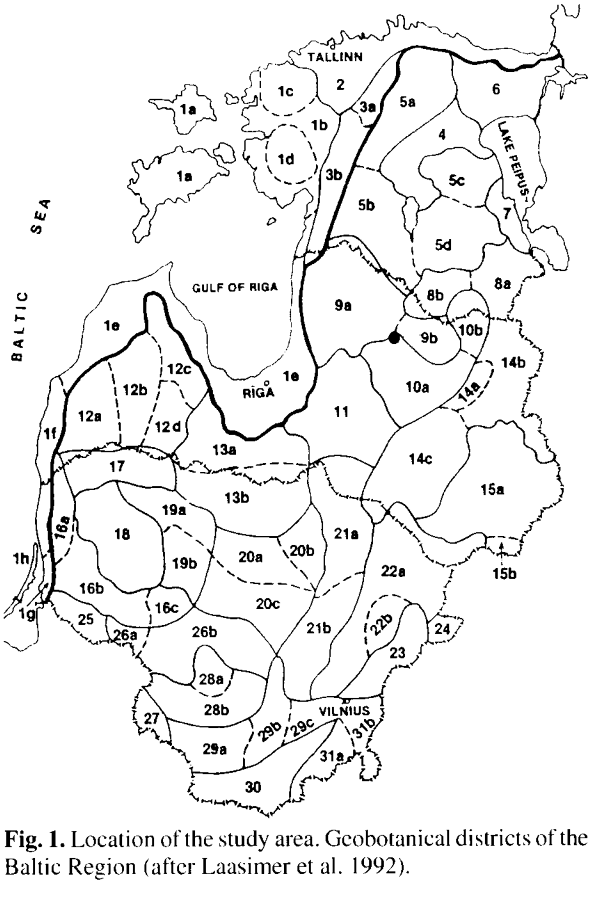

Fig. 1. Location of the study area. Geobotanical districts of the Baltic Region (after Laasimer et al. 1992).

Lake classification

According to earlier lake classifications (Mäemets 1974; Leinerte 1988) the study lakes belong to dystrophic, dyseutrophic and hypereutrophic lake types. Dystrophic lakes are characterized by low water transparency ca. 1 m), brown water colour, accumulation of humic substances and species-poor vegetation. The origin of the humus is the surrounding forests on peat soils or bogs. After the leakage of nutrient rich waters into dystrophic lakes and consequently the accumulation of both the organic and humic substances, lakes are classified as dyseutrophic. In hypereutrophic lakes the water is oversaturated with nutrients and the accumulation of organic substances is very rapid.

Results

Lake characteristics

The studied lakes belonged to dystrophic, dyseutrophic and hypereutrophic lake types (Susko pers.comm.). Most of the studied lakes were small and shallow. The area of four study lakes did not exceed 1 ha and the areas of four other lakes were between 1 and 5 ha. The largest were Kalmodu (18.9 ha) and Cepla (10.4 ha) (Table 1). The maximum depth of the lakes varied between 1 m in Bezdibinis and Podinu lakes to 6.4 m in Cepla Lake (Table 1). The water colour was brown in all the lakes because of the accumulation of humic substances. Therefore the water transparency was rather low – up to 1 m even in the deepest Ceplu Lake. Only two lakes were located on the forest edge, the rest were completely surrounded by coniferous forests (Susko pers. comm.).

Vegetation characteristics and structure

The studied vegetation represented quaking mire vegetation formed in the process of lake terrestrialization. Mainly treeless transition mire vegetation was found in the studied filling-in lakes. In some lakes reed beds were present. The shrub layer occurred in two of the studied sites. The well developed quaking *Sphagnum* carpets with loose to dense, medium-high stands of sedges and other helophytes characterized the vegetation structure. Different vegetation fringes bordering open water can be distinguished (Fig. 2), where often aquatics and brown mosses were observed. Species-poor to moderately species-rich vegetation.

The plant communities

Four transition mire plant communities were distinguished in the studied filling-in lakes and according to the Central European mire classification approach (Dierssen 1982, Pott 1992) assigned to the associations *Caricetum rostratae* Osvald 1923 em. Dierssen 1982, *Caricetum lasiocarpae* Osvald 1923 em. Dierssen 1982, *Caricetum limosae* Osvald 1923 em. Dierssen 1982 and *Carici-Menianthetum* Sóo 1955.

The Carex limosa community

A plant community with *Carex limosa* was described only in Podinu Lake, where it covered the main fen area. Because of the dystrophic type of the lake (Table 1), the species-poor vegetation dominated there. Only 14 plant species were recorded in this plant community. *Carex limosa, Calla palustris* and *Scheuchzeria palustris* were the most common species in the herbaceous layer and *Sphagnum flexuosum* was the dominant moss species.

Table 1. Characteristics of the studied filling-in lakes (Susko pers. comm.). In all lakes the water level was lowered except Klievzers where the change was unclear. In Tela fishing caused some extra nutrient supply, while in Zummers and Klievezers this was caused by recreation.

Lake and its vegetated area (%)	Size (ha)	Max. depth (m)	Lake type	Species number
Podinu (5)	0.59	1.0	Dystrophic	14
Ceplu (20)	10.4	6.4	Dyseutrophic	18
Askina (100)	0.13	1.7	Hypereutrophic	21
Babenis (25)	0.30	1.9	Dyseutrophic	22
Melluzis (36)	1.19	1.7	Dyseutrophic	18
Bezdibinis (~100)	0.5	1.0	Hypereutrophic	32
Tela (23)	2.13	3.8	Dyseutrophic	36
Zummers (14)	1.2	3.1	Dyseutrophic	40
Kalmodu (90)	18.9	1.5	Hypereutrophic	43
Klievezers (~100)	3.16	1.0	Hypereutrophic	50

The Carex-Menianthes trifoliata community

The plant community with *Menianthes trifoliata* was distinguished bordering open water in Askina Lake. The conspicuous cover of *Menianthes trifoliata* characterized this plant community. Associates were *Carex lasiocarpa, Carex limosa* and the moss layer included mainly *Sphagnum flexuosum* and *S. fallax*. The *Carex rostrata* community occupied the rest of the quaking mire area.

The *Carex rostrata community*

The *Carex rostrata* plant community was present in all the studied filling-in lakes and covered the largest quaking mire areas located more landwards from the open water. Species composition was characterized by *Carex rostrata* as dominant species. The most common associates were *Comarum palustre, Menianthes trifoliata, Oxycoccus*

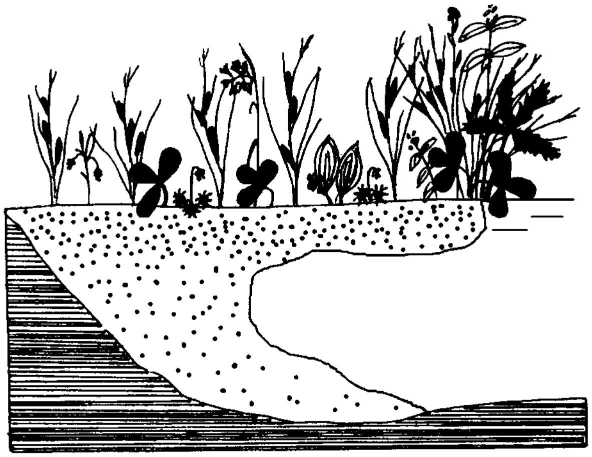

Fig. 2. Profile of the studied filling-in lakes.

palustris, Calla palustris, Carex limosa and *Drosera rotundifolia.* The moss layer was represented by various *Sphagnum* species, mainly by *Sphagnum flexuosum* with small patches of *Sphagnum contortum, S. teres, S. squarrosum, S. angustifolium* and *S. palustre.* (Table 2). The brown moss species *Calliergon stramineum* was observed among the *Sphagnum* species in most of the studied sites. In three studied sites *Chamaedaphne calyculata* was growing, which is a characteristic species of raised bogs and transition mires in eastern and central Latvia. Three rare and protected species in Latvia were found within the *Carex rostrata* community – *Betula nana, Hammarbya paludosa* and *Galium trifidum.* The mean species number in the *Carex rostrata* community was 19.8.

The Carex lasiocarpa community

The *Caricetum rostratae* was separated from open water by a narrow (ca. 1 m) fringe vegetation, where *Carex lasiocarpa* dominated. A *Carex lasiocarpa* community was distinguished here. Besides the different mire plant species also aquatics like *Nuphar pumila, Nymphaea candida* and *Potamogeton natans* were present. In comparison with the studied *Carex rostrata* community, the following plant species: *Cicuta virosa, Scutellaria galericulata, Peucedanum palustre, Galium trifidum, Thelypteris palustris* and *Eriophorum gracile* were more frequent (Table 2). Common associates were *Menianthes trifoliata, Comarum palustre* and *Carex rostrata.* The moss layer was formed mainly by *Sphagnum flexuosum.* Brown mosses like *Calliergonella cuspidata, Calliergon giganteum* and *C. cordifolium* were recorded mainly in this plant community. A different *Carex lasiocarpa* community was found in the Klievezers Lake. In comparison with the other studied *Carex lasiocarpa* communities this one occupied a large area more landwards in contact with the lake banks and was more species rich. The well-developed shrub layer included the following species: *Salix rosmarinifolia, S. pentandra, S. lapponum* and *S. cinerea.* 33 plant species were found, including *Carex lasiocarpa, C. limosa, C. chordorhiza, Menyanthes trifoliata, Comarum palustre, Equisetum fluviatile* and *Oxycoccus palustris* as the most frequent ones. Species richness was supported by diverse moss species. Together with *Sphagnum warnstorfii* and *S. flexuosum* also *Rhyzomnium punctatum* and *Aneura pinguis* were growing there. Rare and protected plant species in Latvia *Galium trifidum* and *Dactylorhiza maculata* were recorded within this plant community. The mean species number in the *Carex lasiocarpa* community was 23.5. *Carex rostrata* and *Carex lasiocarpa* communities were distinguished on mineral substrate in Kalmodu Lake as well, supported by species such as *Nuphar luteus, Comarum palustre* and *Potamogeton natans.*

Table 2. Synoptic table of the studied mire vegetation. 1 = *Caricetum rostratae*; 2 = *Caricetum lasiocarpae*; 3 = *Caricetum limosae*; 4 = *Carici-Menianthetum.* *Only the most important plant species are listed.

Syntaxon Number of relevés	1 112	2 74	3 8	4 5
Ch1 *Carex rostrata*	V^{2}	III^{1}	.	.
Ch2 *Carex lasiocarpa*	+^{1}	V^{2}	.	V^{2}
Ch3 *Carex limosa*	II^{1}	II^{1}	V^{5}	IV^{1}
Ch4 *Menyanthes trifoliata*	II^{3}	I^{4}	.	V^{5}
Class Scheuchzerio – Caricetea nigrae				
Carex canescens	I^{1}	II^{1}	II^{1}	.
Viola palustris	r^{1}	.	.	.
Order Scheuchzerietalia palustris				
Scheuchzeria palustris	II^{1}	r^{1}	II^{1}	II^{1}
Alliance Caricion lasiocarpae				
Comarum palustre	II^{2}	V^{3}	.	I^{1}
Equisetum fluviatile	r^{1}	I^{1}	.	.
Calliergon stramineum	III^{1}	II^{1}	.	.
Aneura pinguis	.	r^{1}	.	.
Eriophorum angustifolilium	I^{1}	I^{1}	.	.
Bryum pseudotriquetrum	.	+^{1}	.	.
Carex diandra	r^{1}	+^{1}	.	.
Calliergon giganteum	.	+^{1}	.	.
Calliergonella cuspidata	.	r^{3}	.	.
Eriophorum gracile	r^{1}	+^{1}	.	.
Class Phragmitetea				
Typha latifolia	+^{1}	II^{1}	.	I^{1}
Lycopus europaeus	r^{2}	I^{1}	.	.
Calliergon cordifolium	.	r^{1}	.	.
Phragmites australis	r^{1}	r^{1}	I^{1}	.
Order Magnocaricetalia				
Alliance Magnocaricion				
Naumburgia thyrsiflora	+^{1}	III^{1}	.	.
Peucedanum palustre	II^{1}	II^{1}	.	I^{1}
Scutellaria galericulata	+^{1}	I^{1}	.	.
Cicuta virosa	+^{1}	II^{2}	.	.
Calamagrostis canescens	.	r^{1}	.	.
Other species				
Calla palustris	III^{2}	III^{4}	IV^{2}	I^{1}
Oxycoccus palustris	V^{2}	III^{2}	I^{1}	V^{1}
Sphagnum flexuosum	V^{65}	V^{26}	V^{43}	V^{39}
Sphagnum fallax	+^{7}	+^{11}	III^{1}	I^{3}
Sphagnum angustifolium	+^{25}	+^{22}	I^{1}	I^{1}
Nuphar pumila	r^{2}	r^{2}	.	IV^{1}
Potamogeton natans	r^{1}	I^{1}	.	I^{1}
Drepanocladus aduncus	r^{1}	r^{1}	II^{1}	.
Lemna minor	.	I^{1}	.	.
Nymphaea candida	.	+^{1}	.	I^{1}
Thelypteris palustris	r^{2}	I^{2}	.	.
Drosera rotundifolia	III^{1}	I^{1}	.	.
Eriophorum vaginatum	I^{1}	.	I^{1}	.
Stellaria palustris	r^{1}	I^{1}	.	.
Hammarbya paludosa	r^{1}	.	.	.
Sphagnum teres	r^{1}	r^{1}	.	.
Sphagnum magellanicum	r^{2}	.	.	.
Carex chordorrhiza	.	I^{1}	.	.
Salix rosmarinifolia	.	+^{1}	.	.
Dactylorhiza maculata	.	r^{1}	.	.
Sphagnum palustre	r^{12}	.	.	.
Salix pentandra	.	r^{1}	.	.
Salix lapponum	r^{1}	+^{1}	.	.
Rhynchospora alba	r^{1}	.	.	.
Chamaedaphne calyculata	I^{2}	.	.	.
Sphagnum contortum	r^{55}	.	.	.
Betula nana	r^{1}	.	.	.
Andromeda polifolia	+^{1}	I^{1}	.	.
Campylium polygamum	.	r^{2}	.	.

Discussion

Terrestrialization *(Verlandung)* is taking place in all the water bodies (Succow & Jeschke 1980). A large number of factors like lake depth, size, size of the catchment area etc. has the influence on lake development (Leinerte 1988; Rieley 1990). The small size and depth of most of the studied lakes (Table 1) (Susko pers.comm.) are good preconditions for lake terrestrialization (Leinerte 1988). The surrounding forests prevent the rapid inflow of above ground waters from the catchment area into lakes and consequently the enrichment of lakes (Leinerte 1988). The influence of other factors towards the terrestrialization predominates. The high percentage of the vegetated area in three lakes (Bezdibinis, Askina and Klievezers lakes) (Table 1) can be explained by the small size and depth of these lakes, but in Kalmodu Lake – through the contact with agricultural land with the subsequent input of nutrient-rich water. All the lakes with the highest percentage of the vegetated area are of hypereutrophic type (Table 1). In four other lakes the vegetated area varies from 23 to 36%. Only 5% of the lake area are covered with vegetation in Podinu Lake despite of its small size (0.59 ha) and depth (1 m), because of the dystrophic type of the lake. Lake terrestrialization depends also on wind action (Leinerte 1988, Susko 1990). In small lakes, where the influence of wind is insignificant, the vegetation develops all around the lake as it was observed in all the small studied lakes. In the two largest Kalmodu and Ceplu lakes terrestrialization was most expressed on the most shallow lakeside sheltered from winds, because in large lakes the lakeside exposed to wind is washed out (Spuris 1958; Leinerte 1988; Rieley 1990) or in small bays or by the inflow of rivers and brooks. Lake terrestrialization is a natural process proceeding in lakes, still besides the natural succession of lakes, land drainage, leakage of nutrient rich water into lakes, fish baiting favour the lake terrestrialization (Susko 1997). In most of the studied localities land drainage with the following lowering of the water level was observed and in two lakes intensive recreation was taking place, which had influence on the lake development. There are rare and protected species in Latvia which distribution is closely related to filling-in lakes and quaking mires. The filling-in lakes can support rare and protected orchids such as *Malaxis monophyllos, Liparis loeselii, Epipactis palustris, Hammarbya paludosa* and *Dactylorhiza incarnata*. Two of the orchids like *Hammarbya paludosa* and *Dactylorhiza maculata* and two other rare vascular plants *Betula nana* and *Galium trifidum* are present in the study sites. A number of *Galium trifidum* and *Hammarbya paludosa* localities were recorded from filling-in lakes of southeast Latvia (Susko 1997). The distribution of *Betula nana* in Latvia is confined to large raised bogs and filling-in lakes mainly in the eastern and northern parts of Latvia. It is a relict species in Latvia and is recorded in many palinostratigraphic records. The species was common and widespread in all of Latvia during the Younger Dryas (Pakalne & Kalnina 1999). The rare aquatic species *Nuphar pumila* characterizes the studied lakes. *Nuphar pumila* occurs in dystrophic, dyseutrophic and even eutrophic lakes in the central and eastern Latvia and grows close to the southern limit of its distribution area (Fatare 1992). Transition mire, moderately rich fen vegetation and also bog vegetation can be found in the quaking mires of Latvia. The studied quaking mires include transition mire vegetation. The most species-poor vegetation occurs in the dystrophic Podinu Lake, where altogether only 14 species were recorded. The largest number of species was observed in the lakes Zummers, Klievezers and Kalmodu (Table 1). It may be explained by the lake enrichment due to recreation in Klievezers and Zummers (Table 1) and due to the location of Kalmodu in contact with agricultural land. The communities bordering open water are more species-rich than the communities located more landwards in filling-in lakes, because of the better nutrient supply due to direct contact with lake water (Zimmerli 1988). The species richness in the *Carex lasiocarpa* community bordering open water is larger than in neighbouring communities. Also there are species strongly confined to the fringe vegetation like *Cicuta virosa* and *Carex pseudocyperus*. Two other species – *Comarum palustre* and *Menianthes trifoliata* – grow in the open water bordering zone and also in neighbouring communities. The most vigorous specimens occur in the vegetation fringe close to open water, which reflects the influence of a better nutrient supply.

The vegetation located close to the lake banks represents more species-rich vegetation, which is also due to the influence of drainage water from the catchment area (Zimmerli 1988). It can be observed in Klievezers, where a species-rich *Carex lasiocarpa* community is found close to the lakeside with a well-developed shrub layer and small hummocks of *Sphagnum warnstorfii*. The *Carex-Menianthes* community characterizes the very beginning of the terrestrialization process in close contact with the lake banks and, at the later stages, separated from the lake banks by other mire communities, e.g. in Askina Lake. Although this community is found only in one of the study lakes, it is common and widespread in many other lakes of Latvia forming floating vegetation mats. The *Carex-Menianthes* community is recorded from mesotrophic lakes in Germany (Pott 1992), where it can start the lake terrestrialization similarly as in Latvia. The filling-in lakes are not the only habitats of *Carex limosa, Carex rostrata* and *Carex lasiocarpa* communities. There are similarities in species composition between the studied filling-in lake vegetation and vegetation in other mire sites in Latvia and in Europe.

The species composition of the studied filling-in lake plant community with *Carex rostrata* is very similar to that recorded from the bog margins in Latvia (Pakalne et al. 1996). In both cases *Carex rostrata* is the dominant species accompanied mainly by *Eriophorum angustifolium, Menianthes trifoliata, Drosera rotundifolia* and *Oxycoccus palustris*. In the moss layer *Sphagnum flexousum* dominates. It is also possible to find *Carex rostrata* community forming a narrow vegetation fringe around bog pools and lakes. In comparison with the studied ones it is a very species-poor community with *Carex rostrata* as dominant species accompanied by *Sphagnum flexuosum, S. magellanicum* and *S. cuspidatum* (Pakalne et al. 1996). Such species-poor *Carex rostrata* community in bog areas is known also from other places in Europe, e.g. in Britain (Wheeler 1984), Ireland (O'Connell et al. 1984). In Latvia the *Carex limosa* community is not restricted to filling-in lakes either. It can be found in bog hollows (Pakalne et al. 1996) associated with *Andromeda polifolia, Drosera rotundifolia, Scheuchzeria palustris* and *Sphagnum cuspidatum* and around bog pools with also *Carex rostrata*. The species composition of the *Carex limosa* community of Podinu Lake resembles that of quaking mires in Switzerland, where the *Caricetum limosae* subassociation with basiphobic *Sphagna*, sociation of *Sphagnum recurvum* ssp. *mucronatum* was distinguished (Zimmerli 1988). In both communities *Carex limosa* and *Scheuchzeria palustris* are accompanied by *Carex canescens, Oxycoccus palustris, Eriophorum vaginatum* and *Drepanocladus fluitans*. Still, there are differences between the communities. In Switzerland *Menianthes trifoliata, Drosera anglica, Carex rostrata, Drosera rotundifolia, Andromeda polifolia* and *Trichophorum cespitosum* occur, but in the studied Latvian community these species are missing. Instead *Calla palustris* is present in the Latvian *Caricetum limosae*.

Menianthes trifoliata, *Drosera rotundifolia* and *Carex rostrata* can be observed in the *Caricetum limosae* of other Latvian mires, but not *Trichophorum cespitosum*, which is found only in the coastal type of raised bogs in Latvia (Pakalne et al. 1996). In Latvia the *Carex lasiocarpa* community is floristically variable as in other countries (Dierssen 1982; Steiner 1993; Pott 1992). It can be distinguished in rich fens, transition mires and on mineral ground in lakes as well. The most species-rich *Carex lasiocarpa* community is found in the Coastal Lowland of Latvia, forming a rich fen system together with other rich fen communities such as *Schoenetum ferruginei* (Pakalne 1994). The studied *Carex lasiocarpa* community bordering open water is of a different type due to their physiognomy – it occupies only a narrow vegetation fringe and due to its species composition. The lack of characteristic rich fen speices, e.g., *Scorpidium scorpioides* and *Drepanocladus revolvens*, the presence of *Carex pseudocyperus*, *Cicuta virosa* and different aquatics, for instance, *Potamogeton natans*, and the sparse moss layer differs the *Carex lasiocarpa* community from those of rich fens and transition mires.

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Vulnerability of plant communities to breakup under global warming: An index of community integrity

Box, Elgene O.

University of Georgia, Geography Department, Athens, GA 30602-2502, USA;
Fax +17065422388; E-mail boxeo@arches.uga.edu

Abstract. Results from recent studies suggest that some familiar plant communities could be vulnerable to significant breakup under global warming, due to different responses of their main defining elements to changing environmental conditions. In order to assess the vulnerability of present-day plant communities to breakup, climatic envelope models were constructed for the main structural elements of some major plant communities (landscapes) of eastern North America, based on the main climatic factors which seem to be best correlated with their current boundaries. Potential changes in species ranges were then studied under plausible global warming scenarios, and an Index of Community Integrity was developed to estimate the changing patterns of community completeness and fitness of the main species. Only very preliminary results are presented here. The question is posed whether such a single-valued integrity index is in fact a useful tool for assessing community integrity and landscape vulnerability under changing environmental conditions.

Keywords: Beech-Maple Forest; Community breakup; Eastern North America; Envelope model; *Fagus grandifolia*; Index of Community Integrity; Species fitness; Vulnerability assesment.

Introduction

During the last Pleistocene glaciation, some plant communities and corresponding landscapes existed in eastern North America which have no present-day analogs, while some important present-day communities either did not exist or were at least not widespread (e.g. Delcourt & Delcourt 1985; Overpeck et al. 1991). The loss during the 20th century of *Castanea dentata* from Appalachian forests shows that, even today, plant communities which we recognize in the landscape may in fact not be entirely stable. Even if no plant community is stable in a strict sense, however, the overlapping ranges of species with similar physiological requirements and often similar physiognomy have resulted in species assemblages which have existed long enough to develop into the ecological and biogeographic units which we recognize today as major communities. Pollen records and other evidence of vegetation redevelopment since the last glaciation suggest that recognizable units similar to most of those of today, such as northern *Fagus-Acer* forest or southern *Quercus-Carya* forest, have existed for many centuries and probably millenia (e.g. Watts 1983).

Under global warming, the geographic ranges of many plant species are expected to shift, generally poleward and upslope. Different tolerance limits, and perhaps changes in the operative limiting factors, will cause co-existing species to respond differently to such changing conditions. If the main structural elements of plant communities do not migrate together, the potential exists for breakup of familiar present-day natural communities over much or even all of their present ranges. Communities do not have to be stable in order to be vulnerable to such breakup, since breakup in this sense represents much greater and faster instability than exists otherwise. Results from a recent study in Florida suggested that some familiar present-day plant communities could be greatly displaced and show significant degrees of area reduction, i.e. breakup, under global average warming of as little as 1 - 2°C (Box et al. 1999).

The possibility of significant community breakup suggests that measures may be needed to estimate the integrity of plant communities and their vulnerability under foreseeable climatic changes. Biological integrity normally implies a degree of wholeness but may also reflect the degree to which processes are functioning normally and main elements are well adapted to environmental conditions ('fitness'). Under global warming, plants will not only shift their locations but will also undergo changes in fitness across their ranges, with different species shifting in different ways. Community wholeness and member fitness may represent the best basis for studying vulnerability, since these concepts, taken together, permit:
(1) description of the potentially stable core areas of communities, where one may expect them to be best developed (main species most fit);
(2) identification of more transitional peripheral areas, which may be more vulnerable to perturbations (species less fit, some perhaps missing); and
(3) identification of environmental gradients which may suggest regions of particular vulnerability under environmental change.

The concept of ecological integrity is not new or old (cf. Frey 1975; Westra 1998). The MFI index (Measured Functional Integrity, cf. Loucks 1998) and IBI (Index of Biological Integrity, cf. Karr 1994) have been actively used in North America for some time. None of the integrity measures which have been presented, however, is designed for predictive use with changing environmental conditions, which may require calibration for large numbers of taxa over large areas. The purpose of this project is thus:
(1) to define a measure of community integrity based on data which could be readily available for large numbers of species, while still meeting specific ecological criteria; and
(2) to explore how such a measure may be used and what information it may provide in a particular situation involving a hypothetical but plausible warming scenario.

The region employed is eastern North America, from eastern Canada to central Florida, including the Appalachian Mountains. This paper presents an Index of Community Integrity, some simple results, and explores initially whether such a single-valued integrity index would be a useful tool in landscape management and vulnerability assessment.

Data and Methods

The basic methodology involves use of climatic envelopes, i.e. *n*-dimensional hyperspaces defined by the putative upper and lower tolerance limits of biological entities relative to sets of climatic variables assumed to represent the main climatic factors limiting their distributions (Box 1981). For plants, the entities can be species, higher taxa, plant functional types or communities (cf. Box 1996, 1987; Box et al. 1993). The main climatic factors and variables which may represent them were discussed by Box (1995). The data required are the geographic ranges of the entities and climatic data from a large number of meteorological stations adequately covering the physiographic heterogeneity of the region of interest. An important shortcoming of envelope models is that envelopes do not include possible metabolic adjustments by plants, such as to higher CO_2 levels and temperatures, which may modify their physiologies and geographic responses to change. There are essentially no data, however, for parameterizing such adjustments, even if their mechanisms were understood (which they are not, for the most part). As a result, in the absence of generally reliable metabolic models, easily calibrated envelope models may still be the only geographically applicable tool for studying possible responses of large numbers of species to climatic changes.

Climatic envelopes are calibrated by iteratively matching range boundaries with the corresponding climatic values and checking the predicted spatial result. Even parameterization based on accurate range maps, however, does not automatically imply reproducibility of the taxon range, since non-climatic factors may also be limiting, at least in some areas. As a result, accurate re-prediction of a taxon range is not circular logic but rather represents confirmation that climate was the overriding control of that range. A study of 120 major woody plant species in Florida confirmed that this climatic approach can capture much of the spatial variability of plant species ranges, even in a region with pervasive control of vegetation patterns by substrate properties and topography (Box et al. 1993).

For the present study, climatic envelopes were constructed and calibrated for over 200 major plant species (mostly woody) of eastern North America, based mainly on range maps by Little (1971, 1977, 1978) but also on other range maps (e.g. Brockman 1984; Jones & Coile 1988; Mellinger 1984; Radford et al. 1968) and previous correlations between vegetation and climate (e.g. Greller 1989; Box et al. 1993). As an example, the climatic envelope of *Fagus grandifolia*, an important canopy co-dominant tree species extending from eastern Canada to northern Florida, is shown in Table 1, along with climatic data suggesting its fitness at Boston (Massachusetts). The 200 species envelopes were then applied to present-day climatic data for about 500 meteorological stations throughout eastern North America and to values (at those sites) representing a hypothetical 2°C global-average warming scenario. This scenario, considered to be realistic for the mid to later 21st century, involves greater warming in winter than in summer and greater warming at higher latitudes and in more continental areas, as suggested by Anon. (1994) and Smith & Tirpak 1989). Under this scenario, winter warming would range from 2 - 3°C in the southeastern USA to more than 5°C in southern Canada, with summer warming of less than half these amounts.

In order to study the wholeness aspect of community integrity, 15 main plant communities of eastern North America were defined in terms of their main structural elements. This is done at two levels:

(1) those species which are required for community occurrence; and

(2) those additional species which are major, characteristic elements but which do not necessarily occur everywhere the community occurs.

For example, *Fagus grandifolia* and *Acer saccharum* are required for the occurrence of Beech-Maple Forest, but beech may only be an 'additional' or companion species in Northern Mixed Forest, which requires *Pinus strobus* and extends further north than the range of *Fagus*. Such definitions for several major plant communities in eastern North

Table 1. Climatic envelope of *Fagus grandifolia* and application to estimate species fitness at a site.

The potential range of a species can be estimated by its climatic envelope, consisting of its upper and lower tolerance limits relative to its main climatic limiting factors:

	Tmax	Tmin	Tmmin	Tabmin	MIy	Pmin	Defy
Maximum	29.0	13.0	9.0	−7.0	***	***	200.
Minimum	17.0	−12.0	−15.0	−40.0	1.10	40.	0.

Tmax = mean temperature of the warmest month (°C)
Tmin = mean temperature of the coldest month (°C)
Tmmin = mean nighttime minimum temperature of the coldest month (°C)
Tabmin = absolute minimum temperature (°C: coldest ever measured, generally over at least 30 years)
MIy = annual moisture index: precipitation / potential evapotranspiration
Pmin = average precipitation of the driest month (mm)
Defy = annual climatic moisture deficit (mm, as obtained from a climatic water budget)

Fagus grandifolia, which occurs from southern Canada to the Gulf of Mexico (western Florida), requires a significant degree of winter cooling (e.g. Tmin < 13°C) but not necessarily continuing periods of sub-freezing temperatures (Tmmin as high as +9°C). It also requires a generally moist climate (MIy at least 1.10 — higher than for most oaks, for example), with no extreme dry month (Pmin at least 40 mm), but can tolerate some degree of cumulative moisture stress over a year (Defy up to 200 mm). Limits which are considered unimportant or unattainable are left open-ended and denoted by asterisks. For the significance of these (and other possible) climatic factors in limiting species ranges, see Box (1995, 1996; Box et al. (1993).

Fitness at a site is estimated by applying the climatic envelope to site climatic conditions, for example at Boston:

	Tmax	Tmin	Tmmin	Tabmin	MIy	Pmin	Defy
Boston	21.8	−2.6	−6.7	−27.8	1.70	80	37

Comparison of the Boston site data and the envelope limits of *Fagus grandifolia* shows that it is well within the range for all variables (dimensions) in its climatic envelope. Normalizing for the different range widths (and units) of the different climatic variables suggests that the closest limiting factor is the annual moisture index MIy – although it is still quite far away from that limit. On a 0-1 scale representing the fraction of total normalized width, the proximity to the closest limit is 0.29. This value, called d_{min}, is used as the estimate of fitness at the site. (For further details see Box 1981, in particular pp. 44 - 45).

America, with their required and main companion species, are shown in Table 2.

Community integrity, as discussed above and as a predictive tool at particular sites, also requires some measure of the relative fitness of the main structural components. The biological data available at a site are the presence/absence of each species and the proximity of each species to its closest climatic limit, as provided by the climatic envelopes on a normalized 0 - 1 scale (see Table 1). This proximity, denoted $d_{\min}$ in earlier envelope applications (e.g. Box 1981), provides the basis for calculating the index of community integrity.

An Index of Community Integrity

The Index of Community Integrity (ICI) is estimated entirely from species fitness data (normalized proximity to closest climatic limit), based on the two-level system of required and companion species described above. A community is considered to occur only if all required components are present, but not all companion species are required. Thus, the ICI has two parts:

(1) a main, multiplicative part based on the fitness of the required species; and

(2) an additive part based on the fitness of additional, companion species.

This two-part definition is necessary so that multiplication of different numbers of companion fitness values (all < 1) does not bias the result. The fitness values are the proximity scores ($d_{\min}$ values) obtained from application of a full set of species climatic envelopes at a site. Calculation of the ICI is explained in Table 3. The Beech-Maple Forest at Boston (see Table 1) can serve as an example. In that case, the $d_{\min}$ values for both beech and maple were 0.29. Using 0.35 as a good $d_{\max}$ value (see step 3 in Table 3), one gets 0.687 for the base ICI value. There are no companion species (OR species) in the definition of beech-maple forest (see Table 2), so step 4 is not needed in this example and the final ICI value is also 0.687.

The ICI can be summarized by its main properties:

- The ICI is based mainly on the occurrence and fitness of the main species which define the community.
- The ICI varies from 0 to 1, increasing as species fitness increases (i.e. species are farther from climatic limits).
- The ICI is independent of the variables and algorithm used for estimating species fitness; nevertheless, comparison of results from different models requires consistency in variables and algorithms.
- The ICI is based on species which are required (REQ) to define the community and on characteristic companion species, only some alternatives (OR) of which must occur.
- The value of the ICI is not affected by the number of defining species occurring, since absence of any required (REQ) species means that the community does not occur at all.
- The ICI is augmented, at least to some extent, by the most fit defining elements, even if these are companion species which are not required (i.e. not REQ or OR species).

Table 2. Definition of plant communities based on their main defining structural elements.

Beech-Maple Forest	
Acer saccharum	REQ
Fagus grandifolia	REQ
Northern Mixed Forest	
Acer saccharum	REQ
Pinus strobus	REQ
Betula lutea	REQ
Fagus grandifolia	
Piedmont Oak-Hickory Forest	
Quercus falcata	OR
Quercus alba	OR
Carya glabra	
Mixed Mesophytic Forest	
Fagus grandifolia	REQ
Fraxinus americana	REQ
Liriodendron tulipifera	REQ
Acer saccharum	REQ
Tilia heterophylla	REQ
Quercus rubra	OR
Quercus alba	OR

Communities are defined by the occurrence of three types of main structural elements: (1) species which must occur (REQ); (2) species in a group of alternatives, only one species of which must occur (OR); (3) other, companion species. Beech-Maple Forest, for example, requires both *Acer saccharum* and *Fagus grandifolia*, and is considered not to occur if either species is absent. Piedmont Oak-Hickory Forest, on the other hand, is considered to occur if either of its two defining *Quercus* elements occurs, since either can be a canopy dominant. Other species (neither REQ nor OR) may also be characteristic of a community and contribute to community integrity by their presence, for example *Fagus grandifolia* in northern mixed forest. Mixed Mesophytic Forest, the most diverse deciduous forest type in eastern North America (windward west side of the central Appalachian Mountains), requires a larger number of defining elements.

- Occurrence of companion species can compensate for lower fitness among the required (REQ and OR) elements — but only to a certain extent (not to exceed ICI = 1.0).
- The value of the ICI is never reduced by the occurrence of additional companion species, since their contributions to the index are added (not multiplied).
- The value of the ICI is 0 if a REQ species or the operative

Table 3. Calculation of the Index of Community Integrity based on proximity to closest envelope limit.

1. Identify the minimum species *basis* for identifying integrity at the site. This basis must include all REQ and at least one OR species and must involve at least half (and at least two) of all species defining the community. All other defining species which occur at a site are referred to as 'companion' species. If not all required species occur at a site, the community is considered not to occur at that site (i.e. fragments of communities may occur, but only up to a point).
2. Order all defining species in order of decreasing fitness, as estimated by proximity ($d_{\min}$) to the closest environmental limit in an envelope model.
3. Calculate the normalized product of the fitness value of all species in the minimum basis: Base ICI = $\pi\, d_{\min}(\mathrm{i}) / d_{\max}$ (π from n to $n_{\min}$) where the $d_{\min}(\mathrm{i})$ values, for each species i, come from envelope processing and $d_{\max}$ is a standard value at least as large as the largest $d_{\min}$ to be encountered, and perhaps somewhat larger, in order to normalize for all sites to be processed. (A good $d_{\max}$ value for this purpose seems to be around 0.35, since individual $d_{\min}$ values rarely exceed 0.5 even for widespread, non-defining species such as grasses. If a $d_{\min}$ value exceeds $d_{\max}$ the fraction is truncated at one.)
4. Beyond the minimum basis (if more species occur), let the "companion" species augment the integrity index as follows. For each additional species:
(a) Calculate the remaining integrity deficit, i.e. def = 1.0 – ICI;
(b) Multiply this remaining deficit by the fitness of the next species i (arranged in descending order, see item 2 above): $x_{\mathrm{add}}(i) = d_{\min}(i) \times \mathrm{def}$
(c) Add this contribution to reduce the deficit (asymptotically):
$\mathrm{ICI} \longrightarrow \mathrm{ICI} + x_{\mathrm{add}}(i)$

This method has the advantage that ICI can never exceed 1.0 – and cannot even reach 1.0 unless an additional species has a perfect fitness value of $d_{\min}(i) = 1.0$.Example: For beech-maple forest at Boston (see Table 1), the $d_{\min}$ values for both beech and maple were 0.29; using 0.35 as the $d_{\max}$ value (step 3), the base ICI becomes 0.687. In this case step 4 is not involved, since there are no other defining species for bech-maple forest.

Table 4. Estimated integrity of Beech-Maple Forest at present and under 2°C global average warming.

Location	Lat	*N*spp	Integrity Index Now	 + 2°C	 Change
Québec, Québec	46.80	24		.392	.392
Sault Ste. Marie, Michigan	46.47		20	.223	.223
Montréal-Dorval, Québec	45.47	40	.073	.544	.471
Burlington, Vermont	44.47	43	.126	.395	.269
Lake Placid, New York	44.28	15		.180	.180
Concord, New Hampshire	43.20	48	.526	.617	.091
Syracuse, New York	43.12	63	.394	.327	-.068
Buffalo, New York	42.93	65	.510	.360	-.150
Albany, New York	42.75	68	.360	.395	.035
Boston, Massachusetts	42.37	70	.687	.327	-.360
Chicago, Illinois	41.98	71	.160	.138	-.022
Hartford, Connecticut	41.93	76	.687	.340	-.347
Providence, Rhode Island	41.73	77	.687	.286	-.401
Akron, Ohio	40.92	76	.360	.235	-.125
New York, New York	40.78	110	.236	.114	-.122
Pittsburgh, Pennsylvania	40.50	86	.184	.082	-.102
Harrisburg, Pennsylvania	40.22	93	.264	.106	-.158
Columbus, Ohio	40.00	81	.184	.118	-.066
Indianapolis, Indiana	39.73	84	.360	.167	-.193
Baltimore, Maryland	39.28	107	.117		-.117
Washington, D.C.	38.85	103	.099	.022	-.077
Charleston, West Virginia	38.37	105	.264	.046	-.219
Lexington, Kentucky	38.03	102	.236	.064	-.172
Charlottesville, Virginia	38.03	108	.183		-.183
Elk Knob, Virginia	36.87	87	.300	.034	-.266
Boone, North Carolina	36.22	58	.555	.027	-.528
Nashville, Tennessee	36.12	89	.065		-.065
Asheville, North Carolina	35.43	100	.137		-.137

The integrity estimates under current conditions suggest that the core area of beech-maple forest, where it is perhaps best developed and far from climatic limits, is in lower elevations of New England. It may potentially extend, however, with reduced fitness, as far west as Chicago and as far south as the foothills of the southern Appalachians (e.g. Asheville). Under average global warming of 2°C, beech-maple forest could move into more of southern Canada but may retreat entirely from all but higher elevations of the southern Appalachians and from areas as far north as Chesapeake Bay (cf. Baltimore), hanging on only with much reduced fitness in remaining areas of the middle and lower northern Appalachians as well as parts of southern New England. Sites are arranged from north to south by latitude. The second column of numbers (Nspp) shows the number of species predicted to occur at the site, out of the 200 in the envelope model.

OR species has a fitness value of zero (i.e. occurs exactly at a climatic limit) — unless the index is augmented by greater fitness among companion species; ICI = 0 means that the community does occur but is exactly at its limit.

Integrity and vulnerability over a range of a communities

In order to assess the usefulness of the Index of Community Integrity, the ICI was calculated for 15 major plant communities across eastern North America, under current climatic conditions and for the 2°C global-average warming scenario described above. The result for beech-maple forest is shown in Table 4. Mapping of such results is being explored and will of course make the results easier to interpret.

The integrity estimates under current conditions suggest that the core area of beech-maple forest should be in lower elevations of New England, where it is indeed best developed, but that it could extend as far west as Chicago and as far south as the foothills of the southern Appalachians. Its main species would have reduced fitness in these peripheral areas, and the community would probably be replaced by forest communities involving species which are more competitive at these locations. Prediction of the range of a community using the ICI thus requires prediction of other possible communities also.

Gradients of community integrity and of vulnerability to warming-induced instability or breakup can be estimated by studying the ICI changes between two scenarios. In Table 4, the column +2°C shows the ICI values for the 2°C global-average warming scenario. The result suggests that Beech-Maple Forest could move into more of southern Canada (where *Acer saccharum* already occurs but not *Fagus grandifolia*) and retreat entirely from all but higher elevations of the southern Appalachians and from lowland areas as far north as Chesapeake Bay. The net effect across eastern North America is a potential loss of area by the Beech-Maple Forest, as suggested by the mostly negative change values in the last column of Table 4. These results are consistent with those for individual species (e.g. Zabinski & Davis 1989), but the ICI provides a quantitative gradient based on the integrated effects of many species.

Conclusion

The Index of Community Integrity provides an integrated quantitative estimate of community completeness and fitness, and conversely of community vulnerability to disruption by climatic change, based on:

(1) present-day correlation between species ranges and climatic conditions; and

(2) application of such information (as envelope models) to large numbers of sites within and around the ranges of the species involved.

The results not only estimate community 'wholeness' over its range but also the 'fitness' of the main species and their potential for migration based on proximity to climatic limits. The Index of Community Integrity can be based on any reasonable measure of species fitness, but the use of readily calibrated climatic envelope models, based on major climatic constraints, provides a relatively easy means of generating the fitness estimates needed to apply the ICI to large numbers of species over large areas.

Vegetation types whose main structural elements are many or which have wide tolerance limits may be least vulnerable to warming-induced instability or breakup. In the real world, however, vulnerability or at least severe stress may also be affected by geographic 'accidents' such as the shapes of the land masses involved and by factors which we still understand poorly, such as metabolic adaptations and the long-term influence on future vegetation potentials of the transient-state vegetation, which is assumed to be quite weedy.

The results presented here are very preliminary, but the example of beech-maple forest does illustrate, to some extent, how potentially vulnerable areas may be identified. Whether any such single-valued index provides useful (and not misleading or artificial) information for natural-area and landscape management, however, may still be an open question.

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Population dynamics of isolated *Nothofagus* stands in southwestern New Zealand

Haase, Peter

Dyckerhoffstrasse 3, D-49525 Lengerich, Germany;
E-mail haasep@t-online.de

Abstract. Isolated stands of *Nothofagus fusca* (*Fagaceae*) beyond the limits of continuous *Nothofagus* forest in the upper Taramakau Valley, South Island, New Zealand, were investigated during two field surveys, separated by 7 - 10 yr. The compound population of 54 sample stands, ranging in size from 1 to > 400 stems, increased by 37.4% (4.2%/yr) and compound basal area increased by 4.7% (0.5%/yr) between the two surveys. Most of the isolated *N. fusca* stands established on sites likely to experience intermittent disturbance, and decreases in population size of 13 stands were associated with recent, in some cases catastrophic, disturbance. Major disturbance by slips induced by earthquakes and/or high orographic rainfall and erosion of terraces by flooding rivers are important factors facilitating the establishment and maintenance of outlier populations of *N. fusca* in the upper Taramakau catchment, which is part of a regional forest ecotone where competition by species of the podocarp-broadleaved forest increases towards the southwest resulting in complete absence of the genus *Nothofagus* in central western South Island.

Keywords: Disturbance; Earthquake; Forest; Pioneer population; *Nothofagus* forest.

Nomenclature: Connor & Edgar (1987).

Introduction

New Zealand has an oceanic, generally temperate and humid climate so that evergreen forest is the climax vegetation in most places below the alpine timberline. Warm temperate forest associations with subtropical relationships are restricted to the northern half of North Island. Cool temperate forests, which occur at higher elevations in the north and at higher latitudes in southern North Island (39° - 41°30' S) and South Island (40°30' - 46°30' S), are classified into two major types (Wardle 1991). The first subtype, podocarp-broadleaved forest, has a 'rainforest' physiognomy with several strata of trees and shrubs, and abundant tree ferns, lianes, climbing plants, and epiphytes in the wetter regions. Beech forest is dominated by one or more of the five native taxa of *Nothofagus*, often to the near exclusion of other tree species.

While native beech forests are common and widespread in New Zealand, *Nothofagus* is rare or completely absent in certain regions with comparatively mild and superhumid climates (McGlone 1985). In South Island, *Nothofagus* dominates the forests in the north and southwest, but it is absent from the central western region, the so-called 'Westland beech gap' (Wardle 1984; Haase 1990). To the north and south of this distribution gap there are forest ecotones, where scattered stands of *Nothofagus*, ranging from single trees to several hectares in size, occur in podocarp-broadleaved forest, successional scrub and subalpine scrub. The establishment of many small isolated *Nothofagus* stands has been dated within the past 500 yr (Wardle 1980; June 1982; Haase 1989a, b, 1991a) and is possibly related to recent environmental changes (e.g. Holloway 1954).

A probable factor limiting the distribution of *Nothofagus* is that abundant seed production occurs only intermittently, usually after hot and dry summers (Connor 1966; Wardle 1984), which makes *Nothofagus* a poor competitor in mild and humid climates (Rogers & McGlone 1994). *Nothofagus fusca* and *N. menziesii* are vigorous colonizers of disturbed sites (Holloway 1954; Wardle 1984), however, and in *Nothofagus*/podocarp-broadleaved forest ecotones, where environmental limits set by climatic conditions and/or biological competition are approached, marginal and outlier populations of these two species should respond with long-term directional changes in population size to environmental stability or instability including variations in climate (e.g. Haase 1989b, 1991a).

The purpose of this research was to monitor changes in population size of isolated stands of *N. fusca* over an extended period and to relate these changes to observed environmental disturbance in order to predict long-term changes in the composition of the regional forests.

Material and Methods

In North Westland, the mainly *Nothofagus*-dominated forests meet their southern limit along a line extending from the Grey River mouth to Lake Haupiri (June 1982; Fig. 1). A forest ecotone then extends south to the Taramakau River and also along the valley of the upper Taramakau River into its southeastern tributaries (Haase 1989a, b, 1990, 1991a, b). The survey was carried out mainly in the southeastern tributaries of the upper Taramakau River which are enclosed by steep, high mountain ranges of 1400 - 2000 m, belonging to New Zealand's Southern Alps.

A prominent feature of the region is the Alpine Fault, a major active fault line, which traces the boundary between the Australian and Pacific plates. Subsidiary fault lines are traced by the Taramakau Valley (Hope Fault) and from Kellys Creek to Lake Kaurapataka (Kelly Fault) (Fig. 1). The Hope and Kelly faults are associated with a zone of micro-earthquake activity with magnitudes below 3 (Rynn & Scholz 1978), but there have been earthquakes with magnitude 7 or greater, which occur with a return time of less than 50 yr (Smith 1978). Two recent strong earthquakes which affected the survey region, the Arthur's Pass earthquakes of 1929 and 1994 had magnitudes of 7 and 6.7, respectively, but had epicentres located to the southeast of the Main Divide (Rynn & Scholz 1978; Arnadottir et al. 1995).

The local rocks are thick-bedded sandstones and siltstones of Late Triassic age which successively grade into higher

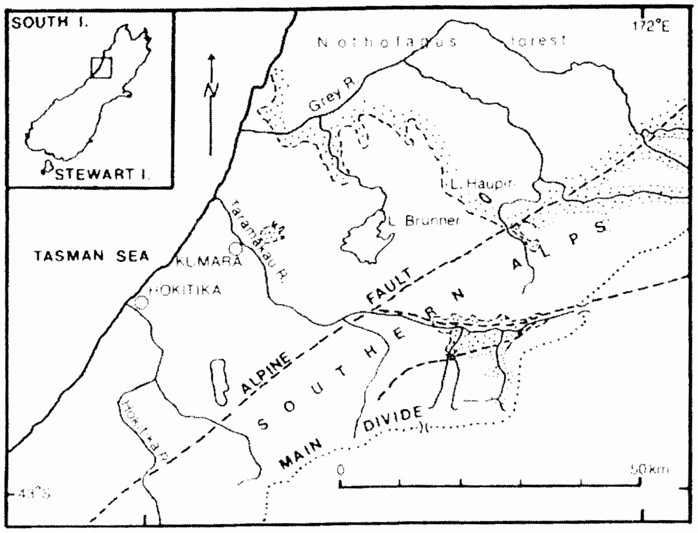

Fig. 1. Map of north Westland and the survey region in the upper Taramakau catchment. The southern limit of *Nothofagus* forest and two large outliers are shown (dotted line, alpine timberline; broken line, non-timberline boundary). West of the Alpine Fault, the *Nothofagus*/podocarp-broadleaved forest ecotone extends south to the Taramakau River. Important fault lines are shown by thick broken lines.

metamorphic stages towards the Alpine Fault. Floodplain gravels and locally extensive debris flows are of Holocene age (Cave 1987).

Soil profile development and soil type are determined mainly by the amount of rainfall, and in the higher rainfall areas most soils are moderately to strongly leached and podzolized.

Because of the insular character and high orographic rainfall, the regional climate is mild and superhumid. Annual rainfall increases from 2500 mm near the western coast to 4500 mm at the foot of the Southern Alps (Anon. 1983a). The nearest rainfall station at Otira (383 m a.s.l.) receives almost 5000 mm of mean annual rainfall. Temperature records for Otira give an annual mean of 9.8°C (February 15.1°C; July 4.2°C; Anon. 1983b).

The survey region is densely forested up to the alpine timberline at 800 - 900 m. Lowland podocarp-broadleaved forest dominated by the tall conifer *Dacrydium cupressinum* and the angiosperm trees *Quintinia acutifolia* and *Weinmannia racemosa* covers the lower Taramakau catchment and extends into the Otira and Deception valleys. The upper Taramakau-Otehake region harbours approximately 5000 ha of *Nothofagus*-dominated forests with *N. fusca* as the major species. On north-facing slopes on the south bank of the Taramakau River, this species ascends to 800 - 900 m and forms the upper limit of tall forest. East of the Otehake River and west of the Otira River, the upper limit of *N. fusca* decreases rapidly and the species becomes restricted to discontinuous stands on the Taramakau floodplain, the westernmost stands are located up to 25 km west of the Otira River mouth. In the lower Otira Valley, isolated stands occur on the southwestern slopes of One Shot Hill, the southeastern slopes of the Kelly Range, and also in the Deception Valley (Haase 1989b, 1991a).

Nothofagus fusca can grow to a height of 24 - 32 m and a diameter of 1.5 - 2.0 m, and reach a maximum age of 450 - 600 yr (Wardle 1984). It is a comparatively light-demanding species and its diameter-class distribution is often more or less continuous, suggesting sporadic recruitment after large-scale canopy disturbance (June & Ogden 1978; Wardle 1984; Stewart & Rose 1990).

Isolated *N. fusca* stands, particularly in montane forest and scrub, are easily identified by their conspicuous light green foliage in spring and early summer. The located stands were visited during two field surveys, the first in 1987-1988 and 1988-1989 and the second in 1997-1998. In each stand, stem diameter at breast height (DBH; 135 cm above the point of origin) of all *N. fusca* trees including dead standing logs was measured with a diameter tape. After the second survey, changes in population size, stem diameter of individual trees and stand basal area were calculated for each stand. Signs of recent and past disturbance were observed on both occasions and the probable cause of mortality of trees was noted.

Results

Of the 56 isolated stands considered, 28 are classified as alluvial stands, located on floodplains, terraces and talus fans (90 - 560 m), the remaining 28 are hillslope stands which occur between 300-940 m. None of the 54 isolated stands of *N. fusca* investigated in 1987-1989 had been eliminated by 1997-1998. The number of isolated *N. fusca* stands increased by two (Table 1). These were recently established saplings, which originated from long-distance dispersal of seed by wind, probably from the nearest estab-

Table 1. Overall changes in number, population size and basal area of isolated stands of *Nothofagus fusca*.

Survey	Stands	Stems	Basal area
	n	*n*	m^2
1987-1989	54	2623	257
1997-1998	56	3603	269
Change	+3.7%	+37.4%	+4.7%
Change/yr	+0.4%	+4.2%	+0.5%

lished isolated stands. The total population increased by almost 1000 stems (Table 1) through recruitment of seedlings into the > 135 cm height class. The compound basal area showed a much smaller increase (4.7%; Table 1) because recruited saplings contributed little to overall wood increment, while death of large trees had a significant negative effect. The population size of individual stands ranged from single pioneer saplings or trees to over 400 stems. Stem numbers increased in 28 stands while there was no change in stem number in 13, mostly single-stem stands and decreases in population size were found in 13 stands. Basal area increased in 43 and decreased in 11 stands.

33 of the 54 isolated stands showed signs of recent natural disturbance at the first survey. Between the two surveys, 18 stands had been affected by various types of disturbance. Catastrophic disturbance was caused by slips (small landslides) in two stands and in another stand by a snapped and fallen *N. fusca* tree of a 150 cm DBH. Dense stands of seedlings of small pioneer trees in all three stands allowed to date this disturbance which was probably related to the Arthur's Pass earthquake of June 1994. In some other stands, catastrophic disturbance had been caused by erosion of river terraces and moraine cliffs. This suggested that earthquakes might be a major factor in the stand history of the local *N. fusca* stands.

Discussion

Pollen profiles from various New Zealand regions have shown that near the limits of its present distribution, population growth of *Nothofagus* has been static or even negative during the past 2000 - 3000 yr, and it has been suggested that *Nothofagus* is non-competitive in humid, mild, low-insolation climates (Rogers & McGlone 1994).

In the *Nothofagus*/podocarp-broadleaved forest ecotone of the upper Taramakau catchment, however, outlier populations of *N. fusca* considerably increased in size over a period of 10 yr, although some of the stands were devastated by disturbance through mass movement. Because of the intermittent seeding and sporadic occurrence of suitable seedling habitats, the short-term variation in population size of isolated stands reported in this paper must be viewed in relation to current population structures. Massive disturbance temporarily decreases population size while at the same time creating new seedling habitats leading to potential subsequent increases in population size. Establishment of dense seedling stands after disturbance leads to large but temporary increases in population size. In the absence of further disturbance and hence, recruitment, the population size initially decreases again because of density-dependent seedling and sapling mortality (self-thinning effect). Long-term trends in population size and possible range extension may thus only become apparent after several decades of field research.

Where *N. fusca* forest is more or less continuous in the survey region, e.g. on north-facing slopes between the Otira and Otehake Rivers, the species covers the complete range of available habitats from stabilised floodplains to the tree line. Outlier stands beyond the limits of continuous forest, however, almost always occupy 'precarious' sites, prone to various types of disturbance and it is likely that *N. fusca* was only able to establish here after a disturbance event and that stands are maintained by intermittent recruitment in the course of recurrent disturbance when biological competition is temporarily reduced.

Such recurrent disturbance is provided by comparatively frequent earthquakes in combination with, or additional to, high orographic rainfall. Each earthquake initiates a series of disturbance events (Fig. 2). The shock waves cause slope failure in the steep terrain leading to rockfalls and landslides with related destruction of the forest cover. Landslide scars and talus deposits are suitable habitats for colonization by *N. fusca*. Large amounts of sediment become

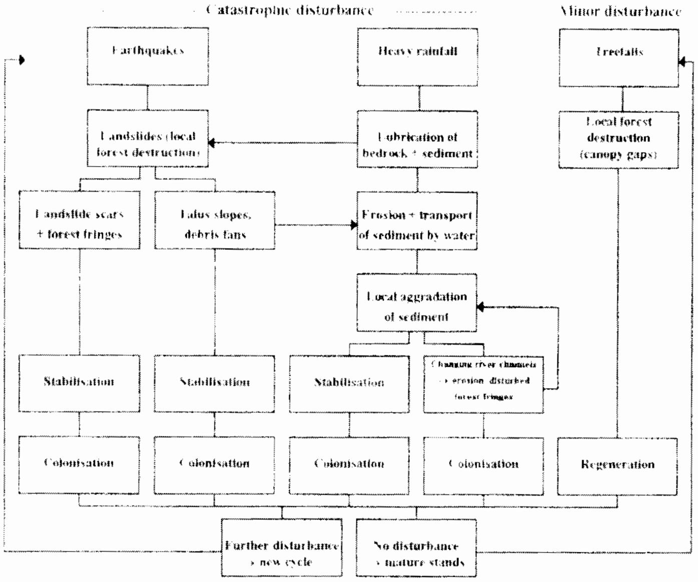

Fig. 2. Flow chart of disturbance-related establishment and persistence of isolated stands of *Nothofagus fusca* in the upper Taramakau catchment, South Island, New Zealand (direction is top to bottom, unless indicated by arrows).

available, which are transported downslope by flooding creeks during rainstorms, leading to local aggradation on lower slopes and in riverbeds in the valleys. These deposits can stabilize and form new terraces, or block river channels which then change course eroding already stabilised and forested terraces in other places. The resulting disturbed forest fringes and new terraces are again suitable habitats for colonization by *N. fusca*. Most of these sites are likely to experience further intermittent disturbance in the future. In the absence of such 'exogenous' disturbance, the ultimate canopy breakdown of massive *N. fusca* trees in old-growth stands, an 'endogenous' disturbance, presents a further opportunity for regeneration of *N. fusca* in isolated stands.

The frequency and intensity of tectonic and climate-induced disturbances will thus affect future numbers and sizes of isolated *N. fusca* stands in the upper Taramakau catchment. Besides temporal variation in tectonic activity, an increasing frequency of rainstorms, such as occur during 'El Niño' events, or a generally more erratic distribution of rainfall, can promote regional population growth of *N. fusca*. To detect such long-term trends in population size and possible range extension will take several decades of field research, however.

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Structure and dynamics of a floodplain alder carr during the late Holocene

Klimeš, Leoš, Pokorný, Petr & Klimešová, Jitka

Institute of Botany, Section of Plant Ecology, Dukelská 145, CZ-379 82 Třeboň, Czech Republic;
Fax +420333721136; E-mail klimes@butbn.cas.cz

Abstract. The late Holocene history of an alluvial alder carr in E. Bohemia, Czech Republic and its vegetation dynamics were studied using pollen, macrofossil and tree-ring analyses together with vegetation analysis. Due to high accumulation rates and good preservation of the palaeo-ecological record, a detailed reconstruction of vegetation changes during the last 2160 yr was possible. After an oxbow had filled up, a peat bog and later an alder carr developed. Pollen and macrofossil analyses indicated cyclic succession in the course of the past 900 yr, with several alder carr and open wetland stages. The last cycle was documented by vegetation analysis and confirmed by tree ring analysis. In the 1880s the current forest margin was established. The centre of the locality was overgrown by the alder carr between 1940 and 1950. Since that time hardly any alder established in the study site. The present dynamics of the tree layer are characterised by a high mortality of suppressed *Alnus* trees, and of *Betula pubescens*, irrespective of tree age.

Keywords: *Alnus glutinosa; Betula pubescens;* Cyclic succession; Late Holocene; Pollen analysis; Population dynamics.

Nomenclature: Ehrendorfer & Gutermann (1973).

Introduction

Alder carrs belong to the most naturally heterogeneous and dynamic ecosystems in temperate Europe (Ellenberg 1986; Prieditis 1997). They are basically formed by hummocks and hollows with permanent standing water. Temporally flooded habitats also occur. Uprooting of mature trees results in gaps where light regime, nutrient availability and competition differ from the closed-canopy forest (Carlton & Bazzaz 1998). Gap centres, usually at slightly lower elevations than their surroundings represent another habitat – small water bodies which persist for many years, until they are terrestrialized (Jeník 1980). The small-scale habitat heterogeneity is reflected in a remarkable mixture of plant species with different soil moisture requirements and tolerance of anaerobic conditions (Döring-Mederake 1991). The long-term dynamics of alder carrs has received insufficient attention (but see Marek 1965; Brock et al. 1989). However, it has been suggested that the alder carrs may persist at a site over more than 800 yr (Marek 1965). The *Alnus glutinosa* stands are usually more or less even-aged in alder carrs (Pigott & Wilson 1978; Tucker & Fitter 1981). Trees belonging to younger age classes are markedly under-represented and establishment of alder seedlings is rare (McVean 1956; Tucker & Fitter 198; Klimešová & Klimeš 1996; Prieditis 1997). It has been speculated that alder carrs follow a cyclic development (Faliński 1986; Remmert 1991) and that the establishment of *Alnus* is restricted to the peat bog stage of this development (Jeník 1980). A similar cyclic development has been reported from several other forested ecosystems (Míchal 1983; Delcourt & Delcourt 1991; Korpel' 1995; Schmidt 1998). Unfortunately, there is little evidence to support or reject this hypothesis in any of the habitats. In alder carrs the peat, containing pollen and macrofossils, is usually mineralised due to its aeration by alder roots so that only a thin layer of it is preserved (Jeník 1980; Rybníček & Rybníčková 1987; Döring-Mederake 1991). Therefore, in most cases the long-term history of alder carrs cannot be studied by using a standard pollen analysis. Data based on other approaches (direct historical observations, archaeological studies, etc.) are also scarce so that little is known about the long-term dynamics of alder carrs in temperate Europe.

The locality 'Na bahně' in E. Bohemia (Czech Republic) is situated at the foot of a pleistocene terrace. Many powerful and persisting springs supply the alder carr with water. Its drying-out is prevented and the water regime is remarkably stable both within a year and between years (Klimešová & Klimeš 1996). Consequently, mineralization of the peat is slowed so that the entire history of the present alder carr could be recorded in the peat. Recent history of the locality has been recorded by several botanists. Rare peat bog plants were reported from the locality at the end of the last century (Hansgirg 1881; Sitenský 1891). In 1924 Mikyška studied the vegetation of the locality. The centre was formed by a peat bog with herbaceous vegetation dominated by *Menyanthes trifoliata, Carex nigra, Potentilla palustris,* large carpets of *Sphagnum recurvum* and *S. flexuosum*, and other heliophilous species (Mikyška 1926), indicating low pH and low nutrient availability (Klimešová & Klimeš 1996). The peat bog was surrounded by an alder carr, locally with abundant *Calla palustris* (Mikyška 1926). In the 1940s the peat bog in the centre of the locality was overgrown with young *Alnus* trees (Mikyška 1964). In the 1980s the vegetation consisted of a homogeneous *Alnus* stand (Rydlo 1981; Klimešová & Klimeš 1996). In 1988 we marked more than 500 trees of *A. glutinosa* and *Betula pendula*, and repeatedly measured their growth until 1998 to evaluate the dynamics of individual tree populations (Klimešová & Klimeš 1996; Klimešová et al. 1997). The stand has also been studied using dendrochronological methods which provided details on the development of the stand during the last cycle (Klimešová et al. 1997).

The aim of this paper is to bring together the available information based on different methods and to reconstruct the development and dynamics of the locality 'Na bahně' during the late Holocene.

The locality

The alder carr 'Na bahně' is situated in the Orlice River floodplain (240 m a.s.l., 50°12'N, 15°58' E), E Bohemia, Czech Republic, at the foot of the youngest (Würm) terrace. The terrace, ca. 5 m in height, surrounding the alder carr from three sides, is covered by a deciduous forest dominated by *Quercus robur*. Towards the Orlice River wet unmanaged meadows invaded by *Alnus* saplings are found. The shortest distance to the river is ca. 150 m. Mean annual air temperature is 7.8 °C, mean annual precipitation is 602 mm (Nové Hradec Králové Meteorological Station, 8.5 km W of the locality; Vesecký et al. 1961).

Data collection

Palaeobotany

A series of exploratory borings was performed in the centre of the locality in spring 1997. The layer of organogenic deposits was up to 0.5 - 5 m deep. A 5-m long core was taken with a 5-cm diameter Russian-type corer (Jowsey 1966). The sediments were analysed for their components according to methods by Troels-Smith (1955), modified by Aaby & Berglund (1986).

Three samples consisting of pieces of wood were taken for ^{14}C dating. The samples were AMS-dated at the Radiocarbon Dating Laboratory, Department of Quaternary Geology, Lund, Sweden. Age calculations were based on a ^{14}C half-life of 5568 yr. The results were calibrated (Stuiver & Reimer 1993) and are reported in calendar time scale.

The samples used for pollen and other microfossil analyses were prepared by the modified acetolysis method (Erdtman 1943). As the lower part of the core had a more or less mineral character, the samples were pre-treated with concentrated hydrofluoric acid for 24 h (Faegri & Iversen 1989; Moore et al. 1991). The extracted microfossils were lightly stained with 0.3 % safranin and mounted in a glycerol-water mixture. In each sample an average of 1500 pollen grains were counted. The percentage values were calculated on the basis of the total sum, including all pollen types.

A macrofossil analysis was performed using the same core as for pollen analysis. The core was cut into 20-cm contiguous samples and their volume was determined. Macrofossils were extracted by heating the sample in a 5% sodium hydroxide solution for 5 min and then sieved under running water. Sieves with mesh sizes of 200 μm, 300 μm and 700 μm were used. The residues were examined under a stereomicroscope and the total amount of macrofossils was counted. In the macrofossil analysis the absolute number of items of each taxon was recalculated to a standard volume of 500 cm^3.

Zones in the pollen and macrofossil data were delimited using Detrended Canonical Analysis (DCA; Hill 1979). Samples were grouped into 'zones' using a simple iterative procedure linking simultaneously pollen and macrofossil samples into groups whose envelopes did not overlap.

Other methods

We made phytosociological relevés in the summer and autumn of 1987, using standard methods described by Mueller-Dombois & Ellenberg (1974). In a belt, 70 m in width and 140 m in length situated across the alder carr we labelled all 830 trees in the autumn of 1987. Trunk girth at the standard 1.3 m height was measured in the autumn of 1987 and in 1998. A comparison between relevés by particular authors was made using DCA. In randomly selected 72 *Alnus* and 14 *Betula* trees growing in the above belt two cores were taken from with a Pressler increment borer at 1.3 m height to count the number of tree rings.

Results

Palaeobotanical reconstruction

Three zones were distinguished by DCA ordination in the core both for pollen and macrofossil data (Fig. 1). The lower zone (160 BC - 680 AD) represented a small oxbow lake, ca. 1.5 m deep, dominated by wetland plants, such as *Myriophyllum spicatum*, *Batrachium* spec., *Potamogeton* spec. and *Nuphar lutea*. The occurrence of some taxa was proved by trichosclereids (*Nymphaeaceae*) and leaf spines (*Ceratophyllum*). The presence of zygospores of the chlorococcal alga *Mougeotia* indicates permanent water. Amphibious plants, such as *Alisma plantago-aquatica*, *Polygonum amphibium* and *Sagittaria sagittifolia* were abundant in the littoral. An adjacent belt of wetland vegetation was formed by sedges (predominantly *Carex rostrata*) and other common wetland plants (*Lycopus europaeus*, *Lythrum salicaria*, *Cicuta virosa*, *Ranunculus flammula*, *Solanum dulcamara*). An alder stand was apparently situated closely to the oxbow lake, because *Alnus* was well represented in the pollen spectrum. *Pinus*, *Carpinus betulus* and *Tilia cordata* grew probably on the adjacent terrace slope.

After the oxbow had filled up a wetland dominated by *Filipendula ulmaria* and *Caltha palustris* was developed (middle zone, 680 - 970 AD). Sedges (*Carex vesicaria*, *C. pseudocyperus* and *C. echinata*) were relatively infrequent there. Although *Alnus glutinosa* pollen were abundant, the number of macrofossils slowly decreased, indicating that

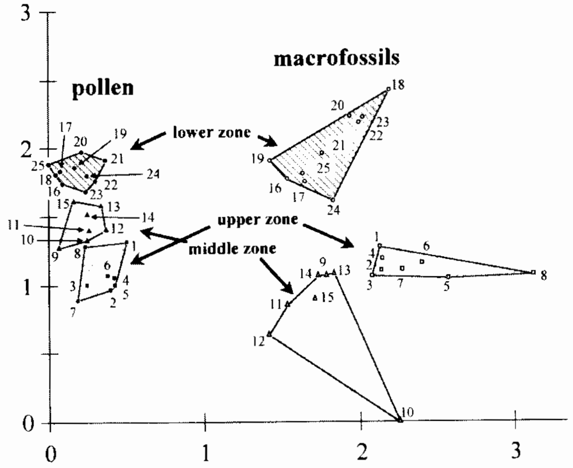

Fig. 1. DCA ordination diagram of the pollen and macrofossil data from a 5-m core. The 20-cm contiguous samples are labelled with numbers; samples belonging to the three zones are in envelopes.

the alder locally declined. Later on a *Sphagnum* dominated fen developed, with *Equisetum*, *Ericaceae* and *Calla palustris*. Since this time the river sediments contributed only little to the sedimentation process and the effect of local springs at the foot of the terrace became dominant. The alluvial wetland changed to a spring type wetland.

The upper zone (970 AD - present) began with a marked vegetation shift. *Sphagnum* decreased and *Potentilla palustris*, *Lycopus europaeus*, *Cicuta virosa*, *Caltha palustris*, *Carex echinata* and *Sparganium minimum* became more abundant in the peat bog. After that the wetland became overgrown with *Alnus* and *Betula*, and a closed forested wetland was established.

The dynamics of *Alnus* and heliophilous wetland herbs showed opposite trends during the past ca. 900 yr, with four or three peaks of *Alnus*, based on pollen and macrofossils, respectively (Fig. 2). The results indicate a cyclic development of the alder carr during the last millennium.

The uppermost two samples of the pollen diagram (20 and 0 cm) included roughly the last 100 yr. In the *Sphagnum* peat layer (16-27 cm) mosses indicating mesotrophic to eutrophic habitats were abundant (*Sphagnum palustre*, *S. recurvum* and *Calliergon cordifolium*). *Sphagnum squarrosum* and *Rhizomnium punctatum* were infrequent. This layer with indicators of an open peat bog corresponds to the stage studied by Mikyška (1926). For more detailed palaeobotanical results see Pokorný et al. (2000).

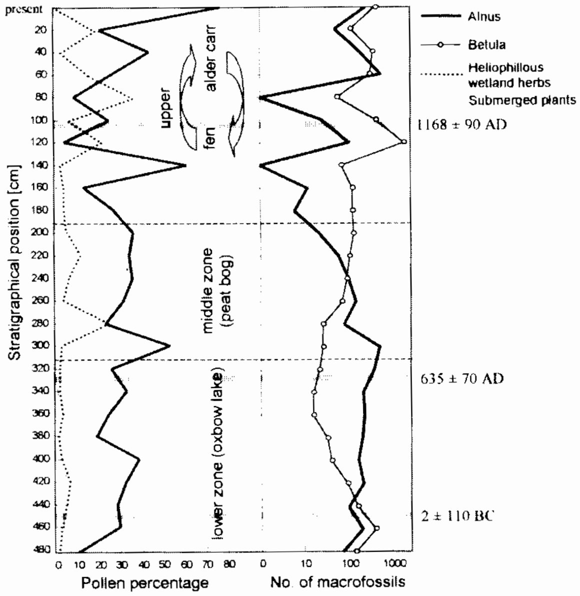

Fig. 2. Synthetic percentage pollen diagram and *Alnus* and *Betula* macrofossil diagram, illustrating local vegetation succession. The three zones were delimited using DCA multivariate analysis (see Fig. 1).

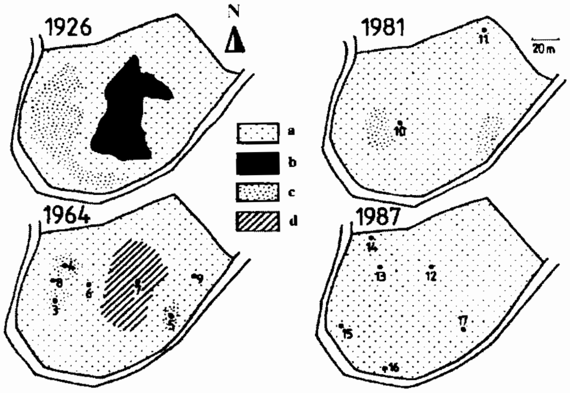

Fig. 3. Map of the locality 'Na bahně' according to Mikyška (1926, 1964), Rydlo (1981) and our research in 1987. Localisation of phytosociological relevés (3 - 17). Some important vegetation types are also given. Relevés 1 and 2 by Mikyška (1926) were recorded in the alder carr, their exact localization is unknown. a = alder carr; b = peat bog; c = alder carr with dominating *Calla palustris*; d = alder carr with dominaning *Lycopus europaeus*.

Vegetation dynamics during the last 100 years

The oldest floristic records from the locality 'Na bahně' by Hansgirg (1881) and Sitenský (1891) include numerous species indicating an open peat bog environment. Some more floristic notes confirming these records were published at the verge of the century. Until the 1930s the centre of the locality was open, with a *Sphagnum* peat bog, whereas the foot of the terrace was covered with an alder stand (Mikyška 1926). The vegetation pattern changed remarkably between 1926 and 1964 (Mikyška 1964; Fig. 3). The central peat bog became overgrown by an alder carr and plants requiring an open canopy disappeared. The species composition of the alder carr surrounding the peat bog also changed markedly between 1924 and 1964. A comparison of the vegetation relevés of the alder carr recorded by Mikyška in the 1920s and 1960s indicates a major change in species composition reflected in a shift of x-coordinates of the sites in the DCA scatter diagram (Fig. 4). Later, the development slowed down. Hence, in the DCA, the envelopes encompassing relevés recorded by Mikyška (1964), Rydlo (1981) and Klimešová & Klimeš (1987) are situated close to each other (Fig. 4).

In 1998 the tree layer was dominated by *Alnus glutinosa*, (nearly 68% of the trees). Another important tree reaching the canopy was *Betula pubescens* (21 % of the trees). The remaining 10% included younger trees of *Ulmus minor*, *Tilia cordata*, *Sorbus aucuparia* and *Prunus padus*, which did not reach the canopy.

The relationship between tree age (*TE*) and trunk girth (*TG*) in 1998 was linear (regression analysis):

Betula: $TE = 0.93 * TG + 40.99$, $R^2 = 0.39$, $P < 0.001$;

Alnus: $TE = 0.94 * TG - 0.415$, $R^2 = 0.37$, $P < 0.05$.

The slope of the regression line was nearly the same for the two species ($P > 0.1$) but the increment differed between them ($P < 0.05$). In *Betula* the increment was close to 0, whereas in *Alnus* it was nearly 41. This difference can be explained by the fast growth of young *Alnus* trees and a stable increment in trunk girth in *Betula*. At present hardly any trees of either species younger than 40 yr can be found in the locality; most *Betula* trees are older than 70 yr. The distribution of the tree age of *Alnus* and *Betula* in the

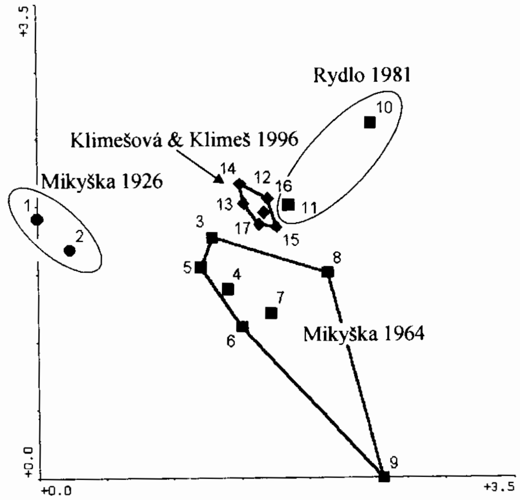

Fig. 4. DCA ordination of the presence/absence data based on relevés (1-17) recorded in the alder carr of the locality 'Na bahně' from 1926 to 1987.

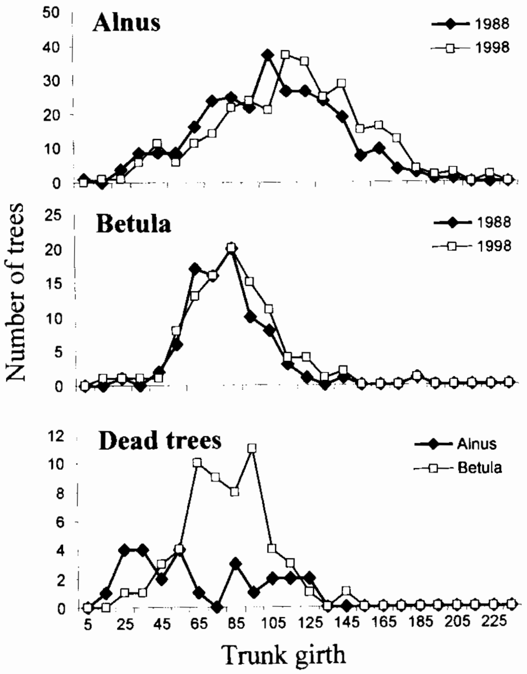

Fig. 5. Changes in size distribution of trunk girths in *Alnus glutinosa* and *Betula pubescens* in the locality 'Na bahně' from 1988 to 1998.

central and peripheral areas of the locality indicated that (1) the central part of the locality was colonized by *Alnus* in the 1950s and (2) the trees of the marginal belt of the locality established at the end of last century.

Current tree dynamics are characterized by ageing of the *Alnus* and *Betula* populations, and hardly any seedling establishment of either species. Trunk girth of *Alnus* trees increased significantly in the past 10 yr (Fig. 5), except for the smallest size classes. In *Betula* the increase was not so apparent because many big trees died during the last decade (Fig. 5). Mortality in *Alnus* was nearly the same in the middle and lower size classes, whereas no mortality has been recorded during the last 10 years in the higher size classes. From 1988 to 1998 8% of *Alnus* trees died, whereas in *Betula* 35% trees died and fell down.

Discussion

The development of the vegetation in the locality followed a classical alluvial successional series (Ellenberg 1986), starting with an oxbow, slowly filled up by sediments, later on developed into a wetland dominated by *Filipendula* and *Caltha*. At that time *Alnus glutinosa* was abundant in the pollen spectra but nearly missing among macrofossils, indicating its presence in the surroundings. Finally, before the second millennium, a *Sphagnum* bog developed and at about 1150 AD an alder carr established. It declined and re-established three times at least. The recent alder carr, situated along the foot of the terrace, established according to tree age, pollen and macrofossil data less than 130 yr ago. The centre of the locality was colonized by *Alnus* ca. 55 yr ago.

Our data show that an alder carr may persist in a locality over more than 800 yr. However, during the whole period the canopy of *Alnus* was not as dense as it is today. Its cover was repeatedly much reduced or even *Alnus* locally disappeared completely. The driving force of the cyclic development of the alder carr is unclear. The changes may be caused by the life history of *Alnus* itself. It cannot establish under a closed canopy and in small canopy gaps – a reduction of the tree layer cover to 30-50% is not sufficient for its establishment (Tucker & Fitter 1981; Korpel' 1995). Vegetative multiplication is also inefficient because the suppressed trees die soon. Therefore, the even-aged *Alnus* stands cannot persist for a time longer than the life-span of the alder, which is about 200 yr (Korpel' 1995), but in the study site usually less than 90 yr (Klimešová et al. 1997). The die-back of most *Alnus* trees in a stand may promote establishment of a peat bog with hollows and hummocks. The soil of the hummocks is relatively dry and therefore more appropriate for *Alnus* establishment than permanently wet sites (McVean 1956). Thus, an autogenous cycle in alder carrs may work, as suggested by Jeník (1980) and Faliński (1986). Alternatively, an allogenous cycle induced by cutting of adult alder trees by humans should be considered. However, the increased human activity indicated by a high incidence of pollen of synanthropic plants was not correlated with the decrease of *Alnus* pollen and macrofossils. Therefore, we do not have any additional evidence to support this explanation. Changes in hydrological regime of the locality could also explain the cyclic development of the alder carr. Human-induced changes in water table (Brock et al. 1989) and long-term fluctuations in water table caused by changes in river discharge (Janssen et al. 1995) have been described as factors enabling alder carr establishment. The pollen analysis, however, does not indicate any disrupt change in water regime of the locality.

The local source of spring water seems to buffer water level fluctuations caused by the river. The same holds for nutrients to some extent. Therefore, we conclude that the autogenous model of the cyclic development of the studied alder carr provides the most probable explanation of the observed pattern.

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Genetic diversity, competitive ability and neighbourhood structure of grassland communities

Herben, Tomáš[1*], Hadincová, Věra[1], Hara, Toshihiko[2], Krahulec, František[1], Pecháčková, Sylvie[1], Skálová, Hana[1] & Suzuki, Jun-ichirou[2]

[1]*Institute of Botany, Academy of Sciences of the Czech Republic, CZ-25243 Průhonice, Czech Republic;*
[2]*The Institute of Low Temperature Science, Hokkaido University, Sapporo 060-0819, Japan;*
[*]*Fax +420267750031; E-mail herben@site.cas.cz*

Abstract. A dominant plant of temperate nutrient-poor grasslands, *Festuca rubra*, possesses remarkable intraspecific differentiation both within and among localities. This differentiation concerns parameters that determine its spatial mobility and competitive ability, such as growth and tillering rate, sensitivity to red/far red light ratio and rhizome length and branching. An implant experiment in their native habitat showed that clones differing in these parameters also fared differently in the field. Our experiment showed that the response in the demographic parameters to the structure of neighbouring vegetation (species composition, biomass) was rather weak; the difference among clones in these parameters was pronounced. This suggests that the genetic composition of a population may have profound effects on the whole community dynamics.

Keywords: Competitive ability; *Festuca rubra*; Implant; Rhizome.

Introduction

A major part of plant ecology is based on the assumption that species can be represented by a set of quantities that are species-specific. Recent examples are species-specific growth forms (Grime et al. 1988), species-specific competitive effects (Silvertown et al. 1994; Law et al. 1997), Ellenberg indicator values (which express species' preferences to ecological factors; Ellenberg et al. 1991). Using similar logic, single species-specific quantities (means) have been typically used as state variables in plant stands to represent a population (variables such as average canopy height, mean population density, etc.; but see Hara 1993; Pacala & Levin 1997).

The same type of reasoning also affects treatment of the parameters of the environment. Again, mean values of the environment are often used to represent growing conditions of individuals (see e.g. Bell & Lechowicz 1994 for an extensive discussion of that matter).

It is rather obvious that each of these parameters has not only its mean, but also variance around this mean (Table 1). These variances may considerably affect dynamical behaviour of such a system (Hara 1993; Pacala & Levin 1997). For example, each individual experiences different environments since densities of neighbouring plants and correlated abiotic factors vary, both in time and space (Bell & Lechowicz 1994). As a result hereof, (1) different individuals of one species may encounter different neighbours, and (2) an individual plant may encounter different neighbours through its life-span (Mahdi & Law 1987). Performance of an individual in a stand is then a function of these environmental parameters. Along similar lines, species-specific parameters of the response are modified by intraspecific/intrapopulational differentiation.

A critical element is the 'interaction' between variation in the environment and genetic variation in the plant. Such interactions are commonly studied both in evolutionary ecology and in applied research on crops and their results are represented as 'reaction norms' which may or may not show genotype × environment interaction (G × E interaction; Via 1994). Most of the experiments are done with respect to variation in a single factor in the environment, often in culture. The critical issue here is that ecologically relevant experiments have to assess G × E interaction with respect to actual environmental variation that a plant encounters in the field: if within-stand variation is the question, then with respect to microhabitat variation. For example, our earlier experiments have shown that aboveground shoot growth and tillering and growth of the rhizome system in *Festuca rubra* is very plastic in response to spectral light quality and that this plasticity differs among genotypes (Skálová & Krahulec 1992; Skálová et al. 1997). These experiments, however, were done in a growth chamber; though every attempt was made to make the treatment differences to reflect environmental variation in the field, it is never fully possible. Therefore the reaction norm has to be evaluated using actual variation in the neighbour density in the field. To do this, we performed an implant experiment with multiplied genetically identical shoots originating from four clones; these shoots were planted back into the grassland to sample the actual range of microhabitats that occur there. To augment the biomass variation among microsites, half of the microsites were fertilised. Using this experiment it should be possible to tell (1) whether the actual microenvironmental variation is 'sensed' by the plant, and (2) whether this response to the environment is affected by intraspecific genetic differentiation. In addition, we assessed (3) how does the environment structure (presence and quantity of neighbouring plants) vary at the fine scale.

Table 1. Examples of components of plant performance in the stand: means and variances.

	Mean	Variance
Environment	Mean neighbourhood composition	Fine-scale variance in the neighbourhood composition
Plant	Species-specific growth rate	Genotypic/inter-individual variation in the growth rate

Methods

Study site

The study site was located in a mountain grassland in the Krkonoše Mts., northern part of the Czech Republic (Severka settlement, ca. 3 km NW of Pec pod Sněžkou, 50°41'42" N, 15 °42' 25" E, altitude ca. 1 100 m). The whole area has a harsh climate; the grasslands under study are not natural, but have been maintained by mowing and occasional manuring. The vegetation is rather short, most of the biomass being concentrated below 15 cm in height (Skálová unpubl.).

Experimental design

Four genetically non-identical clones of *Festuca rubra* sampled in 1987 at the study site were multiplied in the experimental garden in Průhonice. The genetic non-identity of these clones was assessed employing DNA RAPD using two primers. In June 1989, twenty individual shoots of each of these clones (each of them with three leaves) were planted into filter paper tubes of 1 cm in diameter and 5 cm long filled with a mixture of compost and peat. In July 1989, these tubes were implanted into an undisturbed grassland at the study site. They were implanted at regular intervals along four rows (with distance between implants 25 cm), with the clones arranged in a Latin square design. The distance between rows was 90 cm. After establishment, the number of shoots in clusters originating from individual implants and the growth and demography of the shoots were monitored till June 1994. All shoots within the clusters were tagged with coloured plastic rings. For all newly formed shoots, their origin, whether intravaginal or extravaginal, was recorded. In autumn 1992 and in spring 1993 half of the plants were fertilized with a mixture of phosphate, potassium, magnesium, calcium and nitrate and ammonia nitrogen (2.5 g/m^2 of each element) in a factorial design with the clones.

Each year in summer (after the July recording), the vegetation surrounding each implant was recorded. To collect information on neighbouring plants, a 10cm × 10cm plot (further referred to as 'plot') was positioned over the implant (with the implant in the centre). All living shoots of each species of grass and the number of leaves of dicots (mainly *Polygonum bistorta*) were counted in these plots. After counting, the plants within each 10cm × 10 cm plot were clipped at a height of 2.5 cm and the dry mass (dried at 70 °C) of the clippings was taken as an estimate of neighbourhood aboveground biomass.

Data analysis

The data were processed to yield the following variables: (a) natality and mortality over time, (b) intravaginal or extravaginal origin of each shoot, (c) within-season growth rate of shoots. These response variables were analysed for their dependence on clone identity, fertilization, neighbouring biomass and species composition. Species composition was summarised by means of partial principal components analysis (using the program CANOCO; ter Braak 1988). Biomass and year were used as covariables to remove correlation between the first PCA score and biomass that appeared if no covariables were used.

The effects of clone, treatment, neighbouring biomass and identity on natality and mortality was tested using generalized linear models using the Poisson distribution of errors and the log link. The number of shoots in each cluster in the summer of the previous year was used as a covariate. The effects of clone, treatment and neighbours on the mode of tiller formation for each newly formed shoot (i.e. intra- vs. extravaginal) were tested using logistic regression. All calculations using generalized linear models were done using the S-PLUS 4 system (Anon. 1997). The effects of independent variables on shoot size and relative growth rate (RGR) were tested by analysis of variance. A nested ANOVA with clone, treatment, biomass and species composition (first PCA score) as fixed factors and cluster as a nested random factor was used. Neighbouring biomass and PCA scores were divided into two classes according to the position of the mean. The maximum likelihood estimation of the ANOVA effects was used (using program BMDP; Dixon 1990). In all analyses, separate runs were done for the period 1991-1992 (before fertilization) and 1993-1994 (after part of the experimental area was fertilized).

Results

Structure of the neighbouring vegetation

There were only four main heterospecific neighbouring species in the surrounding vegetation (mean densities per 10 × 10 cm ± s.d., minimum and maximum): *Deschampsia flexuosa* (60 ±35, 4, 293), *Nardus stricta* (39 ±45, 0, 217),

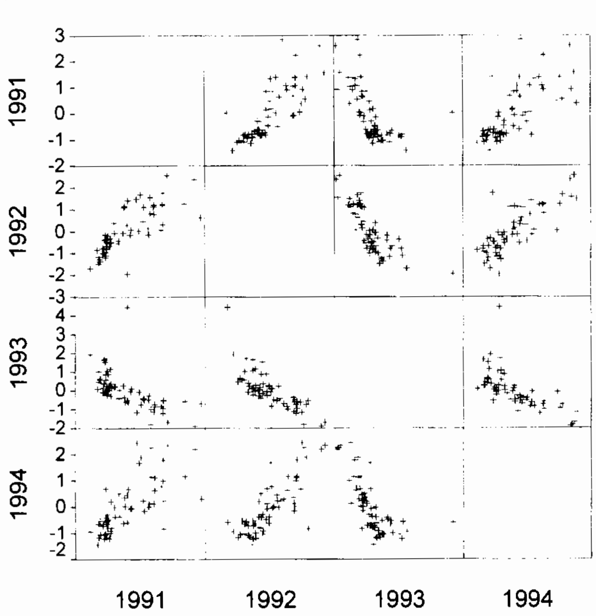

Fig. 1. Matrix plot of the scores on the first principal component axis of composition of neighbouring species recorded in 10 cm× 10 cm plots around *Festuca rubra* implants over four years. Each point refers to one implant. 1991, first principal component axis in 1991; 1992, first principal component axis in 1992, etc. The horizontal axis is scaled exactly the same as the vertical axis.

Anthoxanthum alpinum (20 ±14, 0, 73) and *Polygonum bistorta* (6 ±4, 0, 31). Principal components analysis of the number of shoots of the species present around each *Festuca* shoot cluster revealed strong intercorrelations among these species. The first principal axis accounted for 60.9% of the variation in the neighbouring species composition. The first axis separated neighbourhoods rich in *Nardus* (with negative first axis scores) from those rich in *Deschampsia* and *Polygonum* (with positive first axis scores). There was little change in the species composition over time; the scores of the first axis at individual microsites in different years were closely correlated (Fig. 1).

Total biomass of the vegetation was 2.11 g/10 × 10 cm (± 1.35, minimum 0.20, maximum 7.37). The biomass in individual plots was also correlated over time, but its year-to-year variation was higher than for the species composition and its temporal autocorrelation decays faster than that of the species composition (Fig. 2).

Plant response to the local environment

Total number of shoots, natality and mortality differed markedly between the clones (Table 2). In the first two years of observation (1991-1992), both natality and mortality were affected by the neighbouring species composition; individuals with a high density of *Nardus* in their neighbourhood had consistently lower natalities (results not shown), but the clone × neighbourhood interaction was not significant (i.e. this response was not clone-specific). In the last two years of the experiment (1993-1994), there was no detectable effect of the neighbouring species composition. In this period, natality was affected by neighbouring biomass; interaction clone × fertilization was also significant. In 1993-1994, mortality was not significantly affected by any of the factors.

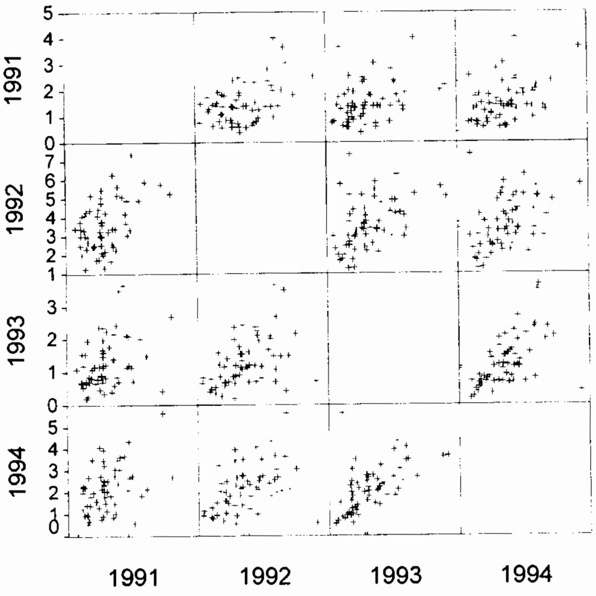

Fig. 2. Matrix plot of aboveground biomass recorded in 10cm × 10 cm plots around *Festuca rubra* implants over four years. Each point refers to one implant. 1991, aboveground biomass in 1991; 1992, aboveground biomass in 1992 etc. The horizontal axis is scaled exactly the same as the vertical axis.

The difference between clones in the proportion of extravaginal shoots was always significant (marginally significant in 1991-1992) (Table 2). The proportion of extravaginal shoots showed little response to environment. Two tests showed significant species composition (first PCA score) × clone interaction (for all unfertilized shoots and for all shoots in 1993-1994). In both cases a larger proportion of *Nardus* increased the proportion of extravaginal shoots in two clones (8, 20), whereas clones 13 and 19 did not respond to *Nardus* density.

There was no significant effect of the neighbouring species composition summarized by the PCA on the growth rate (Table 2). In contrast, biomass of the neighbours rather consistently affected the size parameters, both directly and in interaction with the clone (Table 2). In implants with high biomass of the neighbours, the spring size was invariably higher; the difference persisted throughout the growing season, but was weaker in summer.

Discussion

The experiment shows that the response in the demographic parameters to the structure of the neighbouring vegetation is rather weak. This is surprising since the variation in neighbouring plant density and correlated light levels changes severalfold across microsites (Skálová et al. unpubl.). This may be due to a large number of contrasting stimuli in the field, including soil heterogeneity, sunfleck movement with the stand etc. This phenomenon has important implications for the notion of plant plasticity. Although the plant is able to a remarkably plastic response to the environment, under field conditions this capacity of plastic

Table 2. Summary of clone-specific responses to micro-environment (implant experiment). The following statistical tests were used to test individual response variables: growth rate: nested ANOVA; shoot formation mode: logistic regression; natality and mortality: GLIM (Poisson errors, log link). Neighbour biomass is expressed per area of 10cm × 10 cm; 'neighbour identity' is the first principal component of shoot counts of individual species at this area. C×B = Clone × Neighbour biomass interaction; C×I = Clone × Neighbour identity interaction. + = $P < 0.1$; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

	Clone	Neighbour Biomass	C×B	Neighbour Identity	C×I
Shoot growth rate					
1991-1992		*	*		
1993-1994		+	*		
Shoot natality					
1991-1992	**			***	
1993-1994	***	**			
Shoot formation mode (intra- vs extravaginal)					
1991-1992	+	+			
1993-1994	**		+		**
Shoot mortality					
1991-1992				**	
1993-1994	+			+	

response is exploited by the plant to much lesser degree than under many experimental conditions. Obviously, the *potential* of the plastic response measured by a typical experiment is clearly less relevant to the plant's behaviour in the field than we often think.

A similar result has been found in other studies working with field densities (Fowler 1984, 1995; Bullock et al. 1994). In our view, it gives support to the argument of Law et al. (1993) that the field variation in competitive pressure is not pronounced enough to elicit a really consistent demographic response (see also Fowler 1990). In contrast to this, differences between clones were pronounced and concerned many parameters studied. The differences between the clones were strong enough to override the environmental variation in the field and produced consistent responses, e.g. in proportion of extravaginal tillers or overall natality. As a result, the between-clone differences in sizes of shoot clusters resulting from individual implants were gradually building up. The clone specificity in competition has also been shown by other studies (Taylor & Aarssen 1990; Mehrhoff & Turkington 1995; Miller & Fowler 1993).

An independent DNA RAPD study in the experimental grassland (Suzuki et al. 1999) has shown a high number of genotypes coexisting at a fine scale. This is the case in spite of genetic variation in plasticity which means that some genotypes may be better adapted over a range of microenvironments and should ultimately prevail. This indicates that the selective environments in the grassland does not lead to selection of one or a few 'best' genets. Possible (non-exclusive) explanations are (i) weak selective pressure relative to the age of the grassland, or (ii) differential selection at the seedling stage (this is not accounted for by this study).

The variation in plasticity with respect to microenvironmental variation may also have a community-wide effect. In such a case, the overall effect of one species on an other would depend on the genotype composition of the latter; in addition, the effect of the genetic variation will be coupled with the spatial effects due to the spatial distribution of genotypes in different microenvironments.

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Population dynamics of two winter annual species on a high salt marsh

Luque, Carlos J.[1*], Castellanos, Eloy M.[2], Castillo, Jesús M.[1] & Figueroa, M. Enrique[1]

[1]*Departamento de Biología Vegetal y Ecología, Facultad de Biología, Universidad de Sevilla, POB-1095, E-41080 Sevilla, Spain;* [2]*Departamento de Ciencias Agroforestales, Facultad de Ciencias Experimentales, Universidad de Huelva, Palos de la Frontera, E-21071 Huelva, Spain;*
Fax +34954626308; E-mail cluque@cica.es

Abstract. We have studied the population dynamics of two winter annual salt-marsh species, *Spergularia rubra* ssp. *longipes* and *S. nicaeensis*, in an environment affected by fluctuating stress-causing factors (salinity, rainfall, tidal water level). The study was carried out in the Odiel salt marshes (Huelva, SW Spain). Consecutive cohorts of individual plants were identified with markers in permanent plots. Data from two years are presented in this study. Density rates of all populations were very high at the beginning of each growing season. Seed rain values range from 1 785 000 to 506 000 seeds/m^2, and seed banks exceed 1 580 000 seeds/m^2. Shallow cracks on the ground surface of certain areas play an important role as safe sites and allow a permanent seed bank to be formed. The number of germinated seeds and the seed rain rates were positively correlated with the amount of rainfall of that season. The great quantity of seeds in the seed rain and in the seed bank suggests that these populations have a high growth rate potential.

Keywords: Fluctuation; Life cycle; Odiel; Population ecology; Safe site; Seed bank; Seed rain; *Spergularia nicaeensis*; *Spergularia rubra* ssp. *longipes*.

Nomenclature: Valdés et al. 1987.

Introduction

Population ecology is interested in the number of a particular plant or animal to be found in an area and how and why population sizes change. Hence, information on the phases of the plant life cycle provide useful intervals at which changes that take place in plant population size in relation to time can be analysed (Silvertown 1987). The information about the different phases in the life history of the plant is helpful to understand its population ecology. To know what happens in each phase and in the transition between different phases (age distribution of plants, fate of seeds and seedlings and predators) is vital for the population since it affects the potential members of the next generation. The study of these phases can become very complex. Seed stage constitutes a determining phase of the life cycle of plants. However, it is normally neglected in studies on plant population dynamics, because of the difficulty to work with seeds. The fate of the seed pool determines the population potential. Ungar (1987) emphasizes that few data are available concerning the quantitative relationship between seed production, seed rain and the soil seed bank. Seed rain cannot be considered as an unequivocal estimator of the seed production by surface established at time intervals, though sometimes the estimation can be approximated. Seed rain does not report on the surface seed pool either, since this seed pool can include the seed dormants that did not germinate during the previous season.

Moreover, the seed bank alone is not a good estimator of the seed production, since in fact the seed bank is constantly consumed by seed predators and is highly prone to fungi attacks, moreover, persistent seed can also originate from a previous season. Understanding the dynamics of the seed stage is a critical factor for a better understanding of other phases of the plant population.

In this work we have quantified the seed bank, population dynamics – with the number of born and died individuals by cohorts – and seed rain of two winter annual species (*Spergularia rubra* ssp. *longipes* and *S. nicaeensis*) for two cycles. Both species show high densities both as seeds and as vegetative individuals.

Material and Methods

Study sites and species

The study was conducted at three sites at the Odiel salt marshes (Huelva, SW Spain), which have a maritime Mediterranean climate. The rainfall is variable, with large interannual differences and shows striking differences in distribution during the growing season of plants for different years. During the cycle 1990-1991 the rainfall was 352 mm, whereas the cycle 1991-1992 was drier, rainfall rate down to 279 mm; in both cases below the annual average rainfall in this area (513.3 mm).

The species studied are winter annuals of the genus *Spergularia*, family *Caryophyllaceae*. *S. rubra* ssp. *longipes* populations occur on deposits of drained limestone material deriving from the channels of a nearby port area, locally known as the 'Eucaliptal'. This species is a primary colonizer on the natural marsh.

The other species is *S. nicaeensis* which occurs at two sites. One of the sites is similar to the *S. subra* sites and the other is located on the high marsh and is flooded periodically with higher tides. The first population is called 'Alta' and the second 'Ría'. In this stage of the secondary succession on the high marsh only populations of *Spergularia* appear.

Seedlings and mature plants

During 1990 16 permanent plots, each 5 m × 5 cm^2 in size, were established. In 1991 only five plots per population were used, since it was observed that these were sufficiently representative. Consecutive cohorts were identified with markers.

With this method we managed to control all emerging individuals and to eliminate risks of underestimating the population. The individuals recorded during the last sampling have been considered individuals belonging to the stage of mature plants.

Seed bank

Six seed bank samples were collected in each population with metal cylinders of 5 cm diameter and 5 cm depth. In the laboratory the samples were cut into 1-cm thick layers, and set to germinate in Petri dishes without limitation of water and under laboratory conditions.

Seed rain

Sticky traps were used to estimate the seed rain. These are dishes of 3.4 cm diameter, with a thin layer of vaseline. This substance is sticky and allows to trap the seeds while avoiding any possible dispersal by wind. The edge of these traps was high enough to prevent seeds already lying on the ground to fall onto the traps. In this way an overestimation of seed rain number was avoided. Furthermore, the vaseline is translucent, which makes the seed count easier. Finally, when heated the vaseline liquefies and the seeds are deposited in the bottom of the containers.

Between 20 and 25 containers were used for each population. The traps were always placed on the same place to record the seed rain from the same surface. Seed traps were replaced, carried to the laboratory, and the seeds deposited on each container were counted. The experiment ended when the size of the seed rain diminished. Finally, capsules also fall down on the traps. The seeds inside them were counted too. The count was carried out with the aid of magnifier binoculars.

Results and Discussion

The study began with the analysis of the seed banks of the three populations in 1990. We were able to obtain the previous persistent seed bank of 1989 of the *Spergularia rubra* population (non-germinated seeds produced in previous seasons), since the seed rain of 1989 had not been produced yet. In this persistent bank, 56 350 ± 36 465 seeds/m^2 (mean ± standard deviation) were obtained; the seed rain of 1989 constituted the seed bank of 1990-1991. (Figs. 1, 2 and 3).

Larger seed banks were recorded for the 'Eucaliptal' and 'Alta' populations. The rates of both species were higher than the highest known production of seeds from a seed bank for a flowering plant community: *Spergularia marina* with 471 135 seeds/m^2 as reported by Ungar (1988). The largest seed bank in this salt marsh was obtained in the first population, with a maximum value of 1 581 869 ± 505 271 seeds/m^2.

There are clear differences between the seed banks of the same species (*S. nicaeensis*) in different populations. The seed bank in 'Ría' is considerably smaller than that in 'Alta', probably due to 'Ría' being affected by periodic tidal flooding. The effect of the tide facilitates the dispersion of the seeds, and it is an important cause of seed loss from the seed pool in the 'Ría' population. However, the two populations with no flooding ('Eucaliptal' and 'Alta') presented huge seed banks, because they were not affected by the tidal dispersion process.

Fallen seeds end up in the seed bank of the three populations. When the ground dries shallow cracks may appear on the soil, especially in the 'Alta' site. The high seed bank values found are explained by the fact that the seeds are transported by the wind toward these cracks or traps that serve as 'safe sites' (Harper et al. 1961; Fowler 1988). The seed bank is highly superficial in the three populations. Seeds in the seed bank were most abundant (95%) in the first centimetre of the soil surface and numbers decreased progressively with depth (Table 1).

During the following growing season between 200 000 and 300 000 seeds/m^2 germinated, while only less than 25% reached the mature stage. In these populations a manifest population regulation occurs from the seedling phase to mature plants through dependent mortality process. With these high densities in the three populations, an increase in mortality is observed with high density, whereas mortality decreases with reduced population density (Luque 1996).

On the other hand, in the persistent seed bank of 1990-1991 between 5 and 10% of the seeds recorded in the seed banks remained. The persistent seed bank and the germinated seeds differ greatly from the seed bank content in 1990. So, most of the original seed pool was lost due to several causes (mortality, export, deep dormancy). These losses are essential for the seed banks, especially in disturbed habitats, since an important amount of this seed pool is eliminated. This mortality may be due to predation (mainly by ants), immaturity, fungal attack, decay, etc. Likewise, seed export may also be one of the main causes of the diminishing of the standing seed pool.

The seed rain began during spring time. It was abundant and differed according to the population, more than 1 700000 seeds/m^2 in 'Eucaliptal' and 613 000 seeds/m^2 in 'Ría' being obtained. The two populations with the same species (*S. nicaeensis*) show remarkable differences (613 784 ± 319 535 (in 1990) and 506 364 ± 272 746 (in 1991) seeds/m^2 in 'Alta' as compared with 1 035 841 ± 527 474 (in 1990) and 1 597 836 ± 820 743 (in 1991) seeds/m^2 in 'Ría'). The production of seeds was lower in the first population due to the difference in the number of flowers produced in the plants and to the lower density of the final reproductive individuals. This also accounts for the differences between the seed rain of 'Eucaliptal' and 'Ría' during the two years of study, being larger in the first population during 1990-1991, and 'Ría' in the second year.

Table 1. Number of seeds from different depths in the seed bank (1990-1991) of three populations. ($n = 6$).

	Seeds/m^2 (mean ± s.d.)		
Depth (cm)	Eucaliptal	Alta	Ría
Superficial	1482728 ± 465149	937018 ± 239035	220610 ± 76452
0-1	81657 ± 87746	472965 ± 241076	91334 ± 83330
1-2	15194 ± 22187	96257 ± 56465	9677 ± 12223
2-3	1443 ± 1265	34377 ± 33028	1019 ± 720
3-4	934 ± 1305	3141 ± 2760	764 ± 953

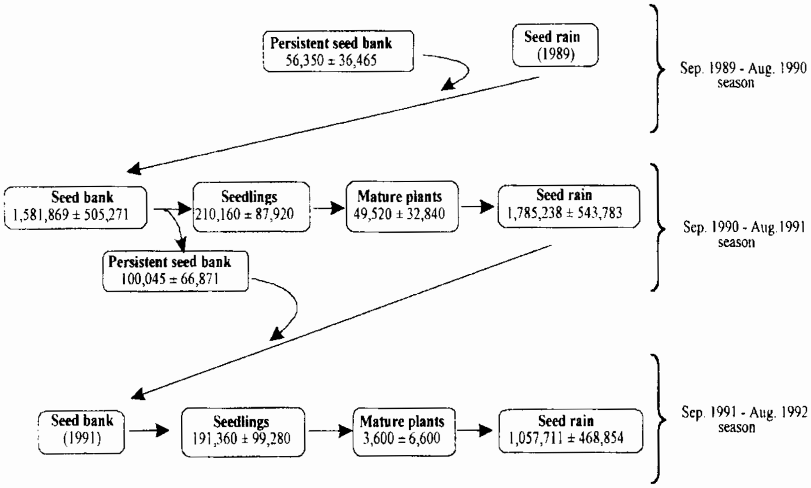

Fig. 1. Diagrammatic life cycles of *Spergularia rubra* ssp. *longipes*, population 'Eucaliptal'. (Mean ± standard deviation per m^2).

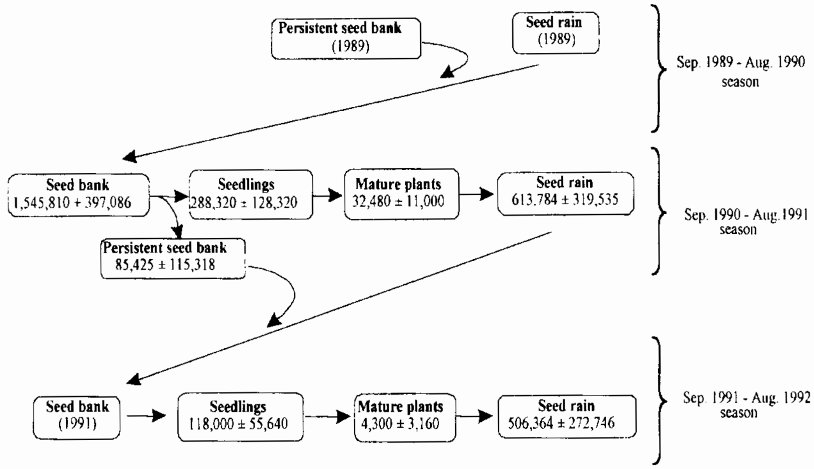

Fig. 2. Diagrammatic life cycles of *Spergularia nicaeensis*, population 'Alta'. (Mean ± standard deviation per m^2)

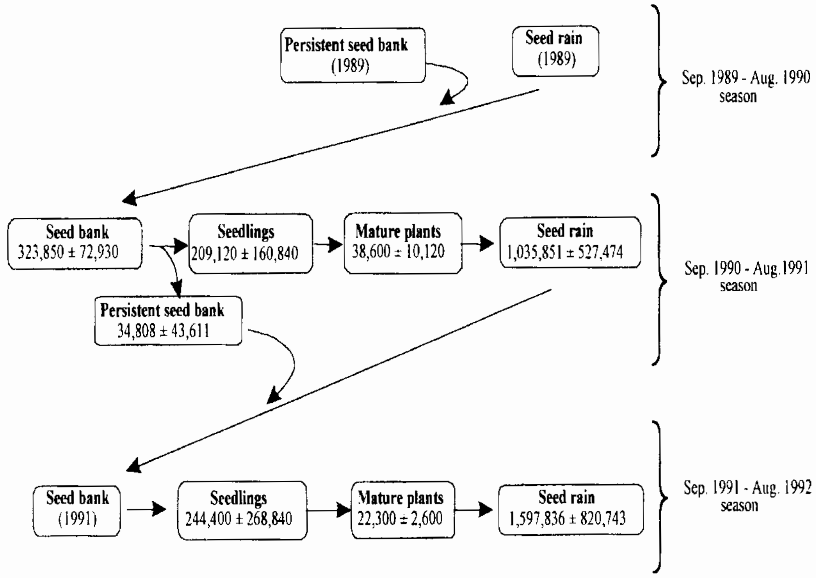

Fig. 3. Diagrammatic life cycles of *Spergularia nicaeensis*, population 'Ría'. (Mean ± standard deviation per m^2).

In the following seed banks (1991) germination rates ranged from 118 000 seeds/m^2 in 'Alta' – where the density was lower in relation to the previous season – to 244 400 seedlings/m^2 in the population 'Ría', increasing in relation to the season 1990-1991. 764 000 seedlings/m^2 were recorded in one of the plots of this population. Meanwhile, the population of *Spergularia rubra* showed densities similar to the previous year.

On the other hand, in the population of *Spergularia nicaeensis* with tidal influence ('Ría') there was an increase in the number of germinated seeds and in seed rain amount from 1990-1991 to 1991-1992, while in the tidal-independent populations ('Eucaliptal' and 'Alta') a decrease in the number of germinated seeds and seed rain is recorded between 1990-1991 (352 mm of rainfall) and 1991-1992 (279 mm).

Conclusions

In this study huge densities have been recorded in the seed rain and seed bank of the three studied populations. We have detected large interannual, interspecific and interpopulation differences in the seed stage of the population dynamics.

Spergularia rubra and *S. nicaeensis* belong to Type III of Thompson & Grime (1979) in relation to the behaviour of the seed bank and the patterns of deposition and germination of the seeds. This group includes species in which most of the seeds germinate soon after they are shed (usually in late summer), but in which a small proportion joins a persistent seed bank. These species tend to produce a large amount of small seeds, which frequently show dormancy (Fenner 1985). High seed rain and abundant seed bank occur frequently in disturbed habitats. The species in the present study perform a strategy that allow them to play a major role as colonizers in disturbed and productive habitats, such as the disturbed middle-high marsh where these populations occur.

The high production of seeds, estimated from seed rain and seed bank in the three populations that we have been studying, together with the strategy of these species induce a practically monospecific grassland.

There is a huge quantity of seeds lost from a phase to the following. This loss is an essential factor in the plant population dynamics in disturbed habitats since a high percentage of the seed pool is eliminated. In spite of the high proportion of exported or decayed seeds, the presence of shallow cracks in the soil acting as 'safe sites' contribute to form a large seed bank that allows the maintenance of the population.

With this study, we have shown the importance of the seed phase in plant population dynamics. Population dynamics during the seed stage proves to be an essential phase in the whole plant cycle and affects decisively following generations.The study of seed dynamics is crucial for a better understanding of many events of the later vegetative phase of plants (high mortality rates, densodependence processes, number of final reproductive individuals, etc).

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Regeneration dynamics in populations of two hemiparasitic species in wet grasslands

Petrů, Martina[1] & Lepš, Jan[1,2*]

[1]*Department of Botany, Faculty of Biological Sciences, University of South Bohemia, Branišovská 31, CZ-370 05 České Budějovice, Czech Republic;*
E-mail martina.petru@tix.bf.jcu.cz;
[2]*Institute of Entomology, Czech Academy of Sciences, Branišovská 31, CZ-370 05 České Budějovice, Czech Republic;* **Fax +42038 5300366; E-mail suspa@entu.cas.cz*

Abstract. Two semelparous biennial hemiparasites of wet grasslands, *Pedicularis palustris* and *P. sylvatica* (*Scrophulariaceae*), have been declining in the Czech Republic due to land management changes. Regeneration was studied in the field both by observation and experiment. Permanent 1-m^2 plots were set up in populations of both species in order to observe spatial patterns of established seedlings under natural conditions. A manipulative field experiment was conducted to test effects of disturbance regimes on recruitment. Treatments such as mowing, litter and moss removal, and creation of artificial gaps were performed in five replicate 0.25-m^2 plots. Seeds were sown into plots and the number of emerging seedlings was monitored over the growing season.

In the permanent plots, seedlings were clustered around mother plants, particularly in *P. sylvatica*. Seeds successfully germinated early, perhaps getting an early season advantage over neighbouring vegetation. However, high seedling mortality was found in late summer, which might be a result of self-thinning and caused by competition. In both species germination percentage in untreated control plots was low as compared to mown plots and plots with gaps. This supports hypotheses concerning the importance of available safe sites for species regeneration. A regular management regime and local soil surface disturbances seem to be important for the persistence of the two species.

Keywords: Disturbance; *Pedicularis palustris*; *Pedicularis sylvatica*; Management; Regeneration niche; Seedling recruitment.

Nomenclature: Rothmaler (1976) for vascular plants; Váňa (1997) for bryophytes.

Introduction

Pedicularis palustris and *P. sylvatica* (*Scrophulariaceae*), short-lived monocarpic species of wet grasslands, have been declining in their habitats over the last decades throughout Europe (Rosenthal & Fink 1996; Karrenberg 1998; Schmidt 1998; ter Borg 1979, 1985). The reasons of their decline in their community are of particular interest when mechanisms of species coexistence in grassland plant communities are studied (see Grime 1979; van der Maarel 1993; Palmer 1994). In the Czech Republic, these species were previously common on traditionally managed grasslands; but most populations have decreased rapidly in size or became extinct because of the cessation of management (usually mowing) or because of fertilizer application (Hendrych & Hendrychová 1989).

Successful establishment of new plants is a critical step in plant life history (regeneration niche; Grubb 1977, 1988). Differentiation of the regeneration niche is a major determinant of diversity in vegetation. Seedling recruitment of both these species is limited by the availability of safe sites (ter Borg 1979; 1985). Seedling recruitment decreases dramatically after cessation of the regular disturbance regime, such as mowing and grazing, traditionally used in European wet grasslands (Bakker 1989). We assumed that seedlings of these *Pedicularis* species recruit in gaps.

The aim of this study is to compare the regeneration dynamics of the two *Pedicularis* species. Seedling recruitment was monitored in permanent plots and the effect of disturbance regimes, including the creation of artificial gaps, was tested by the use of a manipulative experiment.

Material and Methods

Study species

Pedicularis is one of the largest genera in the family *Scrophulariaceae*, with several hundred hemiparasitic species. *P. palustris* is a hemicryptophyte with a winter bud (Hartl 1974). It occurs in irregularly mown or moderately grazed marshes, wet meadows and dune slacks (Hartl 1974). *P. palustris* prefers wet habitats such as marsh meadows, peatbogs and fens of the *Caricion lasiocarpae*, *Molinion*, *Caricion fuscae* and *Calthenion* communities (Dostál 1989). These habitats are inundated for at least several months of the year. *P. sylvatica* is a biennial, rarely perennial, hemicryptophyte with a winter bud (Hartl 1974). It occurs on moist and sandy or peaty soils within open vegetation. It is a characteristic species of the alliances *Violion caninae* and *Juncion squarrosi* and may occur also in *Caricetea canescenti-fuscae* and *Ericion tetralicis* communities (Westhoff & den Held 1969; Oberdorfer 1979; Dostál 1989). It also grows in woodland edges and paths (pers. obs.; ter Borg 1985). Both *Pedicularis* species usually behave as biennials and have short persistent seed banks (Thompson et al. 1997; ter Borg, Masselink, Jensen pers. comm.). After dispersal seeds of *P. sylvatica* will most likely germinate the following spring. Two separate cohorts of *P. palustris* can be distinguished (Watkinson & Gibson 1987). Seeds of one cohort germinate immediately after dispersal in late summer and overwinter as juveniles (winter annuals). The other cohort overwinters in a 'short persistent seed bank' (Grime et al. 1988) and germinates the following spring (biennials).

Study sites

Study sites for both species are situated in South Bohemia, Czech Republic, close to České Budějovice. Mean annual temperature is 7.8 °C and mean annual precipitation is 620 mm (Syrový 1985).

Pedicularis palustris - Dívčice

Observation and field experiments were carried out at Dívčice, 20 km northwest of České Budějovice, 49°06' N, 14°19' W, 380 m a.s.l. This site contains one of the last remaining populations in the region, which has been declining over the last five years from hundreds of generative *P. palustris* to only a few individuals (Bastl pers. comm.). The *P. palustris* population occurs at the border between a wet mesotrophic *Molinion* meadow and a *Caricion gracilis* stand.

Pedicularis sylvatica - Ohrazení

The *P. sylvatica* population was studied in a wet meadow, situated between an agricultural field and pine-oak woodland. The meadow was regularly mown until the late eighties, when it was abandoned. This meadow is located 10 km southeast of České Budějovice, 48°57' N, 14°36' E, 510 m a.s.l. The vegetation is characterized by the *Molinion* alliance.

Spatial pattern of seedling recruitment

Field observations were carried out in one 1-m^2 permanent plot, divided by a grid into 0.1 m × 0.1 m subplots within each species population. In August 1997 all fertile plants (already dead, releasing seeds, hereafter called mother plants) were marked and their position on the grid recorded. Seedlings in each subplot in the grid were counted in May 1998. Seedling spatial patterns were characterized by the variance:mean ratio, both of the number of individuals per subplot and the dependence of seedling number in a cell on the distance of the cell centre from the nearest mother plant.

Manipulative field experiment – effect of disturbance regimes on recruitment

A manipulative field experiment was started in August 1997 in each site. The experiment was arranged in five randomized complete blocks of 0.5 m × 0.5 m plots. Plots were divided into 25 subplots of 0.1 m × 0.1 m. Capsules of both species containing ripe seeds were collected in the beginning of July 1997 (*P. palustris*) and by the beginning of May 1997 (*P. sylvatica*) at the respective sites and stored at room temperature until August. 90 seeds of each species were sown by hand into the nine central subplots to minimize edge effects. By experimental sowing we can eliminate the effects of dispersal and study effects of treatments on germination and establishment only. In each block, the following treatments were used:

P. palustris: (1) untreated control; (2) mowing, where the aboveground biomass was cut and litter removed; (3) litter and moss removed without mowing; (4) small gaps were created (five gaps per plot, 5 cm in diameter cutting the sod about 3 cm deep and turning it upside down).

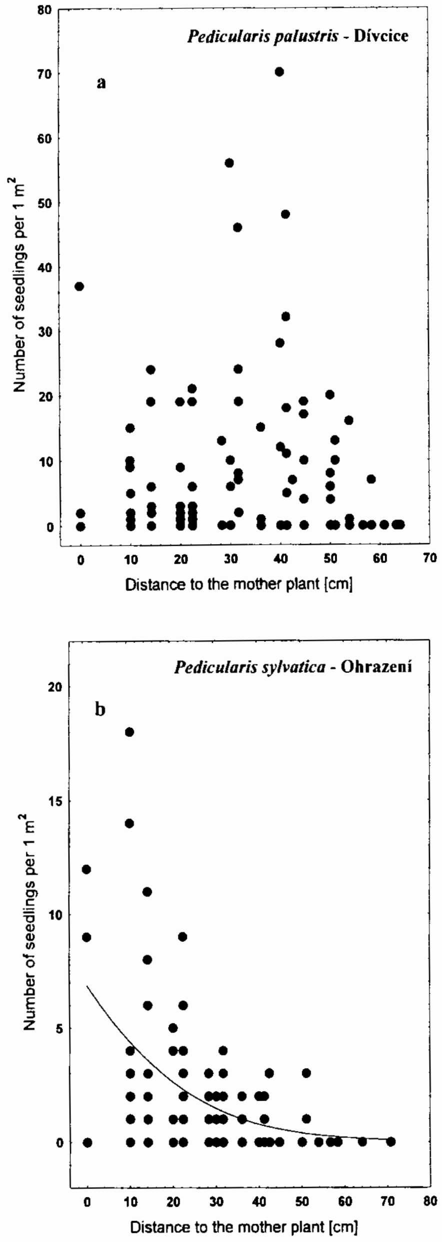

Fig. 1. Dependence of the number of seedlings in a 0.1 m × 0.1 m cell on the distance from the mother plant in **a.** *Pedicularis palustris* and **b.** *P. sylvatica*. The significant relationship ($p < 0.05$) was fitted by LOWESS regression. Note the different scales on the y-axis.

P. sylvatica: (1) control; (2) mowing with litter removal; (3) litter and moss removal; (4) small gaps (five gaps per plot, 5 cm in diameter) were created cutting the sod about 3 cm deep and turning it upside down; (5) large gaps (five gaps per plot, 10 cm in diameter) by cutting the sod about 3 cm deep and turning the cut portion upside down; (6) mowing, where the aboveground biomass was cut and both the litter and moss removed. In order to prevent the burying of seeds and standing water, gaps were shallow. Small-sized gaps only were created in *P. palustris* because of the very wet conditions and in the tall vegetation large gaps would be permanently filled with water. Both small and large sized gaps could be created in the short drier grassland occupied by *P. sylvatica* to study the effect of gap size on seedling recruitment. In drier *P. sylvatica* sites the effect of moss removal in mown plots on seedling establishment could also be studied. The following mosses were found in *P. sylvatica* plots: *Aulacomnium palustre*, *Climacium dendroides*, *Hylocomium splendens*, *Polytrichum commune*, *Rhytidiadelphus squarosus*, *Scleropodium purum*.

The number of emerging seedlings was monitored monthly over the growing season from April to August. In total 25 subplots in each 0.5 m × 0.5 m plot were studied with respect to possible seed dispersion from the central nine sown subplots. Periodic sampling provided information about seedling emergence until June. July and August data provided information on seedling survival.

Data analysis

The LOWESS regression in the non-linear estimation module in STATISTICA (Anon. 1996) was used to fit the relationship between seedling density and distance from the mother plant in permanent plots. A univariate repeated measures ANOVA model in STATISTICA (Anon. 1996) reflecting the block structure of the experiment was used to analyse data from the manipulative field experiment. In the repeated measures analysis the between-subject variation corresponds to differences between observed sampling units (block and treatment) and the within-subject variation corresponds to changes in time. Data were evaluated after logarithmic transformation $x' = \log(x + 1)$. Note that with log-transformed data, the interaction of time and treatment reflects differences in relative changes in time.

Results

Spatial pattern of seedling recruitment

Seedling spatial pattern was clustered (variance:mean ratio >> 1) in both species. In *P. palustris*, the highest number of seedlings was found 30 - 40 cm from mother plants. Only a few seedlings were found either within 10 cm of mother plants or further than 60 cm (Fig. 1a). In *P. sylvatica*, the number of seedlings decreased monotonically with distance from mother plants (Fig. 1b); the relationship was significant ($p < 0.05$).

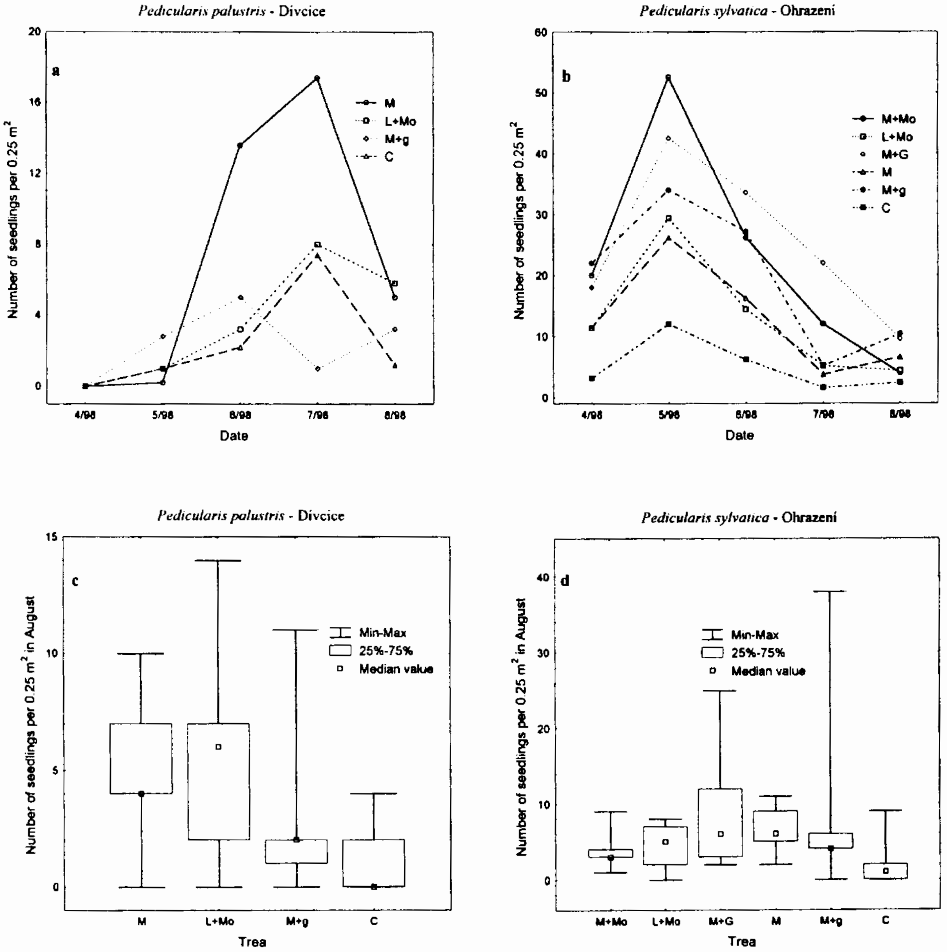

Fig. 2. Germination dynamics of *Pedicularis palustris* seedlings from April (4/98) to August (8/98) in the manipulative field experiment. **a.** *P. palustris*. Treatments were: **M**: mowing with litter removal; **L+Mo**: litter and moss removed without mowing; **M+g**: small gaps created in mown plot; **C**: control. Time × Treatment interaction was statistically significant ($p < 0.05$). For **b.** *P. sylvatica* treatments were: **M+Mo**: mowing with litter removal; **L+Mo**: litter and moss removed without mowing; **M+G**: large gaps created in mown plot; **M**: mowing with litter removal; **M+g**: small gaps created in mown plot; **C**: control. The effect of treatment was statistically significant ($p < 0.05$). Number of seedlings was average number per plot (out of 90 seeds sown). Box and whisker plots of seedling counts in August: **c.** *P. palustris*; **d.** *P. sylvatica*. Differences among treatments were not statistically significant. Note the different scales on the y-axis.

Manipulative field experiment – effect of disturbance regimes on recruitment

P. palustris. Seedling density increased from April to July in all treatments except in plots with gaps. The highest number of seedlings was recorded in July in mown plots (18 per 0.5m × 0.5m plot), in plots with litter and moss removed (8), and in control plots (8). From July to August the number of seedlings declined in these treatments. In plots with gaps the highest number of seedlings occurred in June (5) and some new seedlings were recorded in August (Fig. 2a). The Time × Treatment interaction was significant ($p < 0.05$) revealing differences in dynamics between treatments. High variability within treatments was found in August (Fig. 2c) and consequently differences between treatments were not significant. It should be noted that the control yielded the lowest number of seedlings surviving until the end of the season.

P. sylvatica. Germination mainly occurred in April and May in all treatments varying from 10 in control plots to 54 with moss removal. From May to August the number of seedlings in all treatments declined. However, from July to August the number of seedlings slightly increased in mown plots and in plots with small gaps (Fig. 2b). The number of seedlings differed according to treatment (significant effect of Treatment, $p < 0.05$), but the relative proportions were roughly constant over time (non-significant Time × Treatment interaction). Differences at the end of the season were not significant, probably because of the high variability within treatments (Fig. 2d). Again, the control yielded the lowest number of seedlings.

Discussion

Distribution of dispersed seeds around mother plants (called a 'seed shadow', Fenner 1992) corresponds with a clustered spatial pattern of seedlings found in both species sites. The distance of maximum seedling density can be influenced by the nature of the seed source (Fenner 1992). Differences between species are probably attributable to different plant heights. The height of fruiting *P. palustris* is 30-60 cm, however, plants usually break below the middle. Broken stems fall a distance of 20-40 cm and seeds drop out of capsules at this distance from the base of the stem. Fruiting *P. sylvatica* plants are low and drop seeds in their close vicinity. Consequences of postdispersal seed transport (hydrochory in *P. palustris* and myrmecochory in *P. sylvatica*) need further investigation.

Both species begin their life cycle much earlier than the neighbouring vegetation. We assume that optimal light conditions at this time enable the seedlings to recruit without being outcompeted (see van Tooren 1990; Špačková et al. 1998). This early germination may also be an advantage in their hemiparasitic life history.

The number of established seedlings depends on seed dispersal, germination, seedling establishment and mortality. *P. palustris* had lower germination than *P. sylvatica*. This might be caused by weather and different habitat condition. Rooy & Verhoeven (1985 unpubl.) show that seed germination of *P. palustris* is strongly influenced by water level fluctuation. They found that the best seedling establishment occurred in dry springs followed by wet summers preventing the plants from drying out. In our experimental plots high water levels in March and April 1998 caused poor germination at the beginning of the season. During a later dry period, from May to July 1998, germination percentage increased. A dry summer probably contributed to seedling mortality; in addition to the effects of self-thinning and competition from the established neighbouring vegetation. For example, gaps were exposed to direct sun and became dry during the summer. In mown plots and mown plots with litter removed, seedling establishment was successful (cf. Karrenberg 1998). The unmown control provided the worst conditions for species regeneration. Large variability within treatments probably reflects differences in microclimate, including air humidity (ter Borg 1985). *Pedicularis sylvatica* reached maximum germination in May with the lowest number of seedlings in control plots, and the highest in mown plots with moss removed and plots with large and small gaps. Seedlings of *P. sylvatica* recruited better in large-sized gaps compared to small ones. Extreme values in box and whisker for plots with gaps can be caused, in the case of *P. sylvatica*, by various microclimate and habitat differences causing variability in seedling counts. Litter removal studies (Carson & Peterson 1990; Špačková et al. 1998) have shown that created microhabitats may favour some plant species. However, our results do not show any seedling sensitivity to litter removal, even when in combination with moss removal.

For the *Pedicularis* species studied the lack of a persistent seed bank, with high spring germination and high late summer mortality can cause pronounced between-year fluctuations, making the species prone to local extinction. The seedling establishment phase is critical for population persistence (cf. Křenová and Lepš 1996) and in turn establishment is most influenced by management practices. Our experiments show a positive response of regeneration effort to most disturbance regimes, similar to other parasitic plants (Marvier & Smith 1997). Cessation of traditional management usually results in a decline of safe sites. This in turn causes suppression of seedling recruitment and can eventually lead to species extinction and a decline in species diversity.

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Is sex ratio variation in *Silene otites* affected by drought stress?

Soldaat, Leo L.[1,2] **& Lorenz, Helge**[1]

[1]*UFZ - Centre for Environmental Research Leipzig - Halle, Department of Community Ecology, Theodor-Lieser-Strasse 4, D-06120 Halle, Germany; Fax +49 3455585329;* [2]*Present address: Survey Department, P.O. Box 5023, NL-2600 GA Delft, The Netherlands;*
Email l.l.soldaat@mdi.rws.minvenw.nl

Abstract. The spatio-temporal pattern of sex ratio variation in populations of the dioecious plant *Silene otites* suggests that females are more susceptible to drought stress than males. This hypothesis was tested both in the field and experimentally in climate chambers. Sex ratio at the study site in Central Germany changed from slightly female biased in 1994 to strongly male biased in 1997 and 1998. The percentage of female plants in a year was negatively correlated with summer precipitation, suggesting that not female but male mortality is higher under drought stress. This could be confirmed under experimental conditions in climate chambers, where male mortality was higher when water supply of potted plants was stopped.

Keywords: Climate; Dioecy; Mortality; Spatial segregation of sexes; Vegetation cover.

Nomenclature: Tutin et al. (1993).

Introduction

In many dioecious plants the sexes respond differently to environmental conditions, female plants usually being more sensitive to unfavourable conditions than male plants (Bierzychudek & Eckhart 1988; Dawson & Ehleringer 1993; Freeman et al. 1993; Shea et al. 1993). One often investigated factor in this respect is water supply. In all nine studies mentioned by Bierzychudek & Eckhart (1988), in which the relationship between sex ratio and moisture was investigated, more females were found at wetter sites or more males at drier sites.

Silene otites occurs in dry and semi-dry grasslands from South- and Central Europe to Central Siberia (Hegi 1979). Its sex ratio has often been reported to be male-biased (Knuth 1894; Correns 1928; Westergaard 1958; Weeda et al. 1985), whereas female-bias is the rule in dioecious *Silene* species (Westergaard 1958; Mulcahy 1967; Lloyd 1974; Lovett Doust et al. 1987; Hermanutz & Innes 1994; Lyons et al. 1994; Taylor 1994). However, in dry grasslands in Central Germany Soldaat et al. (1997) found an unbiased sex ratio in *S. otites* in 1994 and an only slightly male biased sex ratio in 1995. Furthermore, they found female biased sex ratios in habitats with high vegetation cover. As a possible mechanisms causing this spatio-temporal pattern they suggested that females are more susceptible to drought stress than males. In this study we describe how the sex ratio developed over five years in relation to summer precipitation and we experimentally investigate the hypothesis that female mortality is higher than male mortality under drought stress.

Methods

Life history of Silene otites

Flowering in *Silene otites* starts in late spring and continues until late autumn, dependent on weather conditions. Part of the seeds germinate directly after seed ripening in early autumn, and a second germination takes place in early summer the next year. In both periods seedling density may be more than 300 plants/m^2. However, survival of the seeds germinated in early spring is extremely low (less than 0.5% of ca. 2000 seedlings in 1994) due to summer drought, whereas autumn seedlings have a much higher probability of survival. Field observations suggest that many young plants do not flower in the first summer after germination. It is not known whether the onset of flowering is primarily determined by plants size, plant age or environmental conditions. Mean life span is ca. 5 yr (Klotz pers. comm.) but individual plants may live much longer.

Annual variation in sex ratio and precipitation

From 1994 to 1998 34 populations of *Silene otites* were investigated in dry grassland on 14 porphyritic outcrops north of Halle (Sachsen-Anhalt, Germany). Each year in August all plants were counted and their sex was determined by visual inspection of the flowers. For details see Soldaat et al. (1997).

Drought stress experiment

From a seed mixture collected from about 25 *Silene otites* plants 117 plants were grown in each of two climate chambers (light/dark conditions = 16/8 h, temperature = 20 / 15°C, relative humidity = 80%). The plants were potted in a 3:1 mixture of sand and potting soil in 0.5 l pots and supplied with ample water. After three months, when most female flowers had formed seed capsules, all plants were watered by placing the pots in a water bath until no water was absorbed any more. At that moment eight plants had died or did not flower. From each climate chamber five plants of both sexes were selected randomly, washed and dried at 45°C in order to determine root and shoot dry weight. The number of rosette-leaves and rosette diameter of each plant were determined. After three weeks without water, when ca. 50% of the plants obviously had no aboveground living biomass any more, water supply was restored. Two weeks thereafter survival could easily be determined by scoring the presence or absence of new leaves.

Results

Annual variation in sex ratio

Both the overall sex ratio in the 34 populations of *Silene otites* and the mean sex ratio changed from slightly female-biased in 1994 to strongly male-biased in 1997 and 1998 (Table 1). In contrast with our expectation, however, the percentage females was not positively, but negatively correlated with precipitation (Fig. 1). Although this relationship was not significant, the pattern suggests that not female mortality, but male mortality is higher under drought stress. On the other hand, drought stress was probably not the main mortality factor in the study area: There was a continuous decrease in plant numbers from 1994 to 1997, despite the high summer precipitation in the latter year (Table 1).

Experiment

In both climate chambers male mortality was significantly higher during the drought treatment (Table 2). This is in contrast with our initial hypothesis, but it explains the relationship between precipitation and sex ratio in the field (Fig. 1). The only difference in biomass allocation between males and females that could be found was a higher number of leaves in female plants (Table 2). This difference, however, has not caused the lower mortality among females, as both the number of leaves and rosette diameter were not negatively but positively related to mortality (ANCOVA, binomial errors, covariate number of leaves: $p < 0.05$, covariate rosette diameter: $p < 0.001$).

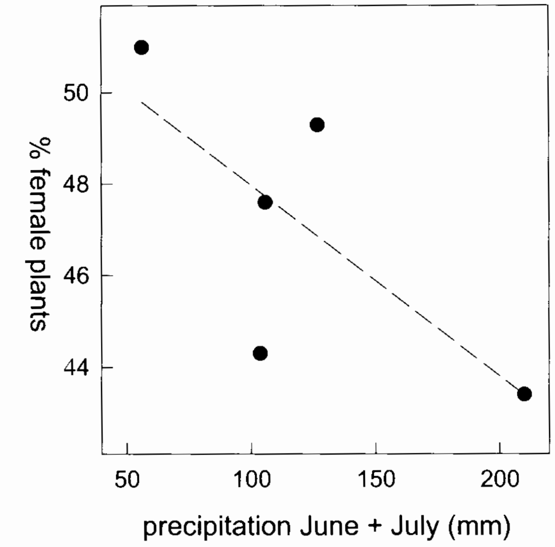

Fig. 1. Overall sex ratio in 34 populations of *Silene otites* in August and summer precipitation (Regression line: $r = -0.724$, $n = 5$, $p = 0.167$). The dotted line indicates an unbiased sex ratio.

Discussion

Both the field data and the results of the experiment are in contrast with the hypothesis that females are more susceptible to drought stress than males. Instead, male mortality is higher under drought stress. These findings are also in contrast with literature data on the spatial segregation of sexes in dioecious plants in relation to environmental conditions. As mentioned in the introduction, the proportion of female dioecious plants is usually higher under wet conditions. A generally accepted explanation for this pattern is that females have less resources to survive environmental stress than males because of the higher investment in reproduction (Bierzychudek & Eckhart 1988). In the experiment reported here, however, differences in biomass allocation between male and female *S. otites* plants seem not to have caused the difference in drought stress susceptibility.

Most plants in which sex could not be determined (see Table 1) were infected with the smut fungus *Ustilago major*. This pathogen forms spores in the flowers and thus sterilizes the plant. Both sexes are equally susceptible to the fungus (Soldaat et al. 1997), which means that the reported sex ratios are not biased due to fungal infection. The mechanism causing male bias in *S. otites* populations remains unknown. If the only environmental effect on sex ratio is the higher male mortality under drought stress reported in this study, then sex ratios can only be unbiased

Table 1. Sex ratio development in 34 *Silene otites* populations and changes in plant numbers from 1994 to 1998. n = total number of flowering plants of which the sex could be determined; n_{st} = total number of plants with stems; n_{nf} = total number of non-flowering plants (% in parentheses).

Year	Sex ratio (% females)				
	Overall	Mean ± s.d.	n	n_{st}	n_{nf}
1994	51.0	52.9 ± 11.5	4960	5445	1758 (24)
1995	47.6	49.0 ± 11.9	3669	4525	927 (17)
1996	49.3	52.1 ± 13.5	2830	3618	972 (21)
1997	43.4	42.3 ± 14.6	1618	2186	1758 (45)
1998	44.3	43.2 ± 11.7	2344	2946	615 (17)

Table 2. Biomass allocation and mortality of male and female plants in the drought stress experiment. The differences between sexes were tested with generalized linear models with sex and climate chamber as factors. Interactions between climate chamber and sex were not significant. The number of leaves, rosette diameter and mortality were higher in chamber 1. Mortality was tested using binomial errors; all other variables were untransformed. *** = $p < 0.001$; n.s. = not significant.

	Male plants		Female plants		
	Mean ± s.d.	n	Mean ± s.d.	n	Sign.
Shoot dry weight (mg)	1.26 ± 0.46	10	1.50 ± 0.57	10	n.s.
Root dry weight (mg)	0.43 ± 0.14	10	0.45 ± 0.21	10	n.s.
Shoot:root ratio	3.10 ± 1.41	10	3.47 ± 0.87	10	n.s.
Number of leaves	61.2 ± 19.0	109	74.9 ± 22.1	117	***
Rosette diameter (cm)	10.2 ± 1.4	109	10.4 ± 1.7	117	n.s.
% mortality chamber 1/2	92/72	38/61	62/26	64/43	***

(under favourable environmental conditions) or female biased (under drought stress). This is not true for the study site: In four of the five years sex ratio was male biased. Furthermore, *S. otites* populations were often reported to be male biased as mentioned in the Introduction. Thus, some mechanism is working in favour of male plants. A possible mechanism is a higher male longevity. Mean longevity of S. *otites* is ca. 5 yr (S. Klotz pers. comm.). Simple calculations showed that the percentage of female plants in a population rapidly decreases if females live five years and males six years. It remains to be studied, however, whether male longevity is higher under field conditions.

We are aware of the fact that the field data is only weak evidence for higher male mortality under drought stress. Moreover, the relationship shown in Fig. 1 could also be explained as a continuous decrease of the percentage females in time, independent of drought stress. Stronger evidence is given, however, in follow-up research in which sex ratio changes in the field are related to estimated water availability (Soldaat et al. 2000).

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The influence of *Carpinus betulus* on the seed bank in natural oak forest, NE Poland

Panufnik, Dorota* & Kwiatkowska, Anna J.

Department of Plant Ecology & Nature Protection,
University of Warsaw, Aleje Ujazdowskie 4, PL-00-478
*Warszawa, Poland; *Fax +48 22 6216835;*
E-mail panufnik@bot.uw.edu.pl

Abstract. In the Bialowieża Primeval Forest, stands of the *Potentillo albae-Quercetum* ('oak forest') have been invaded by *Carpinus betulus* for the last 30 yr, which caused the disappearance of many light-demanding perennials. The influence of *Carpinus* on the species richness and size of the seed bank and the contribution of light-demanding species to the herb layer and seed bank were analysed. The research was carried out in two parts of the forest: with *Carpinus* present only in the herb layer (A), and present in the shrub and tree layers (B). Soil samples were collected and kept in an unheated glasshouse. Emerging seedlings were recorded from 1995 to 1997. In the first year as much as 75% of the species and 80% of the seedlings appeared in the samples from both plots. The herb layer in B was poorer in species than in A. The species richness of the seed bank and the density of seedlings were significantly lower in B than in A. It is remarkable that in B there were twice as many light-demanding species in the seed bank as in the herb layer, while in A these numbers were equal. The species absent from the vegetation might be the most persistent components of the seed bank.

Keywords: Hornbeam invasion; Light demand; *Potentillo albae-Quercetum*; Seedling.

Introduction

The long-term study on permanent plots in phytocoenoses of the *Potentillo albae-Quercetum* ('oak forest'), located in the Bialowieża Primeval Forest, showed that these communities constantly decline in the region (Faliński 1986). It was affirmed that both the number and area of the remaining patches decreased (Faliński 1986; Kwiatkowska 1986; Kwiatkowska & Wyszomirski 1988). This process is directly caused by gradual invasion of the oak forest patches by the hornbeam (*Carpinus betulus*) undergrowth (Kwiatkowska & Wyszomirski 1990). The expansion of *Carpinus* leads to a drastic change of light conditions on the forest floor as soon as *Carpinus* juveniles grow to the shrub layer (Kwiatkowska & Wyszomirski 1988, 1990; Kwiatkowska et al. 1997). At the beginning, the influence of the dense *Carpinus* undergrowth on the herb layer causes in many light-demanding species, typical of oak forest, a decrease in seed production, next a decrease in their density, and finally their disappearance from the patch (Kwiatkowska 1994 a,b; Kwiatkowska et al. 1997). As the seed rain of the light-requiring species is gradually getting poorer and poorer, this may bring about a decrease in the size of the seed bank in the soil. The previous study (Jankowska-Blaszczuk et al. 1998) showed that the soil seed bank in phytocoenoses of the *Potentillo albae-Quercetum* which are undisturbed by man, is relatively large (> 1000 seedlings/m^2), rich (>20 species/m^2) and dominated (> 60%) by the species with high light requirements.

One might suppose that highly light-demanding species do not produce long-term persistent seeds, the interruption of continuous seed input to the soil may cause a decrease in the number of those species in the seed bank, and next in the patches of oak forest that have been invaded by hornbeam for the last 20-30 yr.

The main aim of this study was to verify the hypothesis that *Carpinus* undergrowth influences the density, species composition and species richness of the soil seed bank in the oak forest. Assuming that the seed bank is mainly formed by diaspores being produced within the community we also intended to assess by comparison the persistence of the seeds of those highly light-demanding species that disappeared from the patch after the beginning of the *Carpinus* invasion, but are still present in the seed bank.

In this work the light demands of species are expressed according to the 0-9 scale of Ellenberg (Lindacher 1995) that indicates the ecological optimum of light conditions for species.

Methods

The study was done in the best preserved and described phytocoenosis of the *Potentillo albae-Quercetum* (Kwiatkowska 1994 a, b; Kwiatkowska et al. 1997) in the Landscape Reserve in the Bialowieża Primeval Forest (23°31' - 24°21' E, 52°29' - 52°57' N). The invasion of this community by *Carpinus betulus* began from its northern margin about 30 yr ago (Kwiatkowska 1986). At present, in the marginal part of the phytocoenosis the hornbeam individuals occur in the tree canopy whereas in its central part most of them grow in the herb layer (Kwiatkowska 1994 a, b; Kwiatkowska et al. 1997). In 1994 two permanent plots of 240 m^2 (A and B) were established to analyse both the structure of the herb layer and the size of the hornbeam population. Plot A was located in the best preserved part of the patch and it included the area of the species-rich herb layer with the hornbeam juveniles not higher than herbs. Plot B was established within the same phytocoenosis, in the part with many *Carpinus* individuals in the shrub and tree layers.

The plots (6 m × 40 m) were divided into 60 subplots of 2 m × 2 m. In the summer of 1994, in every 4 m^2 subplot all species of vascular plants were recorded and their frequency (F%) was estimated as a ratio of subplots in which a particular species occurred in all subplots. In 1995 in every subplot the trunk diameter of all hornbeam individuals was measured just above the ground.

In the early spring of 1995, 20 soil samples, with a surface area of 30 cm × 40 cm and 10 cm deep each, were taken from a corner in 20 subplots of 4 m^2, located along the central 2 m × 40 m transect in both plots A and B. After

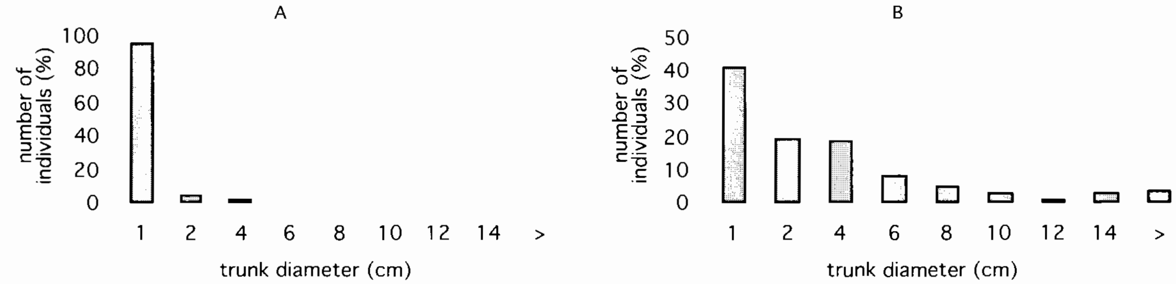

Fig.1. The size structure of the *Carpinus betulus* population in two 240-m^2 plots established in the oak forest: A – with *Carpinus* mainly in the herb layer, and B – with *Carpinus* in the shrub and tree layers.

stems and roots had been removed, the same soil volume from every sample was put into a plastic tray of 30cm × 40 cm. The soil was mixed to stimulate germination. The samples were kept in the unheated glasshouse of the Bialowieža Geobotanical Station for three growing seasons: 1995, 1996 and 1997. For all species (or genera) recorded in the seed bank the number of seedlings and frequency (F% – a ratio of soil samples in which a species was present in all samples) were estimated.

The light requirements of the species found in the herb layer and seed bank were determined using the scale of the light index L of Ellenberg (Lindacher 1995). This scale indicates species which are shade-tolerant (L = 0, 1, 2), moderately (L = 3, 4, 5) or highly (L = 6, 7, 8, 9) light-demanding.

The significance of differences between the mean number of species and seedlings per sample of 0.1 m^2 in both plots was assessed using *t*-tests.

Results

The study plots differed considerably in the amount of light reaching the herb layer due to a high density of the *Carpinus* population in the tree and shrub layers. In plot B the *Carpinus* saplings and trees (trunk diameter ≥ 2 cm) constituted ca. 60% of all individuals whereas in plot A most of the *Carpinus* individuals (95%) did not grow above the herb layer (trunk diameter ≤ 1 cm; Fig. 1).

The influence of the *Carpinus* undergrowth on the herb layer in B after more than 10 yr became evident in a decrease in the number of species with light demand values from moderate to high. In plot A there were more than twice as many such species as in plot B (80 and 35, respectively). The contribution of only highly light-demanding species to the herb layer in A amounted about 50% (Fig. 2), which indicates that the *Potentillo albae-Quercetum* is a thermophilous community. Altogether, there were 86 herb layer species per 240 m^2 in plot A, and 39 in B. Of all species in A 19 (22%) occurred frequently in the patch (F ≥ 60%),

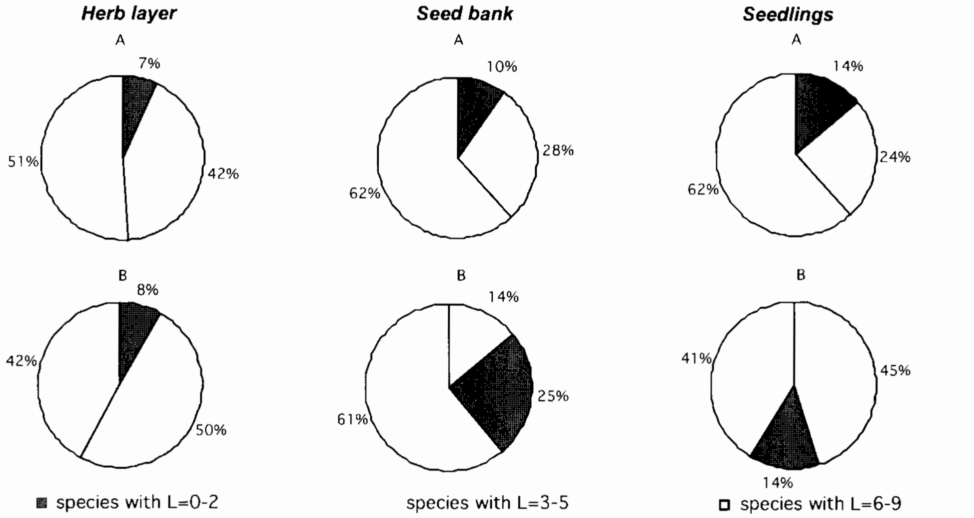

Fig. 2. The contribution (%) of species with different light requirements (shade-tolerant with L=0-2, moderately light-demanding with L=3-5 and highly light-demanding species with L =6-9) to the herb layer and seed bank as well as the contribution of their seedlings to the seed bank in the plots A and B.

Table 1. The mean number of species, including those with different light demands (shade-tolerant with L=0-2, moderately light-demanding with L=3-5 and highly light-demanding species with L=6-9) per 0.1 m^2 and the mean number of their seedlings per 0.1 m^2 in the seed bank samples from the plots A and B.

	A	B
Mean number of species and genera		
Total	22.8 ± 4.9	13.8 ± 3.0
Species with L=0-2	2.1 ± 1.1	2.8 ± 1.0
Species with L=3-5	5.9 ± 1.9	3.3 ± 1.6
Species with L=6-9	12.5 ± 3.1	6.4 ± 2.0
Mean number of seedlings		
Total	154.7 ± 69.9	45.9 ± 45.3
Species with L=0-2	18.7 ± 44.4	12.4 ± 23.7
Species with L=3-5	32.8 ± 24.6	7.1 ± 4.6
Species with L=6-9	78.5 ± 36.1	17.7 ± 7.1

whereas 44 (ca. 50%) did not have frequencies higher than 20% (Fig. 3). Of those rare species as many as 35 were absent from the herb layer in plot B. The presence of *Carpinus* undergrowth in plot B caused a decrease in both the total number of species and frequency of the remaining ones: only four species (ca. 10%) turned out to be relatively frequent (F ≥ 60%).

In all seed bank samples from both plots A and B as many as 75% of species and 80% of seedlings appeared in the first year of observation, 10-15% in the second and 5% in the third year. On the whole, in both cases species with high light requirements dominated the seed bank; they constituted ca. 60% of all species (in A and B) and seedlings (in A). The contribution of those to the seed bank was also higher than to the herb layer in both plots (Fig. 2). Of all species or genera found, herbs dominated the seed bank. The seed bank in both plots turned out to be dominated (about 60%) by species with low frequency (F≤20%) in the soil samples. The contribution of frequent species (F≥ 60%) did not exceed 20% (Fig. 3).

In plot A 3093 seedlings emerged in all samples over three growing seasons (1289/m^2). Of the 76 species of vascular plants found in all samples from plot A, three were trees (two *Betula* spp. and *Carpinus betulus*) and two were shrubs (*Rubus* spp.). The tree and shrub species constituted only ca. 6% of the total number of seedlings. In plot B, in all soil samples 918 seedlings emerged (383/m^2), thus ca. three times less than in plot A. The total number of species also turned out to be smaller in the samples taken in B (56) as compared to A. The same trees and shrubs as in the seed bank in A were found in the seed bank in B. The seedlings of *Salix* spp., that emerged as well, probably came from the contamination of samples by seeds from willows growing near the glasshouse. In the samples from B, the trees and shrubs constituted ca. 17% of the total number of seedlings.

The shading of the forest floor for more than a decade by the *Carpinus* undergrowth and trees in plot B led to a significant decrease in the mean number of moderately and highly light-demanding species (with L=3-9) in a soil sample of 0.1 m^2 ($p<0.001$). The mean number of all seedlings emerging from the seed bank decreased significantly as well, especially of those with moderate to high light requirements ($p<0.001$). The number of seedlings of shade-tolerant species varied considerably among the soil samples from both plots. This variation was strongly influenced by the emergence of *Urtica dioica*, which is also visible in the high (40%) contribution of shade-tolerant species to the total number of seedlings (Table 1, Fig. 2).

Generally, the spatial variation of all seedlings among the samples during three growing seasons was considerable and the coefficient of variation was high in both plots (≥50%).

Discussion

Our results show that even in the patches of the *Potentillo albae-Quercetum*, poorer in species due to the hornbeam invasion and similar to the shady *Tilio-Carpinetum*, highly light-demanding species constituted more than 60% of the seed bank. This confirms the broadly accepted hypothesis that the formation of a persistent seed bank is a survival strategy typical of species with high demands for light (Leck et al. 1989). This study revealed that the invasion by *Carpinus* undergrowth caused a decrease in the number of highly light-demanding species in the herb layer, and in consequence, the number of those in the seed bank. However, most of the highly light-demanding seed bank species were those having been absent from the herb layer for many years. In addition, the contribution of the high light-demanders to the seed bank was higher than to the herb layer. This suggests that seeds of these species are probably long-persistent in the soil (Thompson et al. 1997). In the

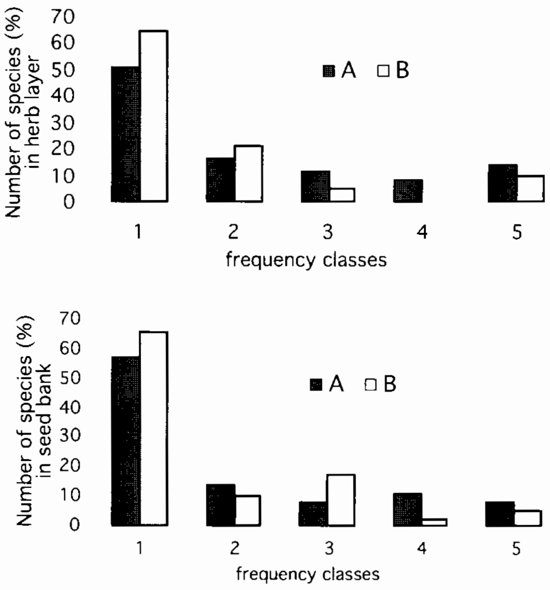

Fig. 3. The contribution (%) of species with frequencies: 1 (1-20%), 2 (21-40%), 3 (41-60%), 4 (61-80%) and 5 (81-100%) to the herb layer and seed bank in the plots A and B.

seed bank in both plots there were also species with moderate light requirements, but their contribution was much lower than to the herb layer. The results showed that diaspores of most highly light-demanding species remain viable in the soil as long as for two decades. The study by Falińska (1999) indicated similar longevity of seeds for species with a high light demand.

For the past 30 yr (15-20 yr of direct influence of the *Carpinus* saplings and trees on the herb layer) the species composition of the seed bank has become much poorer. Thus, the lack of recently produced seeds in the soil brought about a decrease in the seed bank density (the number of seedlings/m^2 about three times smaller) and species richness (the number of all species smaller by ca. 25% and of the highly light-demanding ones by ca. 30%). The negative influence of the tree canopy on the size and species richness of the seed bank was proved in many studies focused on the seed bank changes during secondary succession (e.g. Beatty 1991; Warr et al. 1994; Kalamees & Zobel 1998; Leck & Leck 1998; Falińska 1999). It should be emphasized that the highly light-demanding species found in the seed bank in this study are typical of natural oak forests with sparse tree stands, and without pioneer species. In the landscape changed by man, species spread into habitats with a high influx of light where they form communities of forest edges, meadows and tall herbs.

The Bialowieža Primeval Forest used to belong to the Polish kings and it used to be exploited as an attractive place for game hunting. In the 20th century the area, which had never been deforested, became a strict reserve. The fate of trees in the protected area depends only on the natural dynamics of tree populations and such random events as tree-falls caused by wind or snow. The vegetation in this region was formed after the last glacial period. The communities of the *Potentillo albae-Quercetum* originated 5000 -4000 yr ago, ca. 1000 yr after the shady *Tilio-Carpinetum* had spread into this region (Ralska-Jasiewiczowa & Latalowa 1996). Therefore, it does not seem possible that seeds of the species with high light requirements have persisted in the soil for a few thousand years.

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Competition and resource availability of two graminoids: a mini-rhizotron study

Röttgermann, Matthias

Plattenstr. 5, DE-74229 Oedheim, Germany
Fax +4989 2443 30750; E-mail roettgermann@foni.net

Abstract. Competitive interactions between plants are frequently the determining factor for vegetation patterns within terrestrial ecosystems. In resource limited areas belowground competition seems to play a dominant role. While most studies on this subject use nutrients as the main limiting resource, the present study investigated responses of two competing grass species (*Carex arenaria, Deschampsia flexuosa*) to changes in water availability as a common limiting resource on sandy soils. In a mini-rhizotron experiment with a low nitrogen content of 0.005% (d.w.), relative competition intensities (RCI) were investigated. Values of RCI showed two differing phenomena: 1. Under high water availability *D. flexuosa* exhibited a reduction in root area by competition, whereas *C. arenaria* was not influenced at all. 2. Under low water availability both species showed a decrease in root area.

Keywords: Belowground competition; *Carex arenaria*; *Deschampsia flexuosa*; Relative competition intensity; Sandy soil; Water availability.

Introduction

From the viewpoint of nature conservation inland sand dunes are among the most valuable ecosystems of Central Europe. Although there are descriptive studies of the vegetation dynamics (e.g. Pott 1992) the ecology of these systems and particularly the causal background of plant succession in this system are only poorly understood. As decisive factor for the transition between single states we suggest changes in competitive balances (Tilman 1988, 1985); therefore it is necessary to determine the competitive ability of dominant plants dependent on the abiotic factors. Because of the fact that belowground competition is the dominant interaction in nutrient-limited habitats (Wilson & Tilman 1993), it was essential to investigate the consequences of belowground competition. Especially the first successional stages of inland dunes can be described as continuously nitrogen-poor open stands with patchy distributed densely growing individuals of different plant species. Further, these ecosystems are characterized by an alternating water availability and the resource water itself seems to be important for the growth of the plants (Boorman 1982; Fitter 1997; Onyekwelu 1972; Rode 1995; van Rheenen et al. 1995; Watt 1936; Willis & Jefferies 1963). Because of the fact that the dynamic interactions of root development are important for the competitive balances between plants (Aerts et al. 1989; Shipley 1994) we analyzed the influence of water availability on belowground competition of two dominating grass species of sandy dry grasslands in Germany.

Material and Methods

The species

For the experiments we used two dominant species of these inland dunes with two differing growth forms: *Carex arenaria* (*Cyperaceae*), sand sedge, is a sympodial rhizomatous plant, typical of a variety of mostly nutrient-poor habitats including sand dunes and open woodlands (Oberdorfer 1994; Pott 1992). The species forms extensive perennial rhizome systems, with rhizomes of variable length. *Deschampsia flexuosa* (*Poaceae*), wavy hair-grass, is a thicket grass with a short rhizome. This plant is also perennial and common on sandy soils. Both species are often found on inland dunes in northern Germany and are dominant plants on sandy soils. The plant material used in this study was propagated from four original plants from both species collected in the Senne area near Bielefeld. The original material was collected in autumn 1996 and multiplied clonally in the greenhouse until the start of the experiment in July 1997.

Experimental conditions and design

Belowground competition between *C. arenaria* and *D. flexuosa* was experimentally assessed in mini-rhizotrons (height: 30 cm, width: 50 cm, depth: 3.5 cm) filled with 5.25 dm^3 pure sand. The length of the experiment was one month and we used four replicates. Total nitrogen content of the substrate was similar to the field situation (< 0.005%). Experimental plants for the present investigation were obtained through vegetative multiplication from one genet originating from the inland dunes near Bielefeld (08° 41' 17" E, 51° 55' 04" N). The clonal fragments used consisted of one ramet (*C. arenaria*) and five ramets (*D. flexuosa*) with a rooted rhizome of 10 cm length and a fresh weight of 1 g. A ramet was defined by one shoot with its attached rhizome and roots. Therefore the clonal fragments of the two species had the same fresh weight, the same rhizome length and represented both a juvenile plant of these species. For the mixture treatment one clonal fragment of *C. arenaria* and one of *D. flexuosa* were planted in a mini-rhizotron. For the monoculture each mini-rhizotron contained two clonal fragments of each species. Plants were grown under two different water treatments: (1) high water: plants were watered every second day up to field capacity, and (2) low water: plants were watered up to field capacity only once at the beginning of the experiment (1 July 1997). Consequently the water availability decreased only in the low water treatment and was the crucial resource for plant growth different to the high water treatment. The mini-rhizotrons were kept in a growth chamber under an angle of 30° so that roots could hit the glass wall. The plants grew under the following conditions: temperature: day 20°C and night 15°C; dewpoint of the air: day 12°C and night 12°C; light intensity (12 h/day): 550 ± 50 μmol PAR m^{-2} s^{-1}. Root growth was analyzed every third day by means of image analysis with the software Adobe Photoshop™ 3.0 (Adobe Systems, Inc., 1994, USA.). For this purpose the root system was photographed at a distance of 50 cm with a piece of a graph paper fixed at the glass disk of the mini-rhizotron. All roots of a plant and therefore summarized root length values from the resulting digital images were expressed in cm relative to the grid of the attached graph paper. The different colours of roots of *C. arenaria* (white) and *D. flexuosa* (brown) made it easy to distinguish the roots of the two species. The measurement of total root length of harvested plants showed no significant difference compared to root length measured by means of image analysis from photos taken immediately before harvesting. Apart from determining total root length by means of a scanner (Scan Jet IIcx, Hewlett Packard, USA) and a root analysing program (DIAS, Delta-T Devices LTD, England), the above- and belowground biomass of harvested plants was measured.

Data analysis and statistical design

The relative competition intensities were calculated by the following equation (Goldberg & Scheiner 1993; Grace 1995):

$$RCI = \frac{P_{MONO} - P_{MIX}}{P_{MONO}} \qquad (1)$$

Where P_{MONO} represents the average root length of two plants in the control and P_{MIX} represents the root length of a plant in competition (e.g. Grace 1995). In the control we used therefore a treatment without intraspecific competition and in the competition treatment the plants are subjected to interspecific competition. Statistical analysis was carried out with STATISTICA for Windows (Version 5.0, StatSoft, Tulsa, USA). Differences between the treatments were tested with a two way ANOVA, with factors: control vs. competition and water level. For results with significant effects we used the LSD (least significant differences) post-hoc comparison (Day & Quinn 1989; Köhler et al. 1992).

Results

Root area

Under sufficient water availability, the root growth of *Carex arenaria* was not influenced through competition (Fig. 1a). *Deschampsia flexuosa* showed a tendency towards reduction of the root area under competition and sufficient water availability (Fig. 1b). In the water shortage treatment a highly significant ($p < 0.001$, ANOVA; $F = 3.99$, LSD-test) reduction of the root area of *C. arenaria* in the competition treatment to ca. 50% of the value in comparison to the control could be detected at the end of the experiment (Fig. 1a). The root area of *D. flexuosa* over the overall represented time was influenced under competition (Fig. 1b). In both species the water shortage itself in the control and in the competition caused a considerable and significant reduction of the root area ($p < 0.05$, ANOVA; $F = 8.35$, LSD-test). The root area in the water shortage treatment was reduced to ca. one third of the value of plants with daily water-offering at the end of the experiment after 30 days in *C. arenaria* and *D. flexuosa*. The differences in the measured root-parameters itself could be explained through the species ($p < 0.001$; $F = 11.02$, ANOVA) and the water shortage ($p < 0.001$; $F = 21.34$, ANOVA).

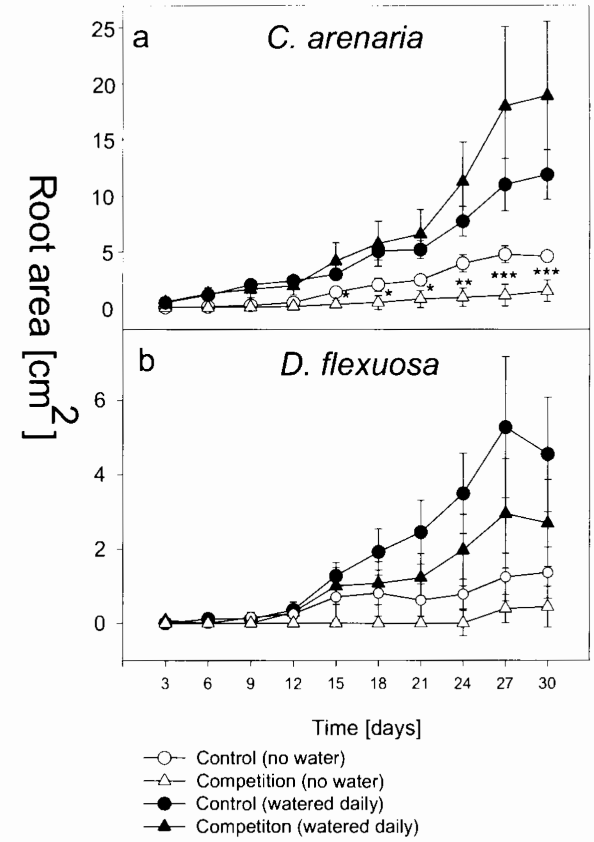

Fig. 1. Root area of *Carex arenaria* (**a**) and *Deschampsia flexuosa* (**b**) under low and high water availability as well as in competition. Significant differences between plants of *C. arenaria* grown in control/competition are shown by stars: *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; ANOVA, LSD-test.

Relative competition intensity

Based on the observed changes in root length the relative competition intensities (RCI) were calculated to compare the standardized level of competition for the two species under study. The low RCI under high water availability (plants watered daily) showed that *C. arenaria* did not experience any competition in the treatment with sufficient water (Fig. 2), while the average RCI of *C. arenaria* under water shortage increased and reached a value of 0.78. *D. flexuosa* experienced already at sufficient water supply competition with an RCI of 0.51. This value increases under water-shortage up to 0.92. However, the water shortage tightened the competition of *C. arenaria* and led to a significant reduction of root area (Fig. 1).

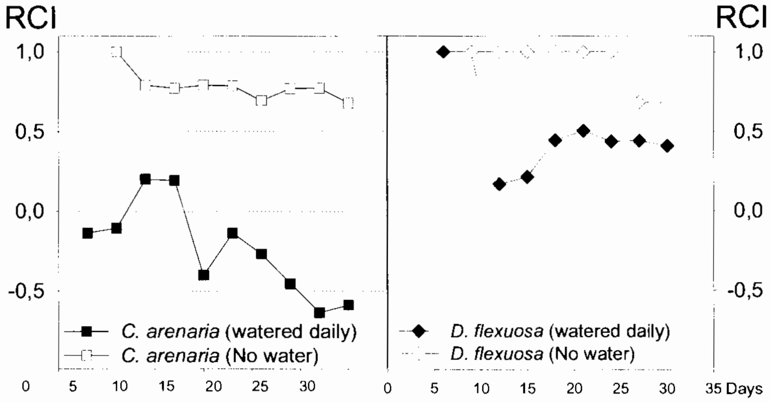

Fig. 2. Relative competition intensity of *Carex arenaria* (left) and *Deschampsia flexuosa* (right) over the presented time of 30 days.

Discussion

With the help of mini-rhizotron experiments we could detect belowground competition between *Deschampsia flexuosa* and *Carex arenaria* under nutrient-limited conditions (e.g. Tilman 1988). The factor water had a considerable influence on the outcome of competition between *D. flexuosa* and *C. arenaria*. *D. flexuosa* showed in competition under high and low water availability a slightly reduced root growth, while root growth in *C. arenaria* was reduced only under low water availability. This shows that the intraspecific competition from other *C. arenaria* (under well watered conditions) is stronger than that of *D. flexuosa*, and does not mean any facilitation. Therefore in watered *C. arenaria* the RCI value is negative, because it compares inter- and intraspecific competition. A comparison of the relative competition intensities showed that the relative competition intensity under water shortage in both species ascends. Moreover roots of *C. arenaria* show a reduced permeability under drought conditions which reduces the ability to acquire resources (Robards et al. 1979) whereas *D. flexuosa* will be able to acquire resources with its fine roots under both wet and dry conditions. So we assume that under drought conditions both species are very sensitive to root competition and that *C. arenaria* should be the superior competitor at high water supply, but the inferior competitor after a period of drought.

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Effects of communal pastoralism on vegetation and soil in a semi-arid and in an arid region of Namibia

Ward, David[1]*, Ngairorue, Ben T. [2], Karamata, Japhet [2], Kapofi, Imanuel[2], Samuels, Rana[3] & Ofran, Yanay[3]

[1]*Mitrani Department for Desert Ecology and Ramon Science Center, Jacob Blaustein Institute for Desert Research, Ben Gurion University of the Negev, Sede Boqer 84990, Israel; [2]Desert Research Foundation of Namibia, 7 Rossini Street, Windhoek, Namibia; [3]Dept. of Ecology, Evolution and Systematics, Hebrew University of Jerusalem, Givat Ram Campus, Jerusalem, Israel;*
**Fax +97276596772; E-mail ward@bgumail.bgu.ac.il*

Abstract. In several semi-arid and arid regions of Namibia, communal pastoralists own large numbers of livestock. Such situations are commonly perceived to lead to the 'tragedy of the commons'. We compared the effects of communal and commercial ranching (with private land ownership) on adjoining ranches in a semi-arid and in an arid region. In spite of far higher stocking densities on the communal areas and the absence of an overall grazing strategy in the arid region, we found no difference in productivity between communal and commercial ranches. In contrast, severe bush encroachment and reduced perennial plant diversity and grass production occurred in the communal ranches of the semi-arid region, in spite of central control of stocking. These results point both to the resilience of arid environments to high stocking levels and the over-riding influence of abiotic variables on environmental quality in the arid environment.

Keywords: Land degradation; Pastoralism; Soil organic carbon; Desert; Grazing.

Introduction

It is widely believed that overgrazing and other human impacts on the environment in communal ranches are greater than in commercially ranched areas in Africa (Archer et al., 1989, Behnke & Abel 1996). This is largely due to the fact that communal areas are not individually owned and may have poor management strategies. Communal ownership is frequently assumed to lead to the 'tragedy of the commons', i.e. land that is not privately owned (known as a 'common' in England) ultimately deteriorates because nobody looks after land they are not personally responsible for (Hardin 1968). However, a number of recent studies have shown that this is not always the case (e.g. Ellis & Swift 1988; Archer et al. 1989; Scoones 1993; Tapson 1993). These last-mentioned studies show that stochastic environmental variation (e.g. in rainfall) may over-ride or mask the impacts of pastoralism on the vegetation in semi-arid and arid regions. Moreover, communal pastoralism in many areas is under the control of village committees or elders (Tapson 1993), and thus there is some management of stock in spite of an absence of individual ownership of land.

In the light of this revised opinion on the effects of communal pastoralism on African rangelands, we set out to determine some of the impacts of communal and commercial (= privately-owned and fenced) rangelands in semi-arid and arid central Namibia. We chose two areas for this study:

1. *Okondjatu*: A preliminary study of the likely impacts of desertification on Namibia indicated that the semi-arid (350 - 450 mm annual rainfall) former Herero land in north-east Namibia was one of the areas most likely to suffer heavy impacts of desertification (Aharoni & Ward 1997) due to high human and livestock population densities. Near Okondjatu, a commercial ranch (Winkelhaak) owned by a single rancher is bordered on three sides by communal ranching area. Stocking rate on the commercial ranch is about half that of the communal areas. The communal areas in the erstwhile Hereroland (now known as Otjozondjupa region) have central control of the number of ranchers per region and waterpoint use by village headmen.

2. *Otjimbingwe*: Stocking rates in the arid Otjimbingwe region (150 - 250 mm annual rainfall) of central-west Namibia are extremely high. In the dry season, the area appears almost completely devoid of grass, as a result of heavy grazing. Furthermore, there has been a change in stock type at Otjimbingwe from predominantly cattle in the 1850s to mostly (75%) goats today (Ward et al. 1998). This suggested to us that grazing productivity may have declined over the last 150 yr to the extent that large grazers such as cattle can no longer be maintained on the land. There is no central management of grazing areas at Otjimbingwe (Ward et al. 2000). Hence, we might expect more of an effect of the 'tragedy of the commons' in Otjimbingwe than in Okondjatu.

Methods

Study areas

Okondjatu: With an average annual rainfall of 349.5 mm (coefficient of variation = 39.0%), the Okondjatu area (20° 58' S, 18° 13' E) falls in the thornbush savanna zone (Van der Merwe 1983). The main tree species are *Acacia erioloba*, *A. mellifera*, *A. reficiens*, *Dichrostachys cinerea*, *Terminalia sericea* and *Grewia flava*. This region is a large plain on Kalahari sands. The communal area has an unfenced interior which makes the regulation of grazing areas difficult. Livestock numbers are high (currently 13.25 ha per large stock unit – where a large stock unit (LSU) is the equivalent of a 450 kg cow). In contrast, Winkelhaak commercial ranch (5764 ha) has a lower stocking density (22.30 ha/LSU) with fenced interior, and stock rotation camps. We recorded vegetation and soil parameters at 100, 200, 300, 500 and 1000 m from each of three water points along three transect lines (see Ward et al. 1998 and Ward & Ngairorue 2000 for sampling design) on communal and commercial areas. Each water point is ca. 2 km apart.

Otjimbingwe: With an average annual rainfall of 165.4 mm (coefficient of variation = 69.4%), the Otjimbingwe area (22° 22' S, 16° 07' E) falls in the desert transition zone known as the Pro-Namib (Van der Merwe 1983). The soils are sandy and are vegetated with *Acacia tortilis*, *Acacia reficiens*, *Boscia albitrunca and Schotia afra*. The unfenced interior makes the regulation of grazing areas difficult. Livestock numbers are high (currently 18.99 ha/LSU). We compared the communal areas of Otjimbingwe with four of the surrounding commercial ranches (Tsaobis, Neu Schwaben, Okomitundu and Davetsaub) have lower stocking densities (40 - 378 ha/LSU) with fenced interiors, and stock rotation camps. We compared two regions of each commercial ranch with two adjacent regions of the communal area of Otjimbingwe (Ward et al. 1998).

Parameters sampled

If there is serious degradation of soil nutrients, then vegetation should not recover after rains. Thus, wet season grass measurements should prove more important than dry season measurements in differentiating between degraded and non-degraded areas. We also examined several parameters of soil quality which may be a reliable indicator of long-term degradation of the environment due to a particular management practice because it reflects the ability of the environment to sustain vegetation for any given rainfall (see e.g. Mokwunye 1996).

1. Plant sampling: We measured grass height using a point-frequency frame (Mueller-Dombois & Ellenberg, 1974), and perennial plant diversity using 250 m long point-centered quarter transects at Okondjatu and the log-series survey method of McAuliffe (1991) at Otjimbingwe. See Ward et al. (1998) for further details of sampling methods.

2. Soil parameters: Soil organic carbon is a good measure of overall soil quality (Foth & Turk 1972; Mokwunye 1996). Organic matter is frequently highly positively correlated with two of the most important soil nutrients, nitrogen and phosphorus, in many African soils (Ward et al. 1998). Total nitrogen, total phosphorus and water-holding capacity were measured using standard techniques. We also used the dry mass of radish plants (*Raphanus sativus*) after 30 days of growth in pots as a bioassay of soil nutrients. See Ward et al. (1998) for further details of sampling methods.

Univariate statistical tests on soil and vegetation parameters reported here were Nested ANOVA, with the number of replicates equal to the number of transects (woody vegetation parameters), the number of times a point-frequency frame was placed on the vegetation (grass parameters), and the number of soil samples.

Results

Grass height

Okondjatu: There was a highly significant difference in grass height between commercial and communal areas in both the wet season ($F = 36.862$, $P < 0.001$, error d.f. = 88) and dry season ($F = 54.160$, $P < 0.001$, error d.f. = 88) of 1997 (Table 1). There was no significant difference in grass species richness between communal and commercial areas ($F = 0.957$, $P = 0.342$, error d.f. = 88) (Table 1).

Otjimbingwe: In the dry period of September 1997, mean grass height on the commercial ranches surrounding Otjimbingwe was significantly greater than on the communal areas (Table 1). In the subsequent wet season (February 1998), mean grass height on the four commercial ranches surrounding Otjimbingwe was not significantly different from that of the communal areas of Otjimbingwe (Ward et al. 1998) indicating that degradation is not occurring because the grass recovers from heavy dry season grazing.

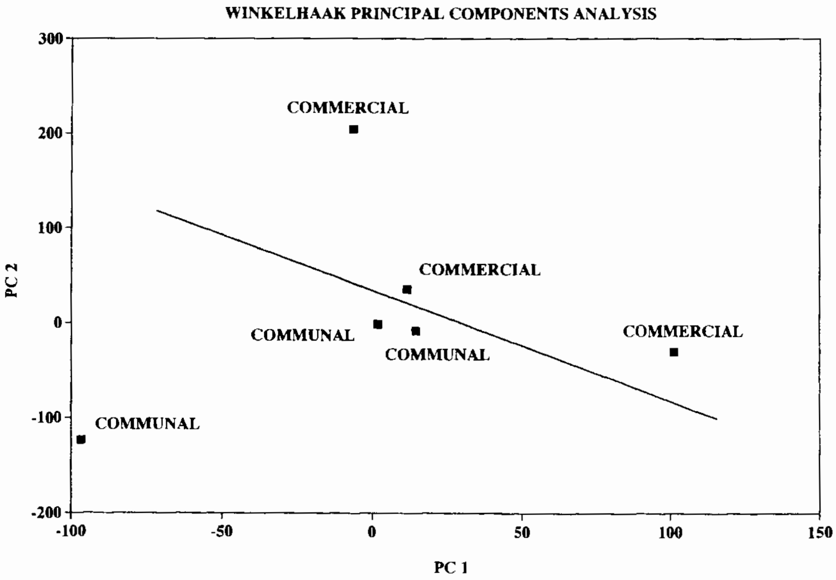

Fig. 1. Principal Components Analysis plot of centroids of perennial plant communities on communal and commercial ranches at Okondjatu. Cumulative % of variance explained by PC axes 1 and 2 = 43.4%. Note that the commercial sites fall on the upper right half of this plot and the communal sites on the lower left. The two species with the highest component loadings on PC1 were *Acacia mellifera* (positive loading) and *Grewia flava* (positive loading), while the two species with the highest loading on PC2 were *Acacia reficiens* (positive loading) and *Dichrostachys cinerea* (negative loading). All four of these species are commonly recorded as bush encroachers.

Table 1. Vegetation and soil parameters in communal and commercial ranches at Otjimbingwe and Okondjatu. Species diversity (= Shannon-Wiener index) and species richness values for Okondjatu are per 50 m transect. Woody cover in Otjimbingwe is % cover and Okondjatu no. of individuals/m^2. Values are means ± 1 S.E. * = significant difference ($p < 0.05$) between commercial and communal ranches. For statistical tests of Otjimbingwe comparisons, see Ward et al. (1998).

	Otjimbingwe		Okondjatu	
Parameters	Communal	Commercial	Communal	Commercial
Grass height (cm) wet season	13.3 ± 1.4	10.4 ± 1.6	16.0 ± 1.7	37.1 ± 3.4*
Grass height (cm) dry season	9.8 ± 0.9	21.0 ± 1.1*	11.6 + 1.4	32.5 + 2.5*
Grass species richness	not sampled	not sampled	3.07 ± 0.21	3.60 ± 0.29
Woody species richness	3.7 ±1.2	4.1 ± 0.6	3.4 ± 0.4	4.5 ± 0.2*
Woody species diversity	0.82 ± 0.09	0.86 ±0.14	0.63 ± 0.13	1.015 ± 0.11*
Woody cover	11.3 ± 3.3	11.8 ± 3.3	0.3 ± 0.1	0.3 ± 0.1
Organic carbon (%)	0.61 ± 0.07	0.57 ± 0.06	1.31 ± 0.29	0.63 ± 0.10*
Nitrogen (ppm)	386.35 ± 33.74	329.60 ±18.79	not sampled	not sampled
Phosphorus (ppm)	9.10 ± 0.59	9.67 ± 0.53	not sampled	not sampled
Water holding capacity (%)	not sampled	not sampled	6.05 ± 0.98	2.80 ± 0.39*
Bioassay (g)	0.88 ± 0.14	0.77 ± 0.16	0.28 ± 0.04	0.26 ± 0.04

Perennial plant diversity

Okondjatu: Woody plant density did not differ significantly between communal and commercial areas (F = 0.003, P = 0.960, error d.f. = 48). There was a significantly higher woody plant species richness (F = 5.271, P = 0.029, error d.f. = 48) and diversity (F = 5.151, P = 0.031, error d.f. = 48) on the commercial areas than on the communal areas (Table 1). There was also a difference between commercial and communal areas in vegetation community structure (Fig. 1).

Otjimbingwe: There was no significant difference in percentage plant cover, species richness, or species diversity of perennial plants between communal and commercial areas (Table 1, Ward et al. 1998). We also found no significant difference between commercial and communal ranches in vegetation community structure using detrended correspondence analysis (Ward et al. 1998).

Soil

Okondjatu: There was a significant difference in percentage organic carbon (F = 4.900, P = 0.035, error d.f. = 28) and water-holding capacity (F = 9.454, P = 0.005, error d.f. =28) between communal and commercial areas. These results could be due to the higher level of defecation around waterpoints in the communal areas caused by higher stocking rates. This is suggested by the negative correlation between % organic carbon and distance from the water point (range of $r = -0.70 - -0.99$). There was no significant difference in total dry mass of radish plants (bioassay) between the communal and commercial areas (F = 0.128, P = 0.723, error d.f. = 28; Table 1).

We performed a multiple regression analysis to determine whether there was a significant effect of soil quality (parameters as recorded above) on the first and second principal components in the principal components analysis of vegetation community structure. We found no significant correlation between either PC1 or PC2 and all three soil parameters we measured (PC1: F = 1.384, P = 0.446, error d.f. = 4; PC2: F = 0.485, P = 0.727, error d.f. = 4).

Otjimbingwe: There was no significant difference in percentage organic carbon, total nitrogen, total phosphorus, water-holding capacity or in total dry mass of radish plants (bioassay) between Otjimbingwe and the four commercial ranches (Table 1; Ward et al. 1998).

Discussion

We found that the commercial ranch Winkelhaak differed from the surrounding communal areas at Okondjatu in most vegetation parameters and several soil parameters (Table 1, Fig. 1). It is clear that heavy stocking in the communal areas has led to bush encroachment and dominance by *Acacia mellifera*, *A. reficiens* and *Dichrostachys cinerea*. This increase in dominance has led to a decline in perennial species diversity. Bush encroachment occurs as a result of overgrazing: grass and trees are in competition, and the grass is usually dominant on account of its ability to more efficiently sequester resources (water and soil nutrients) at the soil surface than the trees. Moreover, few rainfall events are of sufficient magnitude to facilitate recruitment (germination + survival) of trees in these semi-arid environments. When overgrazing occurs, the grass is removed and soil resources are freed up for the trees. Once sufficient rain falls, trees can recruit *en masse*. Up to 65% of northern semi-arid Namibia may suffer from this problem (Quan et al. 1994). In Namibia, these bush-encroaching tree species are well-protected by thorns and are mostly inaccessible to cattle. Thus, productivity of the bush-encroached communal regions of Okondjatu is lower than that of the commercial ranch,Winkelhaak, both because of lower grass availability and increased bush density. Thus, in spite of central control of stocking in the communal areas of the former Hereroland (Otjozondjupa), we recorded negative effects of the heavy stocking (which is twice that of the commercial ranch). It is worth noting that the commercial ranch studied here also shows signs of heavy grazing and is bush encroached in parts.

In contrast to the results from semi-arid Okondjatu, we found few differences in long-term impacts on the environment between the communal and commercial ranches near arid Otjimbingwe (e.g. Table 1). The major difference between sites at Otjimbingwe was that the communal area had less grass than the commercial ranches in the dry season of 1997 (Table 1). This result indicates a negative short-term effect of the higher stocking rate in the communal areas. The lower stocking rates of the commercial ranchers may benefit them in that they have more grass per animal for longer into the dry season than the communal ranchers. However, the vegetation and soil quality have not declined as a result of the heavier grazing on the communal areas because wet season grass productivity is the same in communal and commercial areas of Otjimbingwe.

While our results indicate that there is very little difference between commercial and communal ranches at Otjimbingwe, this should not be taken to mean that no degradation of land has occurred. In another study we have shown that water points on the communal areas of Otjimbingwe that have been in use for at least 150 yr display lower vegetation productivity and lower soil quality than those that have only been in use for 5 - 10 yr (Ward & Ngairorue 2000; Ward et al. in press). Therefore, we do not exclude the possibility that slow, long-term degradation has occurred on both commercial and communal ranches at Otjimbingwe. If this is indeed the case, the lack of difference between commercial and communal areas indicates that there is no linear relationship between stocking rate and impact on soils and vegetation. Rather, it would appear that there may be a threshold effect.

The differences in the effects of communal pastoralism on the environment between Otjimbingwe (arid, not centrally managed) and Okondjatu (semi-arid, centrally controlled) are contrary to our expectation based on type of management. We believe that the high inherent variability in rainfall tends to mask the relatively smaller impacts of pastoralism in arid regions such as Otjimbingwe (see also O'Connor 1985; Venter et al. 1989; Milchunas et al. 1989; Parsons et al. 1997). In contrast, in semi-arid regions such as at Okondjatu, there is sufficient (and reliable) rainfall to allow large-scale tree establishment and bush encroachment following heavy grazing. Hence, greater efforts should be expended in producing more effective stock management strategies in semi-arid regions rather than in arid regions of Namibia (see also Aharoni & Ward 1997).

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Phytocoenotic intensity and stand organisation in *Pinus sylvestris* forest

Zagidullina, Asyia T.

Saint-Petersburg State University, Department of Plant Ecology and Vegetation Sciences, Universitetskaja emb., 7/9, Saint-Petersburg 199034, Russia;
Fax +78123281472; E-mail asya@az2828.spb.edu

Abstract. In order to study mechanisms of forest community integration, the concept of phytocoenotic intensity (PHI) was introduced. PHI reflects the transformation of ecological conditions by surrounding plants at a given point of space and time and can be estimated via canopy parameters for any point of the forest community. The estimation of the influence of this intensity upon a given point can be calculated on the basis of a hypothesis about the additive character of the superpositions of the individual phytogenic tree fields.

Plots in different forests were chosen in areas with comparable soil regimes but with different stages of post-fire regeneration and with varying structure. In each plots coordinates and some parameters of trees, recruitment and ground cover were recorded. Data were analysed with the help of the author's programs.

The functioning of the of the *Pinus sylvestris* forest rich in lichens and the feathermoss *Pleurozium schreberi* is dependent upon plural interactions between its components. These interactions have different intensity and take place on different levels of community organisation. The main part of these interactions is comparatively weak. Nevertheless, PHI, caused by the surrounding trees, is very important for community formation. This intensity regulates the formation of a stand mostly; besides, PHI can influence other layers of a forest community through the canopy changes.

Keywords: Canopy; Phytocoenotic field; Phytogenic field; *Pinus sylvestris*; Plant interaction; Russian Karelia.

Introduction

One important line in modern vegetation science is the study of structure and functioning of plant communities, particularly, the main components of forest communities and internal interactions between them. Internal interactions, notably interference between individuals, is important for the dynamics of plant populations and communities, because formation, growth and reproduction of plants are strongly dependent on the parameters of the surrounding individuals (Harper 1977; Weiner 1982; Peterson & Squiers 1995). Effects of neighbour influence, leading to the reduction of growth rate, changes in morphogenesis and reduction of reproductive potential, are usually treated as competition which is one of the possible interference types (Weiner 1982). However, when it is necessary to describe interactions correctly, the terms 'competition' and 'interference' are not convenient enough because (1) they combine both influence (cause) and effect (result) and, (2) they refer to processes not limited in time.

The main influences of individuals upon other individuals take place through the transformation of environmental conditions (Ipatov & Kirikova 1997). In the usual Russian terminology, the part of environmental space, which is changed by a selected plant individual, is called 'phytogenic field' (Uranov 1965). Since the degree of environmental transformation may be different, we may speak of the intensity of this field which characterizes the intensity of an individual influence (Yastrebov 1996). Aggregates of several individual 'fields', including the space of their superposition, in the community gives birth to a resulting 'phytocoenotic field' which can be characterized via its intensity (PHI). The latter reflects the transformation of ecological conditions by surrounding plants at a given point of space (x_i, y_i, z_i) and time (t_i).

The direct estimation of phytocoenotic intensity in real communities seems to be impossible, because transformation of some ecological factors are very difficult to measure. But, obviously, transformation of complex ecological conditions is dependent on number, size, and distribution of individuals in space (Yastrebov & Posnanskaya 1993; Yastrebov 1996; Weiner 1984; Pendrige & Walker 1986). Therefore, indices including these parameters can be used to characterize phytocoenotic intensity in communities (stands) indirectly and may be used for the construction of the appropriate models. The main problem with this estimation is a basic size character. It is justified that, when large bodies of data are collected, the emphasis is on characters, which are simple to measure. For example, the diameter of a trunk (DBH), which is usually used in the analysis of a competition in stands, is very simple for measurement. But it is also closely related to several other characters of a tree (e.g. Usoltsev 1985; Yastrebov 1988; Ipatov & Kyrikova 1997).

As was shown by Yastrebov (1996) for the Karelian *Pinus sylvestris* forest under study, a type with lichens and the feathermoss *Pleurozium schreberi*, the phytogenic field of a pine tree is formed mostly due to transformation of light conditions by the crown. According to Ford & Diggle (1981) and Dai (1996), the photosynthetically active radiation is one of the most limited resources in forest ecosystem, and the light amount, accessible for a tree, is determined by the spatial arrangement of surrounding crowns. Therefore, transformation of light conditions is one of the main components of phytocoenotic intensity in a forest. So, we tried to include the crown parameters in the index of phytocoenotic intensity for the forests stands formed by 'light-demanding' species such as *P. sylvestris* and some other tree species.

One of the most interesting problems is that of a character of cumulative influence in a stand, or, in other words, the interference of phytogenic fields created by different individuals. In our opinion, the given question requires special research, but in this case we use the assumptions of Yastrebov (1996), which confirmed that the pine canopy influence upon any other element of the community has an additive character.

In order to study the role of the phytocoenotic factor in

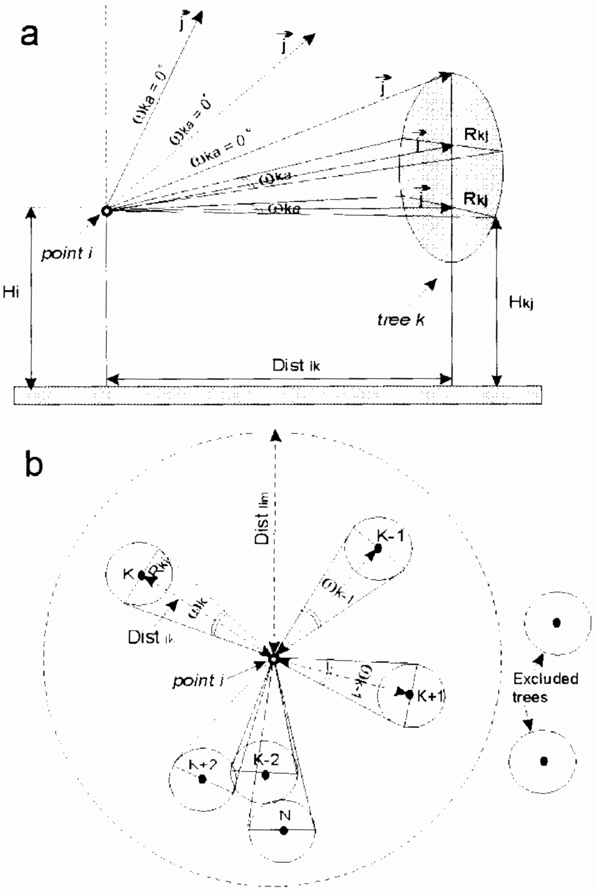

Fig. 1. Estimation of phytocoenotic intensity for the point i. (a) Profile: estimation of the angular part of closed celestial sphere through the ring zone with the step *a*. (b) Plane: estimation of this angular part for one ring zone.

forest organisation we tried to develop an index of phytocoenotic intensity, taking into consideration the questions marked above.

Material and Methods

Data were collected in natural *Pinus sylvestris* forests in Russian Karelia rich in lichens and the feathermoss *Pleurozium schreberi*. In the summers of 1994 - 1998, 23 experimental plots (30 m × 30m in size) were studied. The plots were chosen in forests with comparable bedrock and soil (fluvioglacial sands) but representing different stages of post-fire regeneration and different variants of stand structure. In the plots coordinates of trees and saplings (*Pinus* individuals > 0.2 m but < 3 m in height) were recorded. To consider the influence of the environment, we also measured coordinates and DBH (diameter at breast height equal to 1.3 m) of trees within the 8 m margin around the plot. For each tree inside the plot the values of DBH, height, and horizontal and vertical crown projections (the last was determined in a direction of the greatest crown asymmetry) were measured. Tree age was estimated with the help of an increment borer. In order to take into account the complexity of a real crown and calculate its sizes, we have accepted such assumptions: horizontal projection is a polygon and vertical projection can be measured as a relative length of branches on the whole crown extent. Thus, any crown in space may be assumed as a series of rectangular prisms. Based upon these assumptions, it is possible to calculate the crown volume and the area of its projection at any height. Standard statistical tests were performed with the help of SPSS 8.0, STATISTICA 5.0. For calculation of indices of phytocoenotic intensity, parameters of crowns, etc., a special program was developed by the author in DELPHI 4.0.

Results and Discussion

Calculation of indices of phytocoenotic intensity

In order to study structure and functioning of forest community it is necessary to develop an index which allows to give its clear spatial interpretation, describes the transformation of light conditions, allows us to reveal the joint influence of the surrounding canopy, and also proves the distance $Dist_{lim}$, beyond which the influence of the surrounding individuals is negligible. The essential property of such an index should be a possibility of its calculation for any point of the community space. The developed algorithm of calculation of phytocoenotic intensity index is given below.

An approximate estimation of the influence of the surrounding canopy upon the crown of an individual is an angular part of the celestial sphere, closed by the canopy. Using the sizes of surrounding crowns and their spatial coordinates, it is possible to calculate this part for any point of community space, estimating it for ring zones of celestial sphere successively (Fig. 1B).

At first, we can estimate the part of the closed sky for some tree i in a stand. As all points of the crown space, except for its top (apex), are shaded by some other parts of this very crown, the surrounding canopy influence may be correctly estimated for the top of the tree i (we shall name it H_i) only. Otherwise, at an estimation of phytocoenotic intensity for any other point of the crown, such an influence will be obviously deformed because of self-shading. As the light flow is a vector, directed downwards, it is necessary to value the part of the closed celestial sphere through the ring zones located not lower than H_i. So we estimate this angular part for some ring zone of celestial sphere up from the level of H_i, and set up the proper angle a (Fig. 1A). We choose any tree k of the environment, which is separated from the tree i by a distance $Dist_{ik}$ (less than $Dist_{lim}$). The approximate angular size ($\omega_{i\alpha}$) of the k-tree's crown at given α is calculated like this:

$$\omega_{k\alpha} = 2arctg \frac{R_{kj}}{(Dist_{ik} / \cos(\alpha))}; \qquad (1)$$

where R_{kj} is an average radius of the k-tree's crown on height level j. This level follows from:

$$H_{kj} = H_i + Dist_{ik} \cdot tg(\alpha); \tag{2}$$

As we stated above, the total phytocoenotic field is formed as a result of aggregation of individual phytogenic fields Here it is necessary to determine the character of superposition of the individual phytogenic fields. According to Yastrebov (1996), the pine canopy influence upon any other element of the community possesses an additive character. Then, for a given zone of the celestial sphere, the main component of phytocoenotic intensity in point H_i, representing the surrounding canopy influence, will be the following:

$$\omega_{i\alpha} = \sum_{\kappa=1}^{N} \omega_{\kappa\alpha}; \tag{3}$$

where N is a total number of surrounding trees. If we sum $\omega_{i\alpha}$ for all ring zones of the celestial sphere with a step α, we arrive at:

$$\omega_i = \sum_{\alpha=1}^{90} \omega_{i\alpha}; \tag{4}$$

where α varies from 0° up to 90°. Our calculations were made with a step of 15°. If we assume some other value of α, then, to have the results comparable, ω_i must be weighted through a division by a number of steps. The resulting parameter ω_i reflects the total part of the celestial sphere closed by the surrounding canopy, without the account of the crown overlap (below we shall use 'PHI' for 'ω_i').

Evaluation of a limiting distance for the inclusion of surrounding trees

The essential methodical problem of usage of the most applied indices of phytocoenotic intensity is that of a selection of limiting distance $Dist_{lim}$. The dependence of the angular size of different crowns upon the distance is characterized by the fast asymptotic decrease. Besides, as follows from Eq. 2, H_{kj} grows linearly with the increase of distance from a tree to a given point i and $a > 0$, exceeding the heights of the majority of trees after some distance is reached. Hence, the probability of inclusion of the crown's angular sizes of removed trees in the resulting index of phytocoenotic intensity is very low. Therefore, there is some distance $Dist_{lim}$ which corresponds to the saturation of the index PHI, i.e. the index, calculated at $Dist_{lim}$, and $Dist_{lim} + \Delta$ will not differ statistically. The evaluation of the most useful $Dist_{lim}$ values was carried out on the basis of the similarity analysis of distribution of PHI frequencies, calculated for a series of $Dist_{lim}$: 2.5 - 20 m. With this purpose 100 abstract points were located regularly on each sample plot on different heights. The PHI was calculated for each point as a series of $Dist_{lim}$. The t-criterion of Student was chosen for an estimation of the reliability of distinction of distribution rows (the analysis was carried out at a significance level 0.05). The change of t-criterion of Student with an increase of $Dist_{lim}$ depends on the height of the estimated point. For the set of pair comparison of distribution rows with $Dist_{lim}$ from 2.5 to 7.5 m, all the rows differ significantly. With a further increase of $Dist_{lim}$, the t-criterion value is reduced, coming nearer to the table values. At a comparison of the distributions obtained for values of $Dist_{lim}$ from 7.5 - 15 m, the differences are not significant. So, for the high trees it is possible to estimate PHI with the $Dist_{lim}$ equal to 7.5 m, but the $Dist_{lim}$ for saplings cannot be less than 15 m, especially when studying different-aged tree populations. However, in order to obtain comparable results for all cases it is necessary to select one common distance. Thus, the minimal distance $Dist_{lim}$, for which PHI is practically saturated in all cases, may be chosen as a value of 15 m. The latter was used for further calculations of indices of phytocoenotic intensity.

Estimation of PHI's role in formation of pine trees in a stand

The next step was the estimation of a tree's reaction on the phytocoenotic intensity, for which an index was developed. Obviously such an index is differently reflected by different characters. Therefore, in order to estimate the response to this influence sufficiently, it is necessary to choose characters which reflect the general state of an individual most thoroughly. Particularly, they must possess high information content, i.e. high loadings on the main axes of a Principal Components Analysis (Zlobin 1984). Such characters are crown volume (factor loading on the first PCA-axis = +0.937), radius of a crown projection (+0.912), tree height (+0.920), and diameter of the trunk (+0.906). Somewhat smaller factor loadings were revealed for average growth rate (AGR). The lowest information content was revealed for crown height extension (+0.736).

According to the results of a one-way ANOVA, PHI significantly influences all tree characters indicated above. The dependence of the characters upon the value of index PHI appears to be monotonous, but non-linear. The non-linearity of the dependences does not allow us to estimate the correlations with the help of the Pearson coefficient correctly. Therefore, in order to linearize the dependences, we took the logarithms from the characters and estimated the correlations for them (Table 1). The strongest dependences upon index PHI (−0.66 to −0.73) were revealed for such characters as radius of crown projection,

Table 1. Coefficients of correlation between index of PHI, age of individuals, and some tree characters. All factors are significant at the 0.05 level.

Character	PHI	Tree age
Age	- 0.42	1
Tree height	- 0.73	0.71
DBH	- 0.48	0.71
Crown extension	- 0.66	0.31
Radius of crown projection	- 0.70	0.52
AGR(height)	−0.66	0.13
AGR(DBH)	−0.38	0.20
Crown volume	−0.71	0.52

crown volume, crown extension, AGR and tree height (we used logarithms for all characters). The correlations with AGR (DBH) and DBH were not very high (–0.38 to –0.48). The correlation of index PHI with the individual's age is significant and fairly strong (–0.42). Probably, it is a consequence of the increase of the proportion of trees, which occupy the part of a canopy space with more favourable light conditions in the course of the development of the stand.

Thus, one and the same PHI value is unequally reflected by different characters of pine trees. It is conditioned by features of PHI and tree characters. Because the stem is formed as a result of constant xylem growth, this process is irreversible. Therefore, trunk volume, basal area section and DBH are cumulative characters. Unlike the trunk, the crown is a dynamic system reflecting current phytocoenotic conditions of tree growth, because the crown is being formed as a result of parallel mortality and increment of the shoots (Bertran 1989; Ford & Ford 1990). The balance of these processes is determined by the individual assimilation balance of a branch, which depends on the disposition of this branch in community space. Intracrown balance of mortality and increment is reflected via values for crown characters. PHI is dependent on the total intracanopy balance of mortality and increment. When PHI increases, crown volume reduces, as mortality dominates over increment processes in the crown, whereas in the trunk only decline of increments can take place. Hence, strong dependences between PHI and crown characters are conditioned by high sensibility of the latter to current phytocoenotic conditions.

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How can we define optimal plant functional types?

Pillar, Valério DePatta

Departamento de Ecologia, Universidade Federal do Rio Grande do Sul, Porto Alegre, 91540-000, Brazil;
Fax +55513191568; E-mail vpillar@ecologia.ufrgs.br

Abstract. Models of vegetation response to environmental change on larger scales cannot rely on species because most plant species are geographically limited. To allow ecological predictions beyond the scale of phytogeographical region, the models have to rely on vegetation descriptions using plant types other than the species. The crucial problem, however, is how to define the types. As types may be defined by the combination of trait states, the problem translates into one of trait selection. I argue that we should select plant traits that maximize the perception of association between vegetation and environment and that minimize redundancy. I view trait selection as a two-step procedure. The first step is the selection of a trait set on the basis of previous knowledge and practicability, which is then used for vegetation description. The second step is the ranking of these traits accomplished on the data analytically by computer algorithms in order to find an optimal subset. Since environmental conditions can be described in different ways and vegetation response may not be the same at all scales, we can hardly expect to find a set of traits or plant functional types that would be optimal for all purposes.

Keywords: Arid; Community; Convergence; Data analysis; Grassland; Grazing; Life form; Plant type; South America.

Introduction

The description of communities requires a taxonomy to dissect the assemblage of organisms into populations. We take these populations as operational community components. Pioneer studies in vegetation used taxonomies that recognized plant types by morphology and function (see Du Rietz 1931 and references therein). Vegetation science in this century, however, has been essentially based on species, because species are 'groups of individuals with uniform inheritance and have been for many years the objects of careful investigation' (Braun-Blanquet 1928, p. 21). This view, though, has been criticized. It is quite clear why we need vegetation descriptions with plant types defined by traits and not by species. On a large scale, predictions based on plant species are geographically limited (Woodward & Cramer 1996). On a small scale, species are in some instances too broad and variable that by describing communities by species composition we may not perceive relevant processes occurring below the level of species. The problem has been studied in connection with the Global Change and Terrestrial Ecosystems project of the International Geosphere-Biosphere Programme (IGBP) (Steffen et al. 1992), where these types are designated as 'plant functional types' (PFTs).

Plant types may be defined as a combination of character (trait) states. For instance, a phanerophyte, with deciduous leaves with a given size and thickness class is a type defined by four traits. Methods have been proposed for the analysis of communities described by such multi-trait defined plant types (Feoli & Scimone 1984; Orlóci & Orlóci 1985; Pillar & Orlóci 1991, 1993a). The crucial problem, however, is how to select the traits so that the PFTs will be likely 'functional'. The answer is obviously context-dependent (scale, environmental factors considered), thus we can hardly expect to find a set of traits or PFTs that would be optimal for all purposes. A prevalent approach in the search for PFTs is the selection a priori of a trait set, which is then used for description and interpretations thereafter. Traits may be chosen on the basis of previous knowledge on form-function relationships, after theoretical principles (e.g. Thompson et al. 1996) or because trends of trait variation in ecological space are known or suspected (e.g. Díaz et al. 1992; Skarpe 1996). Feasibility and cost of observation are also important in trait selection (Skarpe 1996; Díaz & Cabido 1997). Traits may also be selected by their correlation with major components in multivariate ordination of the population data alone (Thompson et al. 1996; Chapin et al. 1996). How functional or ecologically relevant are the plant types so derived? Answers have been found by comparing derived ecological predictions to empirical evidence, but this is usually not part of the data analysis *per se*.

Yet, by definition, community descriptions based on PFTs should produce data in which the compositional variation is highly congruent with environmental variation. Consider that we have a data set describing plant types by traits. Consider also that we have two other sets describing communities by the composition of these plant types and by environmental variables. With these data we can therefore evaluate ecological relevance and rank the traits. This can be pursued at early phases of a study, by revealing through analysis a subset of the traits defining PFTs with maximum ecological relevance, which could abbreviate or advance findings of model validation. I will discuss a general approach to the analysis of data based on plant types, describe algorithms for defining optimal PFTs, and give examples with vegetation data from South America.

Methods

The selection of traits to define PFTs is a two-step procedure. The first step is the selection a priori, using any relevant criteria, of a trait set, which is then used in the description of plant populations and communities. The second step is the selection of a subset of traits from the initial set, which is accomplished on the data analytically by computer algorithms in order to maximize the congruence between vegetational and environmental variation. The methods have antecedents in Pillar & Orlóci (1993a, b). The analyses used SYNCSA software (Pillar 1998).

For community description we need to delimit plant populations and record their presence or more often their quantities in the community. In the present case, plant populations are PFTs defined as sets of trait states. A PFT is identified as a population containing plants that are similar with regard to the pre-selected traits. This 'population' does not necessarily coincide with a species. If intraspecies variability of the traits is acceptable, a PFT may be formed, as a convenience, by the plants belonging to the same species, within each community or across communities. In this case, two or more species that are identical for the traits evaluated would have to be pooled, but they may be recorded separately and the pooling be done later in the analysis. Depending on the traits selected, the PFT description may be valid for the species anywhere, allowing the use of existing relevés.

The description of the plant populations yields a matrix containing the states of *m* traits in the plant populations. The description of the communities yields a matrix containing presences/absences or quantities of the plant populations in *n* relevés. If the traits are binary, qualitative multistate, or quantitative with a limited number of classes, identical plant populations are likely to appear across and within relevés. In the analysis, identical plant populations are trimmed and have their performances within a relevé pooled (or their presences/absences adjusted), leaving *t* distinct plant types in the rearranged data matrices $\mathbf{C}_{txm}$ and $\mathbf{V}_{txn}$. Matrix **V** can be analysed in a similar manner as a species by a relevé table.

The same set of communities is evaluated with regard to environmental conditions that are relevant for the objective and scale considered. For instance, a study will consider macro-climatic variables if the PFTs are to be optimal to describe or predict vegetation response to climate change (in space or time). Or, it will consider intensity or frequency of grazing and fire if the PFTs are to be optimal to describe or predict vegetation response to disturbance. The environmental information yields matrix $\mathbf{E}_{pxn}$ with *p* variables describing *n* communities.

In the optimization of the trait set a matrix correlation ρ (**D**; **Δ**) measures the magnitude of the association or congruence between vegetational variation and environmental variation. **D** is a dissimilarity matrix of communities based on the composition of plant types (matrix **V**). **Δ** is a dissimilarity matrix of the same communities but based on environmental variables (matrix **E**). Any dissimilarity functions are applicable. ρ is the Pearson's product moment correlation involving $n(n-1)/2$ off-diagonal pairs of corresponding dissimilarities in **D** and **Δ**. ρ (**D**; **Δ**) measures the congruence between variation in **V** and E. The larger ρ (**D**; **Δ**), the larger is the likelihood that the defining traits (or traits not observed but associated to the observed ones) are functional.

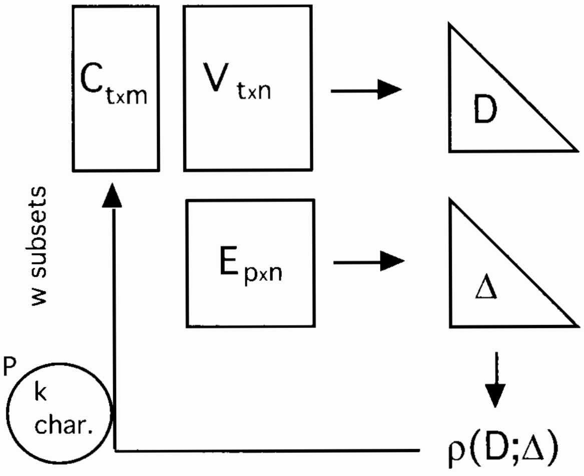

Fig. 1. A general algorithm for the selection of optimal subset of traits to maximize the congruence ρ (**D**;**Δ**) between vegetational and environmental variation.

A subset of the *a priori* selected traits may be used in the analysis to define plant types. This is the foundation of the optimization algorithm (Fig. 1). A subset with *m* traits, taken from the *a priori* selected set (P) with *k* traits, delimits *s* plant populations. This population data is arranged in matrix $\mathbf{C}_{sxm}$, on the basis of which matrix $\mathbf{V}_{sxn}$ is defined. Note that the new number of defined plant types $s \leq t$. Different subsets belonging to P may determine different matrices **V** and congruencies ρ (**D**; **Δ**). A recursive algorithm will search among *w* subsets the one that produces maximum ρ (**D**; **Δ**). This will be the optimal trait subset. The full algorithm will search all possible subsets with sizes varying from $m = 1$ to k, where

$$w = \sum_{m=1}^{k} \frac{k!}{m!(k-m)!} \qquad (1)$$

However, this alternative may be too demanding in computations, since *w* may be too large. We may instead use a stepwise algorithm (as in Pillar & Orlóci 1993b) where the number of trait subsets is

$$w = \sum_{m=1}^{k} (k-m+1) \qquad (2)$$

In this case the algorithm starts evaluating subsets with size $m = 1$, finding among the k traits the one that maximizes ρ (**D**; **Δ**); then evaluating subsets with size $m = 2$, finding among the remaining $k-1$ traits the one that when added to the first maximizes the function, and so on up to subset sizes $m = k$. For instance, for an a priori set with $k = 16$, there will be 65,535 different trait subsets to check in the full algorithm and only 136 in the stepwise algorithm.

Examples

The stepwise and the full optimization algorithms are tried in two different contexts. One example aims at finding an optimal subset of traits to reveal vegetation-grazing relationships at a small scale, the other aims at describing vegetation-climate trends in semi-arid areas at a continental scale.

The first example uses data from the Campos grassland (Boggiano 1995), containing 30 relevés taken in a 0.5-ha

Table 1. Traits used in population description in a small spatial scale study of Campos grassland (Boggiano 1995). Species affiliation was also taken as a 'trait'.

Code	Trait
lf	Life form *sensu* Raunkiaer (phanerophytes, chamaephytes, hemicryptophytes, geophytes, therophytes, other)
g1	Growth form (arrangement of leaves: rosette, caespitose, else)
g2	Growth form (plant inclination: prostrated, erect, both)
g3	Growth form (vegetative spread: stoloniferous, rhizomatous, else)
he	Plant height (7 classes)
tt	Stem tissue type (herbaceous, woody, no stem)
ve	Armature (prickly, spiny, else)
wi	Leaf width classes (in mm 0: leafless, 1: < 2.5 , 2: 2.5 - 5, 3: 5 - 10, 4: 10 - 50, 5: 50 - 100, 6: > 100)
re	Leaf resistance to traction (1 - 4 index)
cr	Leaf cross section (1: straight, 2: folded, 3: rolled, 4: leafless)
tx	Leaf texture (1: herbaceous to 4: sclerophyllous, 5: else)
ev	Ventral epidermal surface (glabrous, glaucous, hairy, tomentose, leafless)
ed	Dorsal epidermal surface (glabrous, glaucous, hairy, tomentose, leafless)
sp	Species

area located in the experimental station of the Federal University of Rio Grande do Sul, near Porto Alegre, Brazil. The sampling used quadrats, 0.1 m × 0.5 m each, located along six transects. Estimates of cover percentage and population description by traits in each quadrat were made for 66 species. The set of traits used in the description is in Table 1. Species affiliation was also taken as a 'trait'; to evaluate the congruence ρ (**D**; Δ) when floristic composition in isolation or with other traits is used to define vegetation patterns. Grazing intensity of the quadrats was evaluated. A grazing intensity index was computed from direct measurements on the communities during a short period of grazing by cattle, after two months of grazing deferment. Details on the methodology and the complete data set is in Boggiano (1995).

The second example uses relevés from mostly semi-arid to arid formations in NE Brazil and NW Argentina (Pillar & Orlóci 1993a). From these, 10 relevé sites are in the Caatinga in Ceará, Brazil, between latitudes 3° 20' and 4° S. The other sites are in NW Argentina, between latitudes 23° and 28° S, with 21 relevés located on a moisture gradient from the driest part of the Chaco in Santiago del Estero to the Monte desert in Catamarca, across the Subandean range, and four relevés located on high altitude (2400-2750 m) Prepuna around latitude 23° S in Jujuy. The species had cover-abundance recorded and were described using 16, mainly morphological, traits (Table 2). No common species are found by comparing the relevés in the Caatinga with the ones in Argentina. Information on estimated annual precipitation of each site was used in the analysis. Mean annual precipitation varied from 540 to 1302 mm in the Caatinga data and from 168 to 1127 mm in the NW Argentina data. Further information is in Pillar & Orlóci (1993a) and references therein. The complete data set is in Pillar (1992) except the relevés from the Prepuna (Pillar et al. unpubl., 1990).

Table 2. Traits used for population description in plant communities of semi-arid to arid formations in NE Brazil and NW Argentina (Pillar & Orlóci 1993a). Stem may refer to a stem-like structure and leaf to a leaflet or leaf-like structure.

Code	Traits
bt	Biological type: 1: bryoid; 2: lichen; 3: pteridophyte; 4: conifer; 5: graminoid; 6: cactoid; 7: other;
gf	Growth-form (states from key in Pillar 1992);
st	Stem tissue type: 1: succulent, 2: herbaceous, 3: woody, 4: no stem;
fu	Stem function: 1: support, 2: support and photosynthesis, 3: no stem;
at	Stem armature: type 1: thorn/spine, other vestures; 2: none; 3: plant with no stem;
du	Leaf duration 1: a-seasonal deciduous; 2: seasonal deciduous; 3: withering;, 4: persistent; 5: plant leafless;
lt	Leaf tissue type 1: succulent, 0: else;
tx	Leaf texture 1 to 5: scale from herbaceous to sclerophyllous; 6: else;
sh	Leaf shape 1: scale, 2: filiform/needle; 3: other; 4: plant leafless;
ar	Leaf arrangement: 1: simple; 2: compound; 3: plant leafless;
ed	Leaf epidermal surface dorsal: 1: glabrous; 2: glaucous; 3: trichomous sparse, 4: trichomous dense; 5: plant leafless;
ev	Leaf epidermal surface ventral: 1: glabrous; 2: glaucous; 3: trichomous sparse; 4: trichomous dense; 5: plant leafless;
wi	Leaf width 1: < 2.5 mm; 2: 2.5 - 5; 3: 5 - 10; 4: 10 - 50; 5: 50 - 100; 6: 100 <; 0: leafless;
le	Leaf length 1: < 5 mm; 2: 5 - 25; 3: 25 - 75; 4: 75 - 125; 5: 125 <; 0: plant leafless;
th	Leaf thickness 1: < 1 mm, 2: 1 - 3; 3: 3 - 5; 4: 5 <; 0: leafless;
he	Plant height 1: <5cm; 2: 5 - 25; 3: 25 - 75; 4: 75 - 125; 5: 125 - 250; 6: 250 - 500; 7: 500 - 1000; 8: > 1000.

The analysis with the grassland data (Fig. 2) revealed an optimal subset of traits related to grazing intensity: leaf width, leaf resistance, leaf cross-section and leaf texture. This subset, when used in the definition of plant types, enabled maximum congruence between variation in community composition and grazing intensity. The stepwise

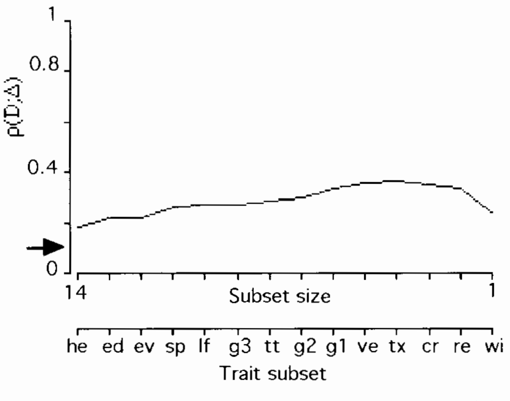

Fig. 2. Profile of maximum congruence ρ (**D**; Δ) at different trait subset sizes in data from subtropical grassland communities. Environmental variation **D** is indicated by absolute differences in grazing intensity. Vegetation composition is described by plant types defined by the traits (codes in Table 1) on the horizontal axis cumulatively from right to left; Euclidean distances define matrix Δ. Stepwise and full algorithms gave identical results. Maximum congruence was found when plant types were defined by leaf width (wi), leaf resistance (re), leaf cross-section (cr) and leaf texture (tx). The arrow points to the congruence when composition was described by species only. Data from Boggiano (1995).

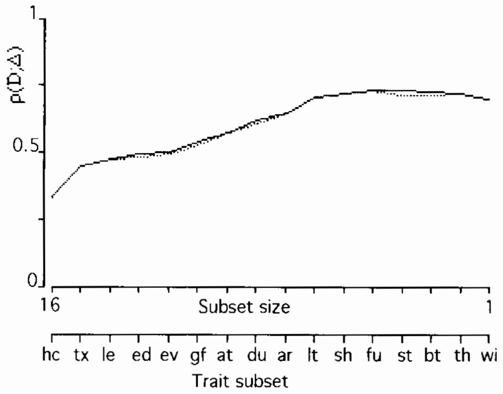

Fig. 3. Profile of maximum congruence ρ (**D**; **Δ**) at different trait subset sizes in data from 35 relevés in semi-arid to arid formations in NE Brazil and NW Argentina (Pillar & Orlóci 1993a). Vegetational variation **D** defined by Euclidean distances. Environmental variation in **Δ** given by absolute differences in mean annual precipitation. The solid line shows optimal congruence found by the full algorithm. The dotted line shows optimal congruence found by the stepwise algorithm. In this case vegetation composition is given by plant types defined by the traits on the horizontal axis cumulatively from right to left (codes in Table 2). When the lines coincide the trait subset is identical in both algorithms. Data from Pillar (1992) and Pillar et al. (unpubl. 1990).

and the full algorithm gave identical results. Note that by using the whole set of traits, or descriptions based on species only, environmental congruence was much lower than the optimal subset. An ordination (see Boggiano 1995) of the relevés with plant types defined by the optimal subset depicted, as expected, a close relationship between vegetation variation and grazing intensity.

The analysis with the 35 relevés in semi-arid vegetation (Fig. 3) indicated an optimal subset of traits related to precipitation which was identical in both stepwise and full algorithms: leaf width, leaf thickness, biological type, stem tissue type and stem function. Plant types defined by these traits revealed vegetation variation with maximum correlation with the variation in precipitation. Again, plant types defined by the complete set of 16 *a priori* selected traits gave a much lower environmental congruence than the optimal subset. The analysis with this data set on a Macintosh with a 240 MHz PowerPC 603ev CPU took 14 seconds when using the stepwise algorithm and 112 minutes when using the full algorithm.

Discussion

The results obtained on the basis of grassland and semi-arid vegetation data sets indicated that there was no advantage in using the more computationally demanding full optimization algorithm over the stepwise algorithm described in Pillar & Orlóci (1993b). The stepwise and the full algorithms revealed identical optimal subsets of traits. When solutions diverged it was at suboptimal subsets.

The examples highlighted the potential for analytical optimization in PFT-based data. The results clearly showed that an optimal subset of traits, taken from an a priori set used for data acquisition, can greatly improve the ecological relevance and, likely, functionality, of the plant types (PFTs) so defined. Moreover, the analysis with optimal PFTs can reveal vegetation patterns with a greater ecological relevance than an analysis based on species composition. It is undeniable, however, that the *a priori* selection of traits is crucial, for the optimization will be useless if the traits are not relevant at the scale and objective intended. In this sense, analytical optimization is an important complementary tool in the definition of PFTs. Furthermore, the analytical optimization provides an objective tool for the assessment of conflicting approaches or theories in the selection of traits. Whether PFTs are functional with respect to the environmental variables considered should not be a question of definition, but something that can be measured and optimized in a given data set. Functionality is here inferred from a measure of congruence, which only proofs association, not cause-effect relationships. Optimization, however, is dependent on purpose. The same set of traits may give a different optimum subset if a different environmental factor is considered.

The existence of PFTs is particularly grounded on the fact that regions of the world with similar climates tend to present similar vegetation structure. This has supported the hypothesis that community evolution is convergent under similar environmental conditions. There are several studies evaluating this hypothesis (e.g. Barbour & Diaz 1973; Parsons 1976; Orians & Solbrig 1977), but convergence is usually defined by the structural similarity of the communities. It is more interesting, however, to evaluate the convergence of vegetation responses to environmental gradients, between distant regions. The example using data from communities in semi-arid areas of the Caatinga and Chaco/Monte in South America is useful in this respect. The joint analysis of floristically disjunct communities found PFTs that were optimal to reveal vegetation variation having maximum congruence with the precipitation gradient. An enlarged joint analysis, involving communities on climatic or disturbance gradients from different continents, may provide the best framework to find optimal PFTs. These PFTs will be the most associated to the given gradients in space and, likely, in time, and therefore the best ones for modeling vegetation change.

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Nested subset analysis as a tool for characterizing plant community composition in Flemish woodlands

Honnay, Olivier[*] & Hermy, Martin

University of Leuven, Laboratory for Forest, Nature and Landscape Research, Vital Decosterstraat 102, B-3000 Leuven, Belgium;
Fax +32 16 32 9760; E-mail olivier.honnay@agr.kuleuven.ac.be

Abstract. A concise introduction to the theory of nested species subsets is presented. A group of biotas is said to be perfectly nested when each species is present in all biotas richer than the most depauperate one in which that species occurs. We shortly discuss the ecological mechanisms generating such nested patterns (i.e. differential extinction, differential colonization, habitat specialization and random sampling). The theory is illustrated with a case study from Flanders (Belgium) where forest-core plant communities exhibit a nested subset structure. The underlying ecological mechanism was one of habitat specialization and not of differential extinction, suggesting that species extinction in Flemish forests mainly occurred in a deterministic way; the process of species relaxation resulting from habitat reduction and subsequent stochastic species extinctions may not have been important.

Keywords: Deterministic extinction; Species relaxation; Forest core plant species; Forest fragment; Habitat fragmentation; Stochastic extinction.

Nomenclature: Delanghe et al. (1988).

Introduction

This contribution offers a concise introduction to the concept of the nested species subsets (for a more extensive review see Worthen 1996). Traditionally, communities have mainly been analysed at the species number level or at the individual species abundance level: z-values of species number-area curves were analysed, species number and the abundance of individual species were related to habitat features, communities were described using rank-abundance diagrams, local species abundance was related with regional species distribution, etc. (e.g. Hanski 1981; Rosenzweig 1995).

Outside vegetation science, the quantification and analysis of an intermediate level of community structure (i.e. community composition, or species co-occurrence) has been relatively underexplored (Worthen 1996). A nested subset structure appears to be a very common form of such a community composition (see Wright et al. 1998 for an analysis of 279 data sets). The theoretical concept that was developed with respect to nested species subsets can be applied to describe and to explain the composition of every species assemblage. The phenomenon has been described in detail e.g. for birds on land bridge islands (Patterson & Atmar 1986), birds in chaparral fragments (Bolger et al. 1992), amphibians in ponds (Hecnar & M'Closkey 1997), plant communities on islands in lakes and in forest fragments (Kadmon 1995; Honnay et al. 1999), ectoparasite communities on marine fishes (Worthen & Rhode 1996), mussel species in rivers (Vaughn 1997), fly communities on mushrooms (Worthen et al. 1996; Worthen et al. 1998), mammals on mountain tops (McDonald & Brown 1992) and rodents in desert habitats (Patterson & Brown 1991).

We aim at giving an introduction to the nestedness concept and to the ecological mechanisms generating nestedness. We will refer to recent literature and illustrate the concept with a case study form the Flanders region of Belgium (fully discussed in Honnay et al. 1999).

Definition and Measures

A group of biotas is said to be perfectly nested when each species is present in all biotas richer than the most depauperate one in which that species occurs (Patterson & Atmar 1986) (Fig. 1). A whole set of procedures has been developed to detect and to quantify a nested community structure. In all cases, the starting point is a data matrix with presence-absence data of species versus habitat fragments. The most easy procedure is to apply a Mann-Whitney U statistic for each species separately, after ranking the habitat fragments with respect to species richness. The Mann-Whitney statistic detects if one individual species is more likely to occur in species rich habitat fragments than in species poor fragments. Tail probabilities can then be combined using Fisher's method (Fisher 1970) to generate a matrix-wide nestedness measure (e.g. Schoener & Schoener 1983; Simberloff & Martin 1991; Hecnar & M'Closkey 1997).

More sophisticated methods are based on the comparison of the data-matrix order with the average order of e.g. 1000 randomly generated matrices; resulting from a Monte-Carlo simulation (e.g. Patterson & Atmar 1986; Cutler 1991; Wright & Reeves 1992; Lomolino 1996). This group of methods normally results in one matrix-wide nestedness measure. The matrix structure or order is quantified by measuring the deviation from perfect nestedness (i.e. counting the number of unexpected presences or absences of species) after ranking the habitat fragments with respect to species richness. In our opinion the best way to quantify nestedness is to use Atmar & Patterson's method which uses a combination of a thermodynamic measure of order and a Monte-Carlo simulation (for further details see Atmar & Patterson 1993, 1995).

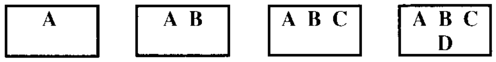


Fig.1. Example of a perfectly nested dataset. When a species occurs in a habitat fragment it also occurs in each fragment that contains more species (from Honnay & Hermy 1998).

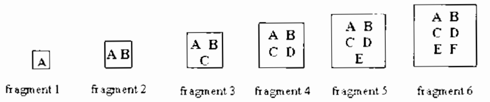
Ecological mechanisms generating nested subset patterns

Nestedness occurs when species are distributed non-randomly with respect to a common set of extrinsic variables (Patterson 1990). This non-random community composition urges for the identification of the external factors that structured community assembly. In the literature four ecological mechanisms generating nested subsets have been described, which are not mutually exclusive.

Differential extinction

Nested communities were first explicitly addressed in a conservation biology context, studying faunal species relaxation on oceanic (land bridge) islands – e.g. Schoener & Schoener 1983; Simberloff & Levin 1985; Patterson 1987; see also the incidence functions of Diamond (1975) – and on habitat islands (Patterson & Atmar 1986; Bolger et al. 1992). The mechanism that is supposed to generate nestedness in this context is relatively simple, as is shown in Fig. 2, which can be read as a time series, from right to the left, or as a snapshot, representing an archipelago of habitat fragments. As a result of shrinking habitat size, the population sizes of the different species are also decreasing and the populations become the subject of stochastic extinction processes (*sensu* Shaffer 1981). The populations fall under their MVP (Minimal Viable Population) and, consequently, go extinct from the habitat patch. The depicted species distribution pattern (i.e. perfectly nested, and with a perfect rank correlation between species number and fragment area) results from differential extinction which is the result of differences in MVP between species.

Applications which are associated with a species pattern generated by differential extinction are the determination of the minimal required habitat area for an MVP of a species and the prediction of extinction-prone species (McDonald & Brown 1992; Atmar & Patterson 1993). The theory has also led to the re-opening of the SLOSS-debate (Wright & Reeves 1992; Worthen 1996). The applicability of the nestedness concept in conservation biology and its relevance for the design of nature reserves has been criticized by Simberloff & Martin (1992), Cook (1995), Skaggs & Boecklen (1996) and Boecklen (1997).



	Species A	Species B	Species C	Species D	Species E	Species F
Fragment 1	1	0	0	0	0	0
Fragment 2	1	1	0	0	0	0
Fragment 3	1	1	1	0	0	0
Fragment 4	1	1	1	1	0	0
Fragment 5	1	1	1	1	1	0
Fragment 6	1	1	1	1	1	1

Fig. 2. Example of a perfectly nested dataset exhibiting a perfect rank correlation between fragment area and species richness. The underlying ecological mechanism is species relaxation. As a result of fragment area reduction, species will become extinct in a predicable order that is directly correlated to their MVP. Habitat quality is considered homogeneous and there is no species migration between fragments (from Honnay & Hermy 1998).

Differential colonization

Another possible mechanism that generates nestedness is the different ability of species to colonize new, relatively isolated habitat patches. Isolated habitats will contain only a subset of species with very good dispersal abilities. The issue has been addressed by Patterson (1990), Kadmon (1995), Worthen & Rhode (1996) and Honnay et al. (1999). The capability of differential colonization abilities to generate nestedness is strongly scale-dependent. On a landscape scale it is to be expected that neither excellent dispersers (because they are occurring even in the most isolated habitat), neither the least dispersing species (because they cannot leave their patch to colonize even the closest habitat) will contribute to a nestedness pattern (Honnay et al. 1999).

Habitat specialization or 'nested habitats'

Differences in habitat specialization between species cause that some species occur almost everywhere (generalists), while other species are confined to well-defined abiotic conditions (specialists). It is possible that habitats are nested, i.e. that if a habitat type occurs in a certain patch, it will also occur in all most habitat-rich patches. This means that rare habitats only occur in habitat rich patches. It can be expected that patches characterized by a high habitat diversity potentially contain all species from the available species pool (including specialists), while habitat poor patches will only contain generalists. It has to be noted that the measurement of habitat diversity is largely scale dependent and a function of the organisms which are studied (see the case study). Because habitat diversity and patch area are mostly correlated, nested species subsets resulting from nested habitats can easily be confused with a species pattern that resulted from habitat reduction and consequent species relaxation (Kodric-Brown & Brown 1993; Honnay et al. 1999).

Random sampling

It is known that species-area relations can be generated from sampling effects. Because large areas constitute large samples and thus contain more individuals, they will also contain more species simply by chance (Connor & McCoy 1979; Coleman et al. 1982). Abundant species will have a higher probability of being present in a certain habitat patch, simply by chance, potentially producing a nested subset pattern (Bolger et al. 1991; Cutler 1994). Worthen (1996), however, concluded that the specific conditions under which passive sampling produces nestedness are still unclear and that more research is needed.

Separation of nestedness generating mechanisms

It is not always easy to separate the different nestedness generating mechanisms, especially because the mechanisms are not mutually exclusive. Different techniques have been proposed to distinguish between external variables generating nestedness. Some authors have claimed that the nestedness measure they developed is able to distinguish between different mechanisms. Wright & Reeves (1992) suggest that their C measure of nestedness is able to distinguish between differential extinction and differential colonization-born nestedness patterns. Cutler (1994) claimed his nestedness measure *U* to be able to distinguish between extinction based and random sampling based nestedness patterns. The most flexible, and to our opinion the best way to detect the nestedness generating mechanisms is to rank habitat fragments according to one or more of the potential external variables (e.g. according to patch area and patch isolation), to quantify the degree of nestedness, and to compare this with the average degree of nestedness of 500 or more randomly generated data matrices (Lomolino 1996; Honnay et al. 1999; and see further). It has finally to be noted that it is possible to exclude mechanisms but that it may be difficult to finally accept one single mechanism.

Nested forest plant communities in Flanders: species relaxation or nested habitats?

Nested forest plant communities

In western and central Flanders, 156 forest fragments (mean patch area 39.4 ha, median 14.0 ha) were surveyed for the presence/absence of 75 'true' forest plant species. The definition of a true forest species is based on field experience and literature references (cf. their phytosociological behaviour according to Ellenberg et al. 1991, see also Honnay et al. 1998a, b). True forest species are confined to the inner core habitat of the forest because they entirely depend on the forest microclimate for their survival and regeneration. Flemish forests have an extremely long history of fragmentation and human interference; Tack et al. (1993), studying historical herbaria, give evidence of a clear decline of the overall plant species richness in these forest fragments, at least since the 19th century.

The plant species composition of the surveyed forest fragments exhibited a significant nested subset pattern; if a species occurs in a certain fragment, it also occurs in nearly all species richer fragments (see Honnay et al. (1999) for further details). An interesting consequence of the highly significant nestedness pattern, is that relatively rare plant species, which exhibit also a strong individual nestedness pattern, can function as an indicator species for true forest plant species richness of Flemish forest patches (Table 1).

Looking for the underlying ecological mechanism

We tested three hypotheses with respect to the nestedness generating mechanism: species relaxation, differential colonization and nested habitats. We used G.I.S. analysis tools (Arc/Info) to calculate the total forest area within a radius of 500 m around a forest patch. This variable was then used as an inverse isolation measure (see also Grashof-Bokdam 1997). We also generated an overall synthetic habitat diversity measure for each of the 156 forest fragments by performing a Principal Component Analysis on five inventoried habitat diversity variables (forest shape index, number of soil textures, number of soil moisture levels, number of soil types and a slope index). The scores of the forest patches on the first factor axis were taken as habitat diversity measures.

Table 1. True forest plant species which can be used as indicator species for total true forest plant species richness in Flemish forest fragments. The species exhibit a highly nested spatial pattern ($p < 0.0001$) and are relatively rare (occurring in < 25% of the forests). Median and minimal true forest plant species richness of the fragments where the indicator species occur are given (from Honnay et al. 1999).

Indicator species	Median species richness	Minimal species richness
Narcissus pseudonarcissus	43	32
Melica uniflora	44	29
Chrysosplenium oppositifolium	39	17
Dactylorhiza fuchsii	42	17
Veronica montana	36	19
Mercurialis perennis	33	14
Sanicula europaea	37	14
Chrysosplenium alternifolium	34	12
Paris quadrifolia	35	11
Lysimachia nemorum	34	12

Secondly we tested if the observed species distribution pattern could be regenerated by ranking the patches according to patch area, patch isolation, and the derived habitat diversity measure. Therefore we used Monte-Carlo based simulation algorithms (see again Honnay et al. 1999). The external variable which was responsible for the nested subset pattern of the data matrix was habitat diversity, meaning that the species relaxation hypothesis and the differential colonization hypothesis could be rejected. The community composition of forest plant species in forest fragments in Flanders is caused by differences in habitat specialization between the different species. The species relaxation hypothesis is rejected, i.e. patch area is a poor predictor for community composition. Supposing that patch area is closely related to population size, there is no reason to expect that stochastic extinction processes (demographic, genetic or environmental stochasticity (Shaffer 1981; Pimm et al. 1988) have seriously affected plant populations. The plant extinction in Flanders was probably guided by deterministic factors like e.g. forest grazing or abandonment of coppice management. Honnay et al. (1998a) came to a similar conclusion after an analysis at the species number level; the community composition analysis by means of the nested subset analysis, however, provides much stronger evidence for this deterministic hypothesis.

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Limitations and extensions of the carousel model in boreal forest communities

Maslov, Alexandr A.[1, 2*]
& van der Maarel, Eddy[2]

[1]*Institute of Forest Science, Russian Academy of Sciences, Uspenskoe, Moscow region, 143030 Russia;* [2]*Department of Plant Ecology, EBC, Uppsala University, Villavägen 14, SE-75236 Uppsala, Sweden;* **Fax +70955616590; E-mail am@ilan.msk.su*

Abstract. Small-scale dynamics of vascular plants and cryptogams were studied between 1980 and 1998 in 10 natural forests of different types in the Moscow region, Russia, and Central Sweden . Data sets of several thousands of 20 cm × 20 cm permanent quadrats – with time lags of one or five years – to assess fine-scale species turnover. The main aim was to find out extensions and limitations of the 'carousel model' (van der Maarel & Sykes 1993) in boreal forests. The general model was tested by calculating cumulative species frequencies and cumulative species numbers. We found in nearly all forest types that the cumulative species number at small scales grows very slowly as compared to species-rich grasslands. Since forests often show a heterogeneous, patchy structure, we need a more complex carousel model to describe species turnover, i.e. one with a community circuit and several patch circuits.

Keywords: Fiby forest; Fine-scale turnover; Forest dynamics; Moscow region; Species mobility.

Nomenclature: Tutin et al. (1964-1980); Corley et al. (1981).

Introduction

To elucidate the high degree of mobility at fine scales in species-rich grasslands on the limestone plateau of Öland, Sweden, van der Maarel & Sykes (1993) developed the phenomenological 'carousel model'. They postulated that most species in such communities move around in the community and can eventually reach most of its microsites. Similar types of dynamics were found in other grassland types (e.g. Herben et. al. 1993; Sykes et al. 1994).

Van der Maarel & Sykes (1993) pointed out that their grassland is species-rich and subjected to periodic disturbances (drought), rather homogeneous, grazed by cattle, nutrient- and water-deficient, and rich in annual species. It is still unclear whether the model can be applied in a more general way, and particularly, in boreal and boreo-nemoral forest communities that are known to be heterogeneous, rather species-poor, and not subjected to periodic catastrophic mortality (Sykes et al. 1994). The main idea of this study was to test the carousel model in several types of Russian and Swedish forest floor communities and find possible extensions and limitations of the model.

Investigation areas and Methods

Nine natural forest stands, not disturbed by logging or grazing, were selected for comprehensive studies during the years 1980-1983 in forest reserves of the Moscow region (Maslov 1989). Permanent sample plots were established, usually 40 by 50 m each. One plot of the same size was established in 1993 in the primeval forest of Fiby near Uppsala, Sweden. This plot was situated in one of the classical gap plots – no. 1 – initiated by Rutger Sernander (1936; cf. Hytteborn et al. 1991). The predominant tree species both in the Swedish and Russian plots were *Picea abies* and *Pinus sylvestris* accompanied by *Populus tremula*, *Betula pubescens* and *Tilia cordata* in some mixed stands.

Rooted presence (rooted frequency) was recorded for all vascular and bryophyte species – while omitting herb and dwarf shrub seedlings (with cotyledons). The quadrats of 20 cm × 20 cm were situated in several parallel transects of 50 m long. The number of quadrats ranged from 1000 to 4000 per plot. In Fiby the analysis was done yearly from 1993 till 1998 in 1000 quadrats. In the Moscow region the time interval was always 5 yr, and the total number of repetitions was four.

Species with a frequency of at least 1 % in any one year (called 'common species') were selected for further testing of the carousel model. Cumulative frequency of the common species was calculated as the total number of quadrats in which the species occurred in any one year. Mean cumulative species number (cumulative richness per quadrat) was obtained by counting the number of species in the first year and adding species newly appearing in later years (van der Maarel & Sykes 1993). Species mobility (turnover rate, *TR*) was calculated as the reciprocal value of the species persistence value *V*; *TR* = 1 – *V*, where *V* is a tetra point correlation coefficient (cf. Herben et al. 1993; Økland 1995).

Results

In the herb-rich *Picea-Populus* forest in Fiby, 54 species of vascular plants and bryophytes were found in the transects. Of these, 40 species were common (Table 1).

During the investigation period of 6 yr only 15 of the 40 species showed a clear increase in cumulative frequency, i.e. more than 10 %. For most species cumulative frequency increased very slowly. Several dominant species, notably *Deschampsia flexuosa*, *Hepatica nobilis*, *Vaccinium myrtillus* and *V. vitis-idaea* show an increase of less than 10 %. For only one species, *Maianthemum bifolium*, the cumulative frequency passed the limit of 80 % and became a 'highly frequent' species.

The cumulative species number on 20cm×20cm quadrats increased on average from 6.9 in 1993 to 10.4 for the period 1993-1998 (Table 1). This means a mean increase per year of 0.7, which is clearly lower than in the Öland grassland with 1.6 on plots of 10 cm×10 cm (van der Maarel & Sykes 1993), though not extremely low. The cumulative number of 10.4 is still far from the total number of common species, 40.

Table 1. Cumulative root frequency of 40 common species in 1000 20 cm × 20 cm quadrats and cumulative species numbers in Herb-type spruce forest Fiby (Central Sweden). ↑ = increasing annual frequency; ↓ = decreasing annual frequency, ↑↓ = highly pulsating species. Figures with increase in cumulative frequency more than 10% in bold.

	Cumulative root frequency (%)					
Year	93	94	95	96	97	98
Anemone nemorosa ↑↓	**16**	**48**	**59**	**62**	**64**	**65**
Campanula persicifolia	2	3	3	3	3	3
Carex digitata	11	13	14	15	15	16
Carex montana	5	5	5	6	6	6
Convallaria majalis	18	21	23	24	26	27
Deschampsia flexuosa	19	21	22	23	23	23
Fragaria vesca	7	8	9	9	9	10
Geranium sylvaticum	3	4	5	5	5	5
Hepatica nobilis	49	53	55	56	57	57
Hieracium murorum	3	3	4	4	4	4
Lathyrus montanus	10	13	14	15	16	16
Lathyrus vernus	**22**	**28**	**31**	**32**	**33**	**33**
Linnaea borealis	7	9	10	11	11	12
Luzula pilosa	13	15	17	18	19	21
Maianthemum bifolium	**63**	**72**	**74**	**77**	**79**	**80**
Melampyrum sylvaticum	**24**	**30**	**32**	**34**	**34**	**35**
Melica nutans	1	1	1	1	2	2
Milium effusum	7	8	10	11	13	16
Mycelis muralis	**3**	**5**	**7**	**8**	**10**	**13**
Orthilia secunda ↓	4	5	6	6	6	7
Oxalis acetosella ↑	**24**	**30**	**34**	**37**	**40**	**44**
Paris quadrifolia	**13**	**20**	**24**	**27**	**28**	**29**
Ribes alpinum	2	2	3	3	3	3
Trientalis europaea	**27**	**38**	**44**	**47**	**49**	**52**
Trifolium medium	1	2	2	2	2	2
Vaccinium myrtillus	34	37	38	39	41	41
Vaccinium vitis-idaea ↓	34	37	39	40	41	41
Veronica chamaedrys	**33**	**39**	**42**	**45**	**45**	**47**
Veronica officinalis	2	3	3	4	5	5
Vicia sepium	**20**	**26**	**29**	**31**	**33**	**34**
Viola riviniana	**35**	**41**	**44**	**45**	**46**	**47**
Atrichum undulatum ↑	2	2	2	3	3	3
Dicranum polysetum	9	11	11	12	12	12
Dicranum scoparium	7	8	10	11	12	14
Hylocomium splendens	**51**	**56**	**59**	**62**	**64**	**67**
Plagiochila asplenioides	8	9	9	9	9	9
Plagiomnium affine	16	16	18	20	21	23
Pleurozium schreberi ↑	**17**	**22**	**25**	**27**	**30**	**32**
Ptilium crista-castrensis	16	16	17	18	19	21
Rhytidiadelphus triquetrus	**53**	**57**	**58**	**60**	**62**	**64**
Mean cumulative species no.	6.9	8.4	9.1	9.6	10.0	10.4

In a rather similar, also mixed *Picea-Populus* forest in the Moscow region, with fewer species, the results are more similar to the Öland results. After four repetitions, nine out of 22 common species show an increase in cumulative frequency of more than 10%. The number of highly (> 80%) frequent species has increased from one to three. But we should keep in mind that the time lag there was 5 yr instead of 1 yr.

The cumulative species number on 20cm×20 cm quadrats increased on average from 3.9 in 1980 to 6.5 for the period 1980-1995, which is 0,65 per analysis. Such low increases in species cumulative frequency and cumulative species number were also found in most other forest communities in the Moscow region.

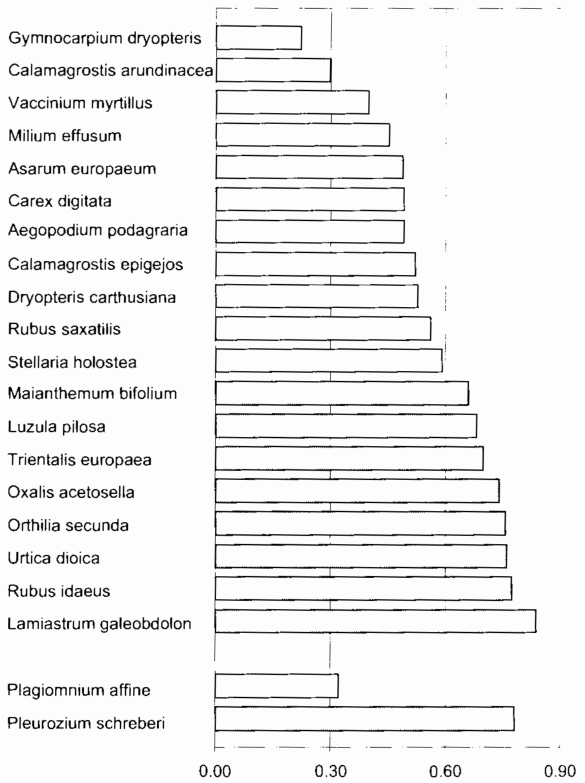

Fig. 1. Mean species turnover rates $TR = 1 - V$ from 1980 to 1995 in an *Oxalis*-type mixed *Picea-Populus* forest in the Moscow region; based on four repetitions with a time lag of 5 yr.

Another way to demonstrate the carousel model is the calculation of species mobility or 'fine-scale turnover' (Rusch & van der Maarel 1992). In the present paper we understand 'single-species turnover' as the tendency of a species to change position within the community by colonizing new (micro) sites, leave them, and occupy them later again.

A wide range of species turnover rates is shown for the *Oxalis*-type of the *Picea-Populus* forest in the Moscow region (Fig. 1). Two species, *Gymnocarpium dryopteris* and *Calamagrostis arundinacea*, have a rather low turnover rate (< 0.30). On the other hand there are eight species, including one bryophyte, *Pleurozium schreberi*, with a high mobility (> 0.60). The most mobile species are the clonal *Rubus idaeus* and *Lamiastrum galeobdolon*. Such wide ranges of mobility rates were also found in most other forest communities in the Moscow region.

Discussion

The boreo-nemoral (south taiga) old-growth forest communities in Russia and Sweden described here differ in several ways from the alvar grassland. They are known to be heterogeneous, i.e. both patchy and stratified. They are not grazed by cattle, but rootings of wild boar (*Sus scrofa*) create fine-scale disturbance both in the Moscow forests and Fiby. Most boreal forests suffer periodically from strong winds. Large canopy gaps formed by severe storms

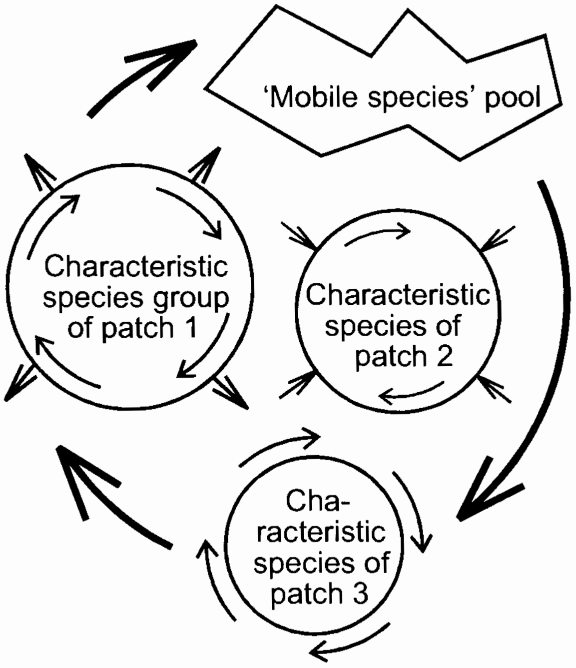

Fig. 2. Phenomenological model of a 'complex carousel' in forest communities. Mobile species from the community species pool move around the entire community, local patch species may move within patches. The arrows indicate movements of species in space as well as changes in multi-species patch size. In the figure patch 1 increases: 'developing patch', patch 2 decreases: 'regressing patch', patch 3 does not change: 'stable patch'.

are found both in Fiby and the Moscow region. In contrast to grasslands, most of our forests are well supplied with water and are moderately rich in nutrients. Regarding species life forms, there are very few annual species in boreal forests, the only common ones being *Melampyrum* spp. In the *Avenetum* ca. 15 % of the species are annuals.

Considering all these differences between species-rich grasslands and natural boreal forests we did expect that the carousel model in forests could face some problems. Indeed, in nearly all forest types, the small scale species accumulation proceeds much slower than in grassland. Where in the alvar grassland the number of highly frequent species (with cumulative frequency > 80 %) increased from 11 to 40 % after 5 yr, in Fiby forest there was an increase from 0 to 2.5 %. Such slower species accumulation could be partly explained by lower numbers of annuals and less frequent severe disturbances like drought. There is also a methodological difference between the two analyses: the basic subplots compared – 10 cm × 10 cm in the grassland and 20 cm × 20 cm in the forest – but this is compensated for by the usually larger size of plant shoots in forest communities.

The following difference between forests and grasslands was found essential. Forest species may have a high turnover rate from year to year but a slow increase in cumulative frequency. This can hardly be explained by the 'simple carousel model'. When looking, for example, at *Anemone nemorosa* (Table 1) a relatively fast increase in cumulative frequency during the first two years was followed by years of little (near to zero) change. *A. nemorosa* was one of the most mobile species in the Fiby spruce forest, and the low increase in cumulative frequency after two years of observations could be explained by its limited distribution within the community in certain patches. Some species in the forests only move around in certain parts while other parts are not colonized. According to distribution maps, in the Fiby forest *A. nemorosa* could not reach the upper 'boreal' part of the slope dominated by *Vaccinium myrtillus*, *Deschampsia flexuosa* and *Hylocomium splendens*.

This means that in heterogeneous forest communities, a simple carousel model with only one large 'turnaround circle' is not realistic. As was already foreseen by van der Maarel & Sykes (1993) several circuits may exist in patchy plant communities, in relation to gap formation and recolonization, and also in relation to topographic variation. Moreover, there is clear temporal variation linked to patch dynamics. To extend the carousel model to forest communities we suggest now the idea of a '*complex carousel model*' with a community circuit and several patch circuits (Fig. 2).

This model includes two types of dynamic processes. The first type is the single-species dynamics as described in the original carousel model. The second type is 'patch dynamics', including small-scale gap dynamics (see van der Maarel 1996).

Species which a high dispersal capacity and broader range of habitats can move around the whole plot community at relatively high speed. They are the 'circulating' and/or 'pulsating' species in the terminology of van der Maarel (1996) or the 'mobile species' according to Zobel et al. 1998. Examples in the forests described here include *Melampyrum* spp., *Pteridium aquilinum*, *Trientalis europaea*, *Luzula pilosa*, where *Melampyrum* is a typical 'circulating' and 'pulsating' species, while *Pteridium aquilinum* is only circulating – its fronds can spontaneously arise at various places in the highly complex rhizome system (see Maslov 1989).

A second type of species can move around in some of the patches and during part of the dynamic cycle. They are usually clonal species with limited vegetative spread. They could still, but more slowly, move around in the community as their particular patch type develops in other parts of the stand as a result of patch dynamics (Fig. 2).

We intend to further develop and quantify the 'complex carousel' by characterizing patch structure through floristic classification and by calculating cumulative frequency and cumulative richness in separate patches. We also intend to apply it to other types of vegetation.

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Fine-scale coalition structure in *Brachypodium* grassland

Virágh, K.[*]**, Bartha, S. & Botta-Dukát, Z.**

Institute of Ecology and Botany, Hungarian Academy of Sciences, H-2163 Vácrátót, Hungary;
[*]*Fax +3628360110; E-mail viragh@botanika.hu*

Abstract. Previous landscape-scale studies found two characteristic species coalitions, a xeric and a mesic one, in *Brachypodium pinnatum*-dominated loess grasslands developing after deforestation in Hungary. Fine-scale patterns of interspecific associations were detected in various patch types (Forest type, Transitional-, and Steppe type) of these grasslands to test the self-similarity of vegetation pattern, i.e. whether the same coalitions appear at coarse and fine scales. Micro-maps of rooting individuals (or ramets) of vascular plant species were recorded in 20 × 110 grids of contiguous 5 cm × 5 cm micro-quadrats. Spatial associations between species pairs were detected by information theory methods. Coalition structures were analysed by permutation tests. We found a tendency for self-similarity in the Transitional-, and the Steppe types. However, constraints due to dominance and rarity, and the related vegetation patterns can mask the differentiation into xeric and mesic species groups at fine scales.

Keywords: Information theory; Randomization test; Self-similarity; Spatial scaling; Species association; Xeromesophilous grassland.

Introduction

Environmental patterns are often of fractal nature, therefore it is reasonable to expect that vegetation also has some fractal characteristics, i.e. self-similarity across scales. Such self-similar vegetation patterns were reported from tallgrass prairie (Collins & Glenn 1990) and from the ecotone between short grass prairie and desert grassland (Gosz 1993). In Hungarian loess grasslands, the medium-scale differentiation, i.e. the existence of a patchwork with alternating dominance of mesic and xeric species groups was described by Zólyomi & Fekete (1994) and by Fekete et al. (1998). In the present paper, we will analyse the trends of differentiation (according to the moisture and light gradients) at finer scale. Coarser-scale vegetation patterns are often physiognomic and compositional structures, which are relatively easy to detect and classify. When resolution is close to the size of individuals or ramets, the pattern becomes stochastic (van der Maarel & Sykes 1993), and we loose the ability of visual description, and the background mechanisms become less obvious. Because fine-scale patterns are non-physiognomic, we need to use spatial statistics to reveal the fine-scale patterns of coalitions. We will use spatial associations to detect these patterns.

Our hypothesis is that the vegetation is self-similar, i.e. similar structures of mesic and xeric coalitions appear also at finer scales. If there is a fine-scale spatial differentiation between the xeric and mesic guilds, we expect more positive and less negative associations within these guilds and more negative and less positive ones between them.

Material and Methods

The study site is situated in a landscape protection area in the northern part of Hungary, 25 km east of Budapest, within a hilly landscape at 200 - 300 m a.s.l. Mean annual temperature of the site is 9 °C and mean annual precipitation is about 600 mm. Transitional soil types between brown forest soil and chernozem on loess substrate are typical here . The area was formerly covered by dry *Quercus pubescens* oakwood, which was cut in the early 1900s (Anon. 1883, 1943). However, deforestation was incomplete and resulted in a heterogeneous mosaic of secondary successional habitats. The forest management activity stopped and the site has only occasionally been grazed since then. During a landscape-scale survey of the vegetation (Fekete et al. 1998) some remnants of oakwood, shrubland, and a patchwork of various xero-mesophilous grasslands on the northeast slopes were found. The successional relations of grassland patches are complex, however, there is a clear direction of differentiation from the xeromesophilous forest vegetation to the xerophilous loess steppe vegetation (Virágh & Bartha 1998). Three typical patch types (Forest type, Transitional-, and Steppe type) of *Brachypodium pinnatum* dominated grasslands were selected for the present study (Table 1),

Micro-maps of rooting individuals (or ramets) of vascular plant species were recorded in 20 × 110 grids of contiguous 5 cm × 5 cm micro-quadrats in June, 1993. From the basic grid data, computerized samplings were carried out (Podani 1984, 1987). Because spatial associations are scale-dependent (Podani et al. 1993), we surveyed four sampling unit sizes (5 cm × 5 cm, 5 cm × 10 cm, 5 cm × 15 cm, and 5 cm × 20 cm) at fine scales. Due to the asymmetry of the field grids, elongated sampling units were used to decrease potential edge effects. Our methodological study showed that elongated quadrats can be appropriate for detecting interspecific associations (Bartha & Horváth 1987). Associations between two species were computed from a 2 × 2 contingency table and they were expressed by their mutual information, I(A,B) (Juhász-Nagy & Podani 1983). Significant associations were detected by Monte-Carlo randomization tests (Site-model; Watkins & Wilson 1992), randomizing the positions of individuals (presences) of species with the same frequency as in the field. Significance of observed value was calculated as the proportion of Monte-Carlo randomizations in which the random I(A,B) is equal to or more extreme than the observed value. 2500 randomizations were applied in each test. The signs of associations were detected from the observed frequencies of diagonal cells of the 2×2 contingency tables (Kershaw 1964). To avoid artefacts due to rarity, species with

Table 1. Guilds and some textural attributes in three patch types of *Brachypodium pinnatum* grassland.

Mesic guild: *Brachypodium pinnatum, Betonica officinalis, Campanula persicifolia, Chrysanthemum corymbosum, Pulmonaria mollis, Veronica chamaedrys, Viola hirta;*

Xeric guild: *Achillea pannonica, Adonis vernalis, Agropyron repens, Astragalus onobrychis, Bothriochloa ischaemum, Bromus erectus, Carex humilis, Chamaecytisus austriacus, Chrysopogon gryllus, Euphorbia pannonica, Festuca rupicola, Helianthemum ovatum, Koeleria cristata, Medicago falcata, Phleum phleoides, Thlaspi jankae, Thymus pannonicus, Viola rupestris;*

Indifferent guild: *Briza media, Carex caryophyllea, Centaurea sadlerana, Falcaria vulgaris, Filipendula vulgaris, Galium verum, Pimpinella saxifraga, Seseli annuum, Silene vulgaris, Teucrium chamaedrys, Trifolium montanum.*

Type	Forest-	Transitional-	Steppe-
Total species richness	50	60	53
Number of frequent species:			
frequency % > 1	16	26	21
% of total species number			
mesic species	62	52	32
xeric species	25	46	54
indifferent species	13	2	14
Relative cover %			
mesic species	70.4	36.7	15.9
xeric species	8	39.4	51.3
indifferent species	21.6	24.9	32.8
Three dominant grass species			
Relative cover %			
Brachypodium pinnatum	66	35	14.9
Festuca rupicola	3.6	19.7	38
Bromus erectus	0	6.8	5.6
Frequency %			
Brachypodium pinnatum	79	63	52
Festuca rupicola	23	17.6	20
Bromus erectus	5.5	24.7	25

frequencies less than 1% were omitted from the analyses (Tóthmérész & Erdei 1992). Significant associations were evaluated with respect to species groups. Three groups of species, a 'mesic', a 'xeric', and an 'indifferent' group were defined based on the results of previous studies (Zólyomi 1967; Ellenberg 1991; Zólyomi & Fekete 1994). All the three groups were analysed; however, we present here only the results concerning the mesic and xeric guilds. The mesic, shade-tolerant species and the xeric, light-demanding and drought-tolerant species are different in their resource use, therefore we will call them 'guilds'. If abundances are concerned, the mesic and the xeric guilds form coalitions (patch types) at the landscape scale. However, the spatial differentiation is incomplete and floristically both guilds are present in each patch type in varying proportions (Fekete et al. 1998).

The graph of pairwise associations is often used to describe the spatial structure of plant communities. However, only few attempts (e.g. Yarranton 1973) have been made to statistically analyse a graph structure. In this paper, we test the separation of guilds in the graph by permutation tests. In each simulation step the guild membership array of species was randomly rearranged (the size of guilds remained unchanged), and we calculated the expected frequencies of positive and negative associations within and between random guilds. (An exact test would be performed with generating all the possible combinations, but its number is usually too large.) The numbers of associations within guilds were not tested separately for the mesic and xeric guilds, because they are not independent from each other. On the contrary, the number of artefacts would have increased, the test would have been too conservative, i.e. it would have rejected the null hypothesis less often than it should.

The frequencies were compared to the frequencies of associations observed within guilds and between the original xeric and mesic guilds. Significance of an observed value was calculated as the proportion of randomizations in which the random value is equal to or more extreme than the observed value. One tail-test was done. 10 000 randomizations were used to detect the expected frequencies of associations. Randomization tests were performed for each quadrat size independently.

Results

A large number of significant spatial associations between species was found for each vegetation type. The number of significant associations slightly increases with increasing plot size. The relative number of significant associations ($p < 0.05$), expressed as percentage of the maximum, $s \cdot (s - 1)/2$, where s is the number of species, varies between 7 and 21% (Fig. 1). The numbers of frequent species in the 5.5 m^2 patches of the Forest-, Transitional-and Steppe types are 16, 26 and 21, respectively.

Table 2 presents the results of the randomization tests of coalition structure. In previous studies (Podani et al. 1993; Bartha & Kertész 1998), we found that the scale where an interspecific association appeared depends on the abundance and the intraspecific species pattern. In the present study, four sampling unit sizes were used from 5 cm × 5 cm to 5 cm × 20 cm, which is the range of the sizes of individual plants or ramets. By using multiple sampling unit sizes, we increased the probability of finding significant associations. However, we do not think that the mechanisms that cause the vegetation differentiation at these scales will change considerably within this narrow range of scale. If the pattern of significant and non-significant values changes with scale, it is only due to the various abundances and various autocorrelations of species. Therefore, we accepted a significant deviation from random expectation if there was at least one quadrat size with significant value. Table 2 shows that in cases where significant deviation appears at more than one scale, the sign of direction of differences remained consistent.

The number of associations within- and between guilds is not significantly different from the random expectation in the Forest type. This contrasts with our self-similarity hypothesis. In the Transitional type, the number of positive associations within guilds and the number of negative associations between guilds are significantly higher than the random expectation, which supports our self-similarity hypothesis. Significantly more negative and significantly less positive associations were found between guilds than expected in the Steppe type. There was no significant difference in the number of associations within guilds.

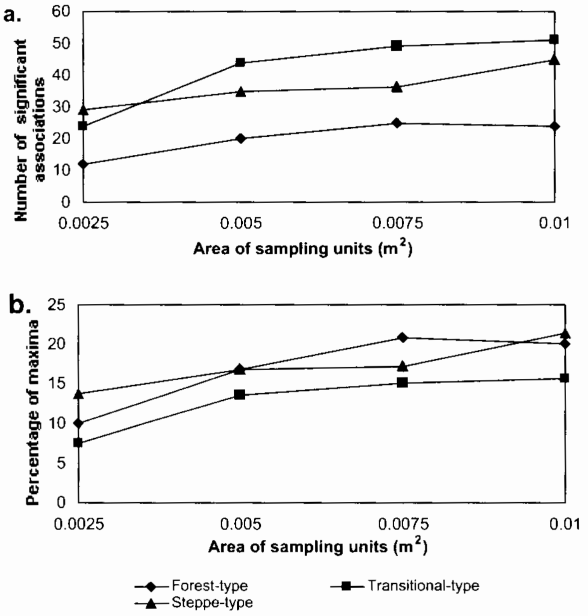

Fig. 1. Number of significant associations as a function of scale. **a.** Number of significant associations ($p < 0.05$) detected in the three vegetation patch types of *Brachypodium pinnatum* grassland. **b.** Number of significant associations expressed as a percentage of maxima $s \cdot (s-1)/2$, where s is the number of frequent species in each vegetation type.

Discussion

Our results show that the trend of the spatial differentiation of mesic and xeric species on microsites of different humidity and light conditions appears at fine-scales as well. However, other factors such as the relative abundance of guilds and the type of the vegetation patterns might mask this assembly rule (Bartha et al. 1995).

If both guilds are abundant (e.g. in the Transitional type), we can find the mesic and xeric coalitions at fine scales. If the abundance of mesic and xeric guilds is considerably different (Table 1), the number of significant associations decreases. Thus, the self-similarity can not be revealed. At an extreme situation the field number is 0 (that is the minimum value), but it can not be significant due to the skewness of the random distribution. We marked these cases in the table as non-tested ones. The species of the subordinated guild occupy the gaps in the matrix of dominant guild. When the gaps become smaller and smaller there is a local exclusion among the species of the subordinated guild that results in an interspecific spatial segregation within guild, i.e. less positive and more negative associations within-guild than expected. Thus, more significant deviations from the random expectation were revealed between guilds than within guilds. The differences in the abundances of xeric and mesic species influenced the graph structure mainly in the Forest type and to a smaller degree, in the Steppe type, while in the Transitional type the results supported our self-similarity hypothesis, i.e. mesic and xeric guilds were separated at fine scales, similarly to the landscape scale pattern.

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Table 2. Number of significant associations within and between guilds. Significant deviations from expected values: * if $p < 0.1$ and ** if $p < 0.05$; Non-significant deviations: ns; Non-tested cases are marked by nt.

			Forest type				**Transitional type**				**Steppe type**			
Area of sampling units (m²)			0.0025	0.005	0.0075	0.01	0.0025	0.005	0.0075	0.01	0.0025	0.005	0.0075	0.01
Between xeric and mesic guilds	positive	field	3	8	7	5	5	7	7	5	5	5	4	7
		random average	2.929	5.338	5.619	5.348	4.391	8.387	8.976	7.543	7.407	9.15	9.16	10.59
		H_1: random > field	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	**	ns
	negative	field	0	0	1	0	1	1	2	6	3	2	3	4
		random average	0.001	0	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001
		H_1: random < field	nt	nt	ns	ns	ns	ns	ns	**	**	ns	*	nt
Within xeric and mesic guilds	positive	field	2	3	4	5	7	12	14	15	8	11	11	11
		random average	3.123	5.673	5.968	5.663	5.992	11.373	12.161	10.291	9.372	11.52	11.517	13.329
		H_1: random < field	ns	ns	ns	ns	ns	ns	ns	*	ns	ns	ns	ns
	negative	field	0	0	2	2	0	1	0	1	0	1	1	4
		random average	0.282	0	1.136	1.121	0.541	0.535	1.076	3.517	1.094	1.091	1.441	2.874
		H_1: random > field	nt	nt	nt	nt	nt	nt	nt	ns	nt	nt	nt	ns
Within xeric guild	positive	field	0	1	0	1	7	11	13	14	8	11	11	11
	negative	field	0	0	1	2	0	0	0	1	0	1	1	4
Within mesic guild	positive	field	2	2	4	4	0	1	1	1	0	0	0	0
	negative	field	0	0	1	0	0	1	0	0	0	0	0	0

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On the responsibility and liberty of the field ecologist

Klötzli, F.

Geobotanical Institute, Swiss Federal Institute of Technology, Zürichbergstrasse 38, CH-8044 Zürich, Switzerland;
Fax +4116321215; E-mail kloetzli@geobot.umw.ethz.ch

Abstract. Ever since science and ethics became separated in the 17th century, ethical aspects have played a minor role in science and ethics did no longer have many contacts with (natural) science. However, the need for scientific field research brought disturbance to natural ecosystems and ethical aspects demanded more and more consideration in modern times, especially regarding socially relevant research (e.g. on conservation biology), adaptable to the local situation, attributes and idiosyncrasies and forcing science to think matters over regarding limits to liberty in scientific research and the interpretation and implementations of scientific results in society.

Modern ethics are an instrument of power to clear the way for an attributive attitude, acknowledging the Kantian principle of universality.

For practical purposes liberty and responsibility in the three steps of scientific research are outlined, viz. in the frame of the scientific problem, in its methods but also in its results, in their publication and implementations.

Keywords: Attributive attitude; Disturbance; Ethic competence; Field research; Globalization; Kantian principle; Local idiosyncrasy; Sociology.

"Liberty of man does not signify that he may do what he wants, but that he must not do what he does not want."
J.-J. Rousseau

An introduction to responsibility and liberty

"Liberty signifies responsibility - that's why so many people are afraid of it". There is quite a lot of truth in these words of G.B. Shaw, a word touching even the author when putting down his talk. But what is hidden behind the expression 'liberty', and what do we imagine by the term 'responsibility'? 'Liberty' has to be understood as a rational action only and has to be demanded of all rational beings. In this sense it is not a simple basis for individuals and their personal wishes. Therefore 'liberty' signifies that I am free to handle or manipulate any item or situation without essentially disturbing the liberty of my neighbours.

'Liberty' is only possible under the discipline of a functioning culture and society (Cramer 1989).

'Responsibility' is more complex and needs an excursion into some more philosophical aspects. There is no collective identical responsibility: it is based on more and better knowledge and position. Man's supremacy must be based on responsibility and this should have the advantage to be on the first place of all other human concessions and strategies in the wide field of conflicts between men and nature. Also, responsibility is based on moral insight and ethic competence (details in Küng 1998; Weischedel 1972; Durr, in Ruh 1997; Fraser-Darling 1986; Ruh 1990,1997; Jonas 1979). Sustainability in land use is man's duty, but it also guarantees his own survival. And right here we are in a dilemma: Since D. Hume's work philosophers distinguish between 'science' and 'ethics'. Science assesses facts, 'all that is', and ethic decides on 'what should be (done)'. Thus science disjoins principally facts and values (Morin 1982; on the loss of nature in philosophy: see Drewermann 1989). There is a certain blindness towards the effects of the scientists' results in our society, in their social and ethic implications in daily life, in the ways society will take up such results and assimilate them into daily needs and general outlook (on science and responsibility see e.g. Sitter 1986). At this point it is appropriate to compare Einstein and his reaction on the implementations and issues of atomic theory in war time.'

There is no 'science and responsibility' to teach us, and there is no 'sociology of science' (Morin 1982). Thus there is no scientific approach to 'responsibility'. Furthermore, we have to avoid two illusions: there is no political conscience which is scientifically motivated, and there is no moral conscience whatsoever guaranteeing a happy end to any practical application of our results, considering all the reactions and feedbacks in our society. And there we are all faced by the paradox situation that more progress in scientific power in our technical culture is coupled with a growing weakness of the scientist in our society. The clash with decision-making politicians inhibits the scientist to assess the complexity between science and society, and in many cases forces one to avoid his intrinsic responsibilities (Morin 1982). Therefore the scientist is urged more and more to sense (instinctively?) the ethic consequences of his activities. We are all obliged to judge the risks of our activities which lead to normative synthesis of values, carried by wisdom and the objective knowledge on man's capacities. At this place one should compare Aristotle who described affirmatively a philosopher having no social responsibility, seeking fulfilment in theoretical considerations, living in political abstinence – which is comparable to the attitude of so many scientists of today. Here philosophy has failed (Arber, Public statement).

The great lacks in bioethics or in the evaluation of biodiversity and species decline, or in biotechnology are quite manifest because hardly any philosopher touched the them (cf. Küng 1998; Ruh 1997; Arber, Public statement).

At this point Kantian philosophy demands another attitude towards society (and nature; Westhoff 1983, 1985). With his 'Categoric Imperative' Kant urges all citizens to ponder over their attitude towards society (see Schulte 1996; Küng 1998): "Act only on that maxim whereby you can at the same time will that it should become a universal law" (translation from Encyclopedia Brittanica). This is rather an expression of the conditions of rationality of conductance than that of its morality. But Kant puts much weight on the power of practical (common) sense and understanding: moral instincts and laws determine our will under absolutely neutral aspects having no inflictions with sympathy. This trigger puts our intentions under the roof of law and order. Man should (still) be free to do his duties for their own sake, including for the sake of nature (details in Schulte 1996).

Too much individualism may deteriorate a whole society - the same society that gives protection and the necessary freedom for the individual, conventions (as e.g. confidence) giving the final stability (Cramer 1989).

Our scientific attitude under the moral laws

The strength of this specific attitude that was shown above should not be much less against nature itself. We should respect the integrity of organisms, populations, and communities, be it analytical or experimental research (on man's attitude towards vegetation see Westhoff 1983; on holism and reductionism see especially Looijen 1998; on man's behaviour see Ruh 1997). Much of our work is not touching the entity of an ecosystem as such, especially work with inventories, structure analysis, microclimate, plant communities, analysis of dispersal, mapping etc. In ecosystems analysis we try to assess reactions, feedbacks and fluxes in all compartments, considering the ecosystem as a network of interrelations: 'no stone is alone'. And we try to be as careful as possible with the soil compartment or in examining production. As a rule we do not dissect the system unnecessarily, we try not to produce artefacts in taking tits and bits of the system out of its context, and we are aware that it is us producing limits or boundaries in a given area (Klötzli 1991, 1995).

A self-chosen boundary signifies respect in front of a 'free area' in nature, ergo an ethic limit (Westhoff 1983; see also Ruh 1997, on 'Ehrfurcht' [awe, reverence] towards nature's structures). Other limits are systematic (too complicated to examine), technical, sociopolitical, or financial, or even physical, driven by our inhibitions to disturb nature, cutting out parts of it or collecting organisms (unnecessarily).

True limits arise in manipulating with material alien to the ecosystems, as e.g. noxious or tracer substances, non-native organisms, or introducing artefacts of all kinds, except adapted or non-aggressive to the system. On the other hand, today's human impacts are comparable to extraterrestrial effects, man's brain is not apt to adjust to a transcendental adaptation, to sense the effects and the power of his influence on his own existence (Klötzli 1991, 1994a, b). "Man is slain by his own brain", often being stuck in his own unethic behaviour (Klötzli 1995). Moral behaviour and thinking demands transcendental directives and selective moral insight (Küng 1998; Arber, Public statement).

Of course, in tackling questions such as carrying capacity, – especially in our stressed forest ecosystems, – underdevelopment, in succession etc. we may be forced to investigate parts of the system – dissect it! – and put it under an artificial stressor. Again this is bearable when reactions of a given system have to be investigated, as e.g. regeneration, effects of buffer zones, reintroduction of eliminated or disappeared organisms, restoration of undesirable states etc.

A further opening in our self-chosen limits are anthropogenic ecosystems, of course, which are itself artefacts by definition, steered and managed by man. In such cases we already touch the aspects of economy and sociology. Mostly, such research is based from the beginning on intense contacts with landowners, tenants and politicians (Klötzli 1991; Anon. 1985; constraints and limits to agricultural use).

In Table 1 my working group has tried to show the influence of liberty and responsibility on the three phases of ecological fieldwork. Be it during the initial phase when tackling a 'scientific problem' or in adjusting our 'methods' or during the last phase when we are assessing our 'results' or finishing discussions and papers we are confronted with constraints in our liberty and the wide frame of our responsibilities.

Since modelling has become a common tool to assess the reactions of ecosystems, assumptions and results have to be corrected according to an analysis of the behaviour of such a system under stress. We know that many reactions are often not foresceable, including the presence/absence of many species which behave in an unpredictable way, often chaotic (in the physical sense), in most systems forcing us to extend such dynamic investigations to more than five, often more than 10 years (Klötzli 1995).

Our scientific attitude against society

If society is involved in our investigations, be it politically relevant or according to our own wish in a sociological context, we try to hang on to an interdisciplinary issue from the beginning, informing and engaging our counterparts from the very start, be it in agro- or silvicultural systems, or in conservation areas. A society involved from the beginning will be more ready to accept the results of our findings and to lend a hand to the expected implementations ('gerichtete Forschung': it is relevant to practical issues, it touches parts of our society and it takes care of practical applications).

Any researcher should take it as his/her duty to give as

Table 1. Liberty versus responsibility in three phases of ecological field work.

	Liberty	Responsibility
Scientific problem	Personal interest	Socio-political consideration
	Creativity	Needs / usefulness
	Scientific progress	Efficiency
	Chance of success	Probability of progress
	Relevance	Auxiliary implications abuse
	Position in scientific community	Funds and time
Methods	Choice	Information
	Research programme	Adaptation
	Scientific interest	Care of public mentality
	Political limits	Appropriate aims
Results and publication	Liberty to publish	Consequences of research
	Interest of society	Attitude / honesty
	Ways of presentation	(Undesirable results?)
	Time and engagement	Popularisation
	Scientific cooperation	(Media, cooperation)
		Control of interpretation

much information as possible to the public – since mostly his grants come from public funds. And it also gives him/her a chance to transmit ecological principles to society, sociopolitically and/or economically. As we all know these ecological principles are as a rule transferable, be it stability s.l., feedback, fluxes and cycles, diversity/diversification, use of energy, co-evolution, and based on these qualifications, there is even a possibility for true sustainable development. However, the scientist often does not have much chance to follow that way, because society lacks the respective receptors, the personal antennas are not receptive or ready, and the will to learn about reactions and limits of complex systems and its implications under daily environmental conditions are not developed, and the full extent of the problem may even be not understood (Klötzli 1994). But often it is the scientist who is to blame. In a coat of 'ethic innocence' one is not aware of the society's demands or even may be at enmity with science.

People are confronted with an ever-changing 'new world' with a new environmental situation (on man's hegemonial demands; see Drewermann 1989). They would actually know their aims but do not know where they stand and which way to go (Klötzli 1991). General 'globalization' s.l. is invading and overlaying all local trends, which are actually better adapted to the local living conditions and accepted by tradition (see Beck 1997; Martin & Mann 1998). It is an unbreakable trend which will stop local trends and habits. It reminds me, by the way, of the more negative aspects of the 'Green Revolution'. Decision makers and financing agencies made so far no distinction between local habits and the habits in their own mighty country. We should not repeat such mistakes, but we are on the way to do so. The 'mighty countries' have their own optics as e.g. what is favourable in agriculture, in conservation practices or in scientific implementations, and they export it to countries not adapted as their own. And in doing so they forget the local ecological, economical and political structures which gave birth to local adaptations, pecularities, idiosyncrasies, and also to local mentality, experience and their ways of fair play. Such attitudes, assumptions and trends should be re-examined. As there will always be favourable and unfavourable areas on our globe (see e.g. Schellnhuber 1997) we should accept a multifaceted world and also a mosaic of globalized, unadapted and unhappy countries. Also amongst us there should be more sensibility and sensitivity to other countries' differences. I guess the experience starts when listening to each other, and it continues when editing articles of compatriots...

Obviously, the only alternative is 'attribution': our brains must be aware of the intentions and ideas of our 'neighbours', and their wishes, knowledge, convictions, feelings and thoughts of progress.

To sum up: To carry responsibility is not only an attitude we are forced to keep up towards our green world. We are also responsible to strengthen our liaisons between countries and regions, and in order to integrate local knowledge too for the benefit of a global endeavour to guarantee as much (bio)diversity as possible in our unique world (on economical aspects see Binswanger 1991 and Studer 1996).

The field ecologist – society and science

What does society expect of our activities, of the ecologist, of the field ecologist? Is it part of an Utopia in the sense of Campanella ('sun-republic') or Thomas Morus? Or is it part of a rough game in science policy, or a realistic part of daily life? What are the concrete aims, seen from the applied side? (On processes in society see e.g. Klöti 1991.)

Normally, society is not aware of their field ecologists, they are 'cryptic people', not like popstars or football teams, models or certain politicians. However, society expects results from the ecologist, since it is aware of a changing environment, confronted with a general eutrophication, oil spills, or – more modern – 'Global change'. Ecology is a sort of a medicine for many. But society is not prepared to believe e.g. that ecologists might have a considerable effect on the maintenance of their landscape. The question is: 'Where is his sociopolitical position, where may the ecologist be seen?'

The active field ecologist is more confronted with local or regional, much less with global problems. Working with public funds one has to consider the sociopolitical environment. Therefore one is also familiar, as we have seen above – with the attitudes and expectations of the farmer, the forester, the engineer and partly the economist and certain important politicians, trying to appreciate the implications of the 'green branches' in practical life, while the ecologist tries to go beyond his/her field in applied science in order to reach society, trying hard to make him/herself understandable. With that in mind, one cannot avoid thinking the political ways, searching to implement his/her findings, often misunderstood and pressed by uncertainties and political intrigues. That is where one has to bring in responsibility and honesty towards society and its needs. Besides these relations one needs to know more how, where and by whom decisions are taken and who is responsible. Only then can one try to learn the specific 'dialects' of decision makers of different background. Is that the start of an Utopia? In the typical Renaissance utopies there is a general tendency to put social and political situations under ethic constraints. Therefore man is confronted with a decrease in liberty – politically spoken. Nowadays, ethic commissions are installed to control the effects of research data which might have impact on political structures or provoke dangerous situations on political thresholds.

Transmitted into our modern research situations, and, consequently considering the question of responsibility in society and science, the scientist should know how to play his instruments in the wide open field of liberty and responsibility keeping in mind to contribute to the education of his society. One may not delegate responsibility to any superior body, it must remain an integrative part of the individual. Such considerations are enabling the birth of a unit of responsible beings, which are independent of any obscure theoretician or single decision makers. Global ethics must grow out of each of us knowing to belong to our global ecosystem and ready to be responsible and to take over the necessary responsibilities (Mislin 1973; Sitter 1985).

With this attitude we approach the last goal we all acknowledge, that is the maintenance of environmental conditions worth living.

Back to society: Under the given circumstances we should hold ourselves back and be free to accept a scientific activity, keeping us responsible, liberal and communicative on the way to more wisdom. We should be aware of our selfborn wisdom – to overcome the schisms between the world of meditation and the world of science, the best service we can offer to society.

A few conclusions for scientific society

The scientific community has its liberties and responsibilities in the frame of society and citizenship and the global situation. Results may be presented not only along the normal scientific pathways. They may also be put in a context where scientists may be urged to think about their social and political, human and ethic implications and repercussions. In other words: A field ecologist may be forced to submit the political aspects of his/her results in a clear and understandable language. Any scientist in such a situation has to be able to express himself on the political glacis as well, although there are a lot of incompatibilities between science, society and the statesman's or governments' political attitudes.

At any rate, a scientist has to be aware that his interests are embedded in a functioning society and that his attitude must be attributive (i.e. to be able to sense the other peoples' intentions, desires etc.). Therefore true scientific responsibility is based on the Kantian principle of universality ('categoric imperative') and not on the utilitarians' selfishness on the expense of the community. This principle could be the basis of planetary responsibility and an appropriate mentality avoiding the ethics of pure success, to be able to forecast sense and the implications of any activity. Humanity would be united into a true community of responsible people, engaged in future events and with respect for nature. In that context ethics are an instrument of power for the scientist, the citizen and society, forming an adaptive community of responsible and free human beings.

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"Liberty signifies responsibility, that's why so many people are afraid of it."
G.B. Shaw

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