

Dry grassland communities on southern Öland: phytosociology, ecology, and diversity

Swantje Löbel^{1*} & Jürgen Dengler²

¹Department of Plant Ecology, Evolutionary Biology Centre, Uppsala University, Villavägen 14, SE-752 36 Uppsala, Sweden; ²Institute of Ecology and Environmental Chemistry, Leuphana University Lüneburg, Scharnhorststraße 1, DE-21335 Lüneburg, Germany; Present address: Plant Systematics, Biocentre Klein Flottbek & Botanical Garden, University of Hamburg, Ohnhorststraße 18, DE-22609 Hamburg, Germany; E-mail dengler@botanik.uni-hamburg.de; Corresponding author: E-mail swantje.lobel@ebc.uu.se

Abstract

We studied dry grassland vegetation on southern Öland, both within and outside the Great Alvar, using the Braun-Blanquet approach. We were able to distinguish 15 associations or equivalent units belonging to three major syntaxa. Dry grasslands on sandy soils (class *Koelerio-Corynepherea*; subclass *Koelerio-Corynepherea*) occurred along the east and west coasts. Weathered rock and outcrop communities (class *Koelerio-Corynepherea*; subclass *Sedo-Scleranthenea*) inhabited shallow skeletal soils, mainly on the Great Alvar. Semi-dry basiphilous grasslands of the class *Festuco-Brometea* occurred on moraine soils, which were the least extreme in terms of soil moisture and nutrient availability. Whereas the first category comprises impoverished variants of widely distributed syntaxa, all *Sedo-Scleranthenea* and *Festuco-Brometea* communities lack direct counterparts in central Europe. The alvar communities proved to be floristically well separated from the others. Species density on 4 m² was highest in the *Sedo-Scleranthenea* (that of the *Gypsophilo fastigiatae-Globularietum vulgaris* with 80 taxa being one of the highest known), intermediate in the *Festuco-Brometea*, and lowest in the *Koelerio-Corynepherea*. Harsh and variable conditions, small plant sizes, and a large local species pool are considered possible causes.

Keywords: Alvar; Biodiversity; Environmental condition; *Festuco-Brometea*; *Koelerio-Corynepherea*; *Sedo-Scleranthenea*; Species richness; Syntaxonomy

Nomenclature: Vascular plants: Tutin et al. (1968-1993); *Allium schoenoprasum* var. *alvarense* and *Silene uniflora* ssp. *petraea*: Jonsell & Karlsson (2004); Mosses: Hill et al. (2006); Liverworts: Grolle & Long (2000); Lichens: Santesson et al. (2004).

Introduction

Since the first visit of Carl von Linné in 1741, Öland has been known for its unique vegetation and outstanding flora. Four vascular plant species (*Artemisia oelandica*, *Festuca oelandica*, *Galium oelandicum* and *Hieracium ×dichotomum*) and several infraspecific taxa (e.g. *Allium schoenoprasum* var. *alvarense*, *Crepis tectorum* ssp. *pumila*, *Helianthemum oelandicum* ssp. *oelandicum*, *Silene uniflora* ssp. *petraea*) are considered endemic to Öland or Öland and Gotland (Rosén 1982; Jonsell & Karlsson 2004). However, Dengler & Boch (2007) found three of these taxa also on alvar sites of the island of Saaremaa, Estonia. Further plant species reach the limits of their geographic range, or occur as outliers on Öland (e.g. Rosén & Borgegård 1999). In central Europe, many of the species of this latter category characterise different dry grassland syntaxa, and one wonders whether these communities also occur on Öland.

Studies aiming to classify dry grassland communities in northern Europe are rare, and their results controversial (e.g. Braun-Blanquet 1963; Hallberg 1971; Westhoff et al. 1983; Krahulec et al. 1986; Dierßen 1996; Dengler & Löbel 2006; Dengler et al. 2006a, b). In northern Europe, generally few attempts have been made to develop supra-regional, hierarchical classifications of vegetation types (cf. Lawesson et al. 1997). One usually relies on informal classifications that are not backed up by vegetation tables (e.g. Pålsson 1999).

Like many other Scandinavian vegetation types, dry grasslands proved to be difficult to assign to higher units of the phytosociological system. Many diagnostic species are missing in northern Europe, whilst at the same time character species different syntaxa frequently occur together (e.g. Diekmann 1995, 1997). The poor characterisation of Nordic vegetation types and the lack of a formal classification cause problems since the EU legislation (e.g. the Habitats directive) is largely based on phytosociological units.

On Öland, dry grassland communities have mainly been studied and described from the Great Alvar, especially by Albertson (1950), Krahulec et al. (1986), and Bengtsson et al. (1988). Krahulec et al. (1986) provided the first modern and comprehensive classification of dry grassland types of the Great Alvar (except the open moss and *Sedum* communities). They distinguished four associations and discussed their position in the phytosociological system but refrained from validly describing these new units. Knowledge about dry grasslands outside of the Great Alvar is limited (e.g. Ammar 1978). However, species distribution maps (Sterner & Lundquist 1986) suggest that some of the alvar communities and other dry grassland types may also occur in other parts of the island. Very little was known about dry grasslands on sandy soils (subclass *Koelerio-Corynephoronea*), even though these are quite interesting from a phytogeographical point of view.

We studied the dry grassland vegetation in the northern part of southern Öland, including dry grasslands on sandy soils (*Koelerio-Corynephoronea*), weathered rock and outcrop communities (*Sedo-Scleranthenea*) and basiphilous grasslands (*Festuco-Brometea*). In the central part of the study area, where the Great Alvar is located, the limestone bedrock is only partly covered by a thin layer of quaternary deposits. Lime-poor moraine soils interchange with residual soils of varying thickness originating from the limestone bedrock. Shallow, weathered soils also occur in the smaller alvar areas on the east coast. Along the Western Landridge, soils are characterised by coarse gravel originating from ancient shorelines. Glacifluvial deposits form sandy soils along the west coast and in the northeastern part of the study area (Sterner & Lundquist 1986).

The aims of our study are (1) to characterise and compare all dry grasslands types that occur within the study area, both floristically and ecologically, (2) to assign them to units of the phytosociological system and to discuss their differentiation on Öland and in comparison with other regions, and (3) to document and discuss their differences in species richness patterns.

Methods

Vegetation sampling

During spring and summer 2001, we made 469 phytosociological relevés of dry grassland vegetation in the northern part of southern Öland. The villages Färjestaden and N Möckleby mark the northern, and Mörbylånga and Alby the southern border of our investigation area (see Fig. 1, below). Dry grassland areas were identified using topographical, geological and species distributions maps (Sterner & Lundquist 1986). Within the areas, sample plots were subjectively chosen according to homogeneity

criteria. We tried to select sample plots that represent the local variation of community types.

Sample plots were 4 m² in size throughout; this size is a compromise between the usually very small plots (1 m² or less) used by many Nordic scientists (e.g. Albertson 1946, 1950) and the sizes suggested for dry grasslands in phytosociological textbooks (e.g. Dierßen 1990). Uniform plot sizes are important for the determination and comparison of many characteristics of communities, e.g. species richness, constancy values and thus fidelity of species (e.g. Dengler 2003; Dengler et al. in press).

All vascular plant, bryophyte, and lichen species (with the exception of epilithic crustose lichens) were identified in the field, or if necessary taken into the laboratory. Abundance was estimated according to the Braun-Blanquet cover-abundance scale in the modified version of Wilmanns (1998). This scale closely resembles that of van der Maarel (2005) but draws the limit between 2a and 2b at 15% instead of 12.5%. All relevés and their precise position data are available in Löbel (2002).

Additionally, species-area analyses were carried out in 31 representative stands representing the five associations on the Great Alvar to be described below. We used a nested-plot design and arranged the subsequent plot sizes (0.0001 m², 0.004 m², 0.009 m², 0.0025 m², 0.01 m², 0.04 m², 0.09 m², 0.25 m², 1 m², 4 m², and 9 m²) in a spiral so that the smallest plot was situated in the centre of the largest. All plants 'rooted' in the respective plots were recorded (grid-point system of Williamson 2003).

Structural and soil parameters

For each plot, several environmental and structural parameters were recorded. Soil depth (cm), micro-topography (cm), cover of bare rocks (%) as well as total and group-specific cover of vegetation (%) were determined in the field. We took a mixed soil sample of the uppermost layer (0-10 cm) at different points of each plot. The samples were dried at 105 °C. For each sample, the soil pH was measured with a pH electrode (WTW). In 130 soil samples, we also determined the content of organic matter (mass %) as loss at ignition (905 °C) corrected for calciumcarbonate.

Mean moisture-values (F-values) according to Ellenberg et al. (1991) were calculated for each relevé, weighting species by the mean coverage (%) that corresponds to their respective cover-abundance value.

Phytosociological classification

The phytosociological classification was undertaken according to the consistent application of the Braun-Blanquet approach proposed by Dengler (2003; see also Dengler et al. 2005). Important aspects of this approach are the objective definition of character and differential species,

and the possibility to describe one 'central syntaxon' within each syntaxon of superior rank. The central syntaxon is characterised by the diagnostic species of the syntaxonomic level(s) above, although it may have insufficient or no character species of its own. The validity of character species is limited to the distribution range of the next higher syntaxon (see also Bergmeier et al. 1990).

We mainly follow the classification scheme of dry grassland types proposed by Dengler (2004a, b), which is based on the evaluation of vegetation data from large parts of Europe. For the basiphilous rock and outcrop communities we adopt the results of our own supraregional study (Dengler & Löbel 2006; Dengler et al. 2006a). The nomenclature of the syntaxa follows the International Code of Phytosociological Nomenclature (Weber et al. 2000).

Ordination

Ordinations were undertaken using Detrended Correspondence Analysis (DCA, Hill & Gauch 1980) with detrending by segments. Three different floristic datasets were ordinated: (1) all species, (2) vascular plants only, and (3) cryptogams only. In addition, we analysed relevés assigned to the three different dry grassland (sub-)classes separately. We used mean species cover (%) in the analyses. Neither down-weighting of rare species nor transformation was applied. Ordinations were performed using the program CANOCO 4.51 (ter Braak & Šmilauer 2002), and ordination plots were created with CANOCO Draw 4.1 (ter Braak & Šmilauer 2002).

Results

Phytosociological classification and floristic characterisation

Table 1 lists the 15 plant communities distinguished, their valid names and their assignment to higher taxonomic units. For details of the nomenclature and synonyms, see Dengler et al. (2003, 2006), Dengler (2004a, b) and Dengler & Löbel (2006). In the text, we do not mention author citations of these syntaxa. In Table 1, the associations are also linked to the units of the Nordic vegetation classification (Påhlsson 1999).

In the synoptic table (see App. 1), we present species constancy values for all associations and for the three different dry grassland (sub-)classes. Character and differential species are indicated by shading. Fig. 1 shows the distribution of stands assigned to the various communities.

Plates 1, 2, and 3 show typical representatives of the main groups: *Koelerio-Coryneporenea*, *Sedo-Scleranthenea* and *Festuco-Brometea*.

Differentiation of the dry grassland (sub-)classes

The diagram of the ordination of all relevés of the first two DCA axes (Fig. 2) reveals a clear floristic distinction between the relevés of the three main groups, *Koelerio-Coryneporenea*, *Sedo-Scleranthenea*, and *Festuco-Brometea*. Separate DCA analyses of vascular plants and

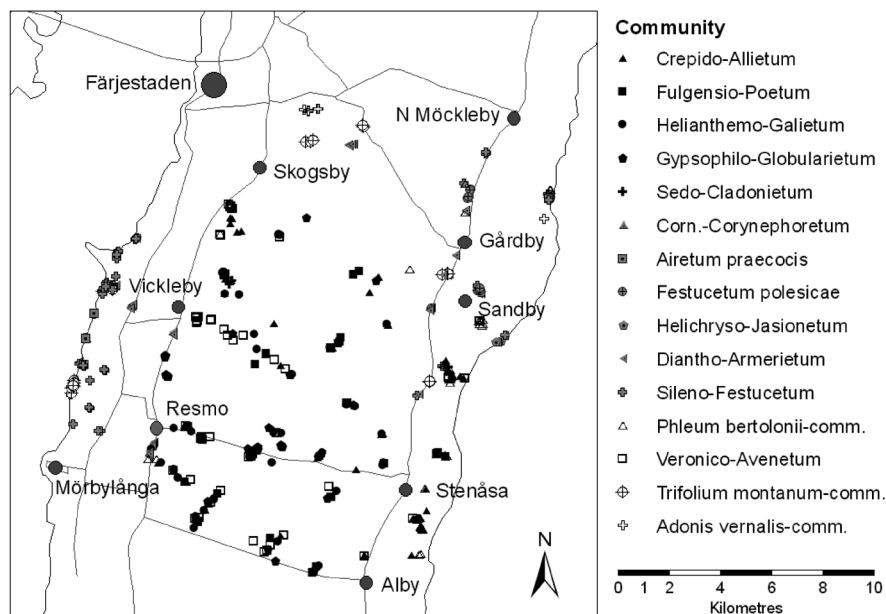


Fig. 1. Investigation area with locations of all sample plots. Dry grasslands on sandy soils (*Koelerio-Coryneporenea*) are restricted to the coastal areas; the *Sileno-Festucetum* also occurs on the Western Landridge. All weathered rock and outcrop communities (*Sedo-Scleranthenea*) except the *Sedo-Cladonietum* only occur in the alvar areas. The *Phleum bertolonii-Saxifraga granulata* community occurs in the smaller alvar areas along the east coast, whereas the *Veronico-Avenetum* is restricted to quaternary deposits on the Great Alvar. The other semi-dry basiphilous grassland communities (*Festuco-Brometea*) occur in the central parts of the island.

Table 1. Syntaxonomical classification of the dry grassland communities of southern Öland. The corresponding units in the Nordic vegetation classification of Pålsson (1999) are given in square brackets. Since this source lacks vegetation tables, the assignments are based on the verbal descriptions only.

Class: *Koelerio-Corynephoretea* Klika in Klika & Novák 1941
 Subclass: *Koelerio-Corynephoreneae* (Klika in Klika & Novák 1941) Dengler in Dengler et al. 2003
 Order: *Corynephoralia canescens* Klika 1934 (central order)
 Alliance: *Corynephorion canescens* Klika 1931
A1 – *Corniculario aculeatae-Corynephorum canescens* Steffen 1931 nom. invers. propos. [5.5.3.1a – *Agrostis vinealis-Corynephorus canescens*-variant]
 Order: *Thero-Airetalia* Rivas Goday 1964
 Alliance: *Thero-Airion* Tx. ex Oberd. 1957
A2 – *Carici arenariae-Airetum praecoxis* Westhoff et al. 1962 nom. invers. propos. (central association) [5.3.1.1c – *Aira praecox-Sedum anglicum*-variant]
 Order: *Trifolio arvensis-Festucetalia ovinae* Moravec 1967
 Alliance: *Armerion elongatae* Pötsch 1962
A3 – *Diantho deltoidis-Armerietum elongatae* Krausch ex Pötsch 1962 nom. cons. propos. [5.2.1.3 – *Festuca ovina-Pleurozium schreberi*-type; 5.4.1.2a – *Festuca ovina-Armeria maritima*-variant; 5.5.3.1 – *Agrostis vinealis-Rumex tenuifolius*-type]
A4 – *Sileno otitae-Festucetum brevipilae* Libbert 1933 corr. Kratzert & Dengler 1999 nom. invers. propos. (central association) [5.4.1.2 – *Festuca ovina-Lychnis viscaria*-type; 5.4.1.7c – *Avenula pratensis-Festuca stricta*-variant]
 Order: *Sedo acris-Festucetalia* Tx. 1951 nom. invers. propos.
 Alliance: *Koelerion glaucae* Volk 1931
A5 – *Helichryso arenarii-Jasionetum litoralis* Libbert 1940 (central association) [5.5.3.1a – *Agrostis vinealis-Corynephorus canescens*-variant]
A6 – *Festucetum polesicae* Regel 1928 [5.5.3.2 – *Koeleria glauca*-type]
 Subclass: *Sedo-Scleranthenea* (Br.-Bl. 1955) Dengler in Dengler et al. 2003
 Order: *Alyso alyssoidis-Sedetalia* Moravec 1967
 Alliance: *Tortello tortuosae-Sedion albi* Hallberg ex Dengler & Löbel 2006
 Suballiance: *Tortello tortuosae-Sedenion albi* (Hallberg ex Dengler & Löbel 2006) Dengler & Löbel 2006 (central suballiance)
B1 – *Cladonio symphycarpiae-Sedetum albi* Tx. 1951 nom. invers. propos. (central association) [5.3.2.1 – *Sedum album-Tortella* spp.-type]
 Suballiance: *Tortello rigentis-Helianthemion oelandici* Dengler & Löbel 2006
B2 – *Crepido pumilae-Allietum alvarensis* Krahulec et al. ex Dengler & Löbel 2006 [5.3.2.1 – *Sedum album-Tortella* spp.-type]
B3 – *Fulgensio bracteatae-Poetum alpinae* (Albertson 1950) Dengler & Löbel 2006 [5.3.2.1 – *Sedum album-Tortella* spp.-type]
B4 – *Helianthemo oelandici-Galietum oelandici* Krahulec et al. ex Dengler & Löbel 2006 (central association) [5.3.2.2 – *Festuca ovina-Tortella* spp.-type]
B5 – *Gypsophilo fastigiatae-Globularietum vulgaris* Krahulec et al. ex Dengler & Löbel 2006 [5.3.2.2 – *Festuca ovina-Tortella* spp.-type]
 Class: *Festuco-Brometea* Br.-Bl. & Tx. ex Klika & Hadač 1944
 Order: *Brachypodietalia pinnati* Korneck 1974
 Alliance: *Filipendula vulgaris-Helictotrichion pratensis* Dengler & Löbel in Dengler et al. 2003 (central alliance)
C1 – *Phleum bertolonii-Saxifraga granulata* community [5.4.1.2 – *Festuca ovina-Lychnis viscaria*-type; 5.4.1.7 – *Avenula pratensis-Fragaria viridis-Filipendula vulgaris*-type]
C2 – *Veronico spicatae-Avenetum* Krahulec et al. 1986 nom. inval. [5.4.1.7b – *Avenula pratensis-Veronica spicata*-variant]
C3 – *Trifolium montanum-Medicago falcata* community [5.4.1.7 – *Avenula pratensis-Fragaria viridis-Filipendula vulgaris*-type]
C4 – *Adonis vernalis-Ononis arvensis* community [5.4.1.7 – *Avenula pratensis-Fragaria viridis-Filipendula vulgaris*-type]

cryptogams (not shown) gave very similar results. The Pearson correlation coefficients of sample scores on the first and second axes were high and significant at $P < 0.05$ ($r_1 = 0.862$ and $r_2 = -0.686$).

Species differentiating the *Koelerio-Corynephoreneae* from both the *Sedo-Scleranthenea* and the *Festuco-Brometea* are mainly species confined to sandy, unstable soils such as *Corynephorus canescens*, *Carex arenaria*, *Jasione montana* and the slightly acidophilous mosses *Ceratodon purpureus* and *Brachythecium albicans*. Other species, e.g. *Thymus serpyllum* ssp. *serpyllum*, *Festuca ovina*, and *Cladonia rangiformis*, which in central Europe are restricted to the *Koelerio-Corynephoreneae* (e.g. Berg et al. 2001, 2004), show a wide amplitude on Öland, and occur in all three major syntaxa of dry grasslands. The same is true for some typical *Festuco-Brometea* taxa, e.g. *Abietinella abietina*.

Sedo-Scleranthenea communities on Öland are characterised by several acrocarpous bryophytes, especially

Tortella spp., *Encalypta* spp., *Didymodon* spp., and *Ditrichum flexicaule* as well as several epilithic lichens. Characteristic vascular plants are *Sedum album* and several small therophytes, e.g. *Arenaria serpyllifolia*, *Erophila verna*, *Hornungia petraea*, and *Saxifraga tridactylites*. Similarly confined to weathered rock and outcrop communities are the assumed island (Baltic) endemics *Helianthemum oelandicum* ssp. *oelandicum*, *Allium schoenoprasum* var. *alvarensis*, *Festuca oelandica* and *Crepis tectorum* ssp. *pumila*.

The *Festuco-Brometea* communities are characterised by many mesophilous species. Typical taxa are *Filipendula vulgaris*, *Veronica spicata*, *Helianthemum nummularium*, and *Asperula tinctoria*. Many *Festuco-Brometea* character species, however, also occur in the *Sedo-Scleranthenea*, e.g. *Anthyllis vulneraria*, *Medicago lupulina*, and *Homalothecium lutescens*.

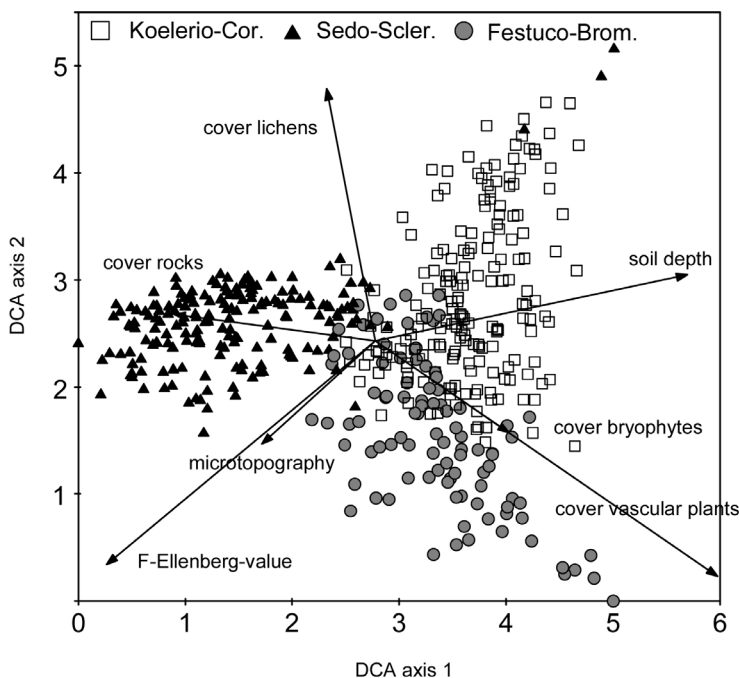


Fig. 2. Ordination diagram with axes 1 and 2 of Detrended Correspondence Analysis; eigenvalues: 0.608 and 0.442. Floristic relationships between dry grassland communities belonging to the *Koelerio-Corynephorena*, *Sedo-Scleranthenea*, and *Festuco-Brometea* are revealed. In addition, correlations of the DCA axes with important environmental and structural variables are indicated.

**Dry grasslands on sandy soils:
*Koelerio-Corynephorena***

In the study area, *Koelerio-Corynephorena* communities occur exclusively on sandy soils outside the Great Alvar. Even though some 'Öland specialities' can be found in these stands, the communities all fit well in widely-distributed associations. We distinguish six such associations (Fig. 3).

The few relevés of the *Corniculario aculeatae-Corynephoretum canescentis* are only poorly characterised. *Corynephorus canescens* dominates the field layer, but the ground layer is poorly developed. The *Carici arenariae-Airetum praecoxis* is characterised by *Aira praecox* and differentiated towards other associations by *Polytrichum*

juniperinum. Floristically, the community connects the *Corniculario aculeatae-Corynephoretum canescentis* and the communities of the *Armerion elongatae*. The associations of the latter alliance are characterised by *Peltigera canina*, and differentiated by *Trifolium campestre*, *Festuca brevipila*, and *Allium vineale*. The *Diantho deltoidis-Armerietum elongatae* includes the characteristic *Dianthus deltoides* and *Armeria maritima* ssp. *elongata*. The *Sileno otitae-Festucetum brevipilae* (Plate 1, p. 19) is mainly negatively characterised, but is differentiated by a high number of basiphilous species. The communities of the *Koelerion glaucae* are characterised by a rather strong continental element and a rich fruticose lichen flora. The *Festucetum polesicae* contains the character species *Koeleria glauca*

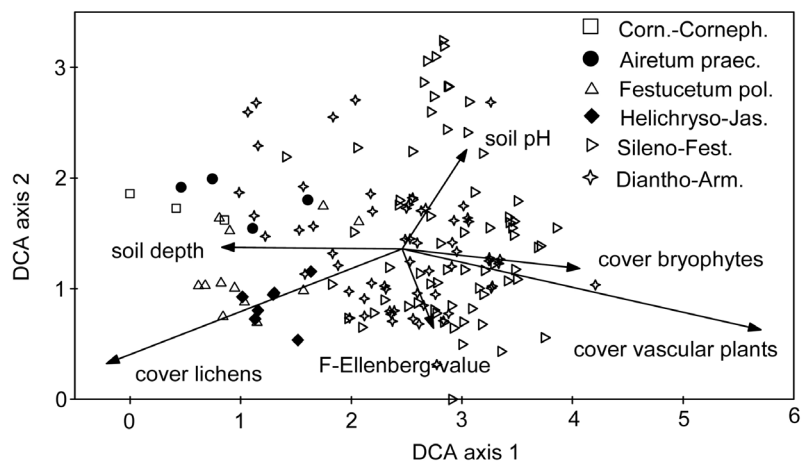


Fig. 3. Ordination diagram with axes 1 and 2 of Detrended Correspondence Analysis of the *Koelerio-Corynephorena* relevés; eigenvalues: 0.471 and 0.350. Floristic relationships between the dry grassland communities in this subclass are revealed. In addition, correlations of the DCA axes with important environmental and structural variables are indicated.

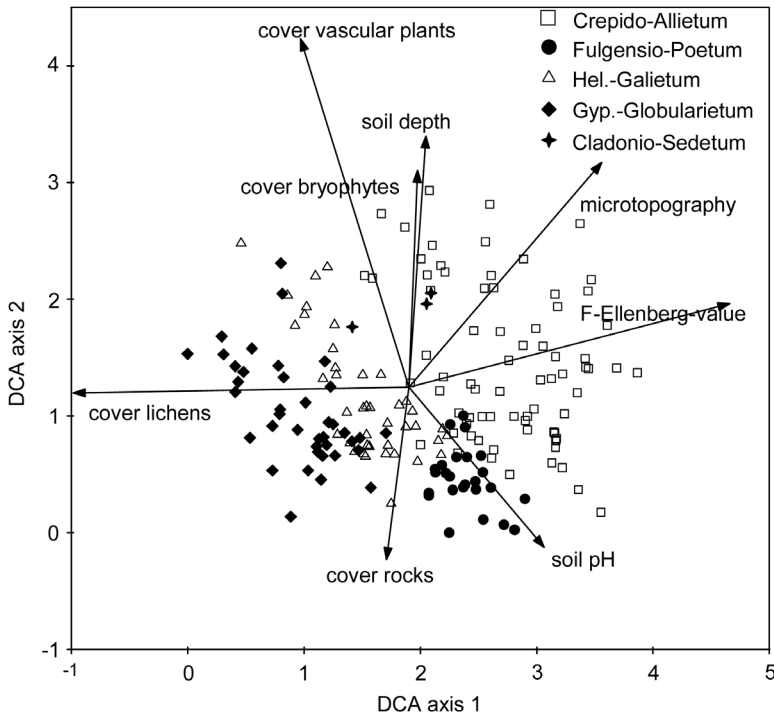


Fig. 4. Ordination diagram with axes 1 and 2 of Detrended Correspondence Analysis of the *Sedo-Scleranthenea*; eigenvalues: 0.431 and 0.322. Floristic relationships between the dry grassland communities of this subclass are revealed. In addition, correlations of the DCA axes with important environmental and structural variables are indicated.

and *Festuca polesica*. The *Helichryso arenarii-Jasionetum litoralis* has no species that characterise it specifically, but it is separated from the *Festucetum polesicae* by the occurrence of several mesophilous species, e.g. *Festuca rubra*.

**Weathered rock and outcrop communities:
*Sedo-Scleranthenea***

We distinguish five associations belonging to the *Sedo-Scleranthenea* (Fig. 4) (for details see Dengler & Löbel 2006; Dengler et al. 2006a).

The *Crepido pumilae-Allietum alvarensis* is characterised by *Crepis tectorum* ssp. *pumila* and the continental *Artemisia rupestris*. The field layer is often dominated by the graminoids *Agrostis stolonifera*, *Festuca ovina*, and *Festuca oelandica*. Several taxa indicating loamy soils such as *Prunella vulgaris*, *Sagina nodosa*, and *Leontodon autumnalis* as well as some rich fen mosses characterise this association. The *Fulgensio bracteatae-Poetum alpinae* is characterised by its rich cryptogam flora, especially the crustose lichen species *Fulgensia bracteata*, *F. fulgens*, *Mycobilimbia lurida*, and *Toninia sedifolia*. *Sedum album* is the dominating vascular species; in addition, several

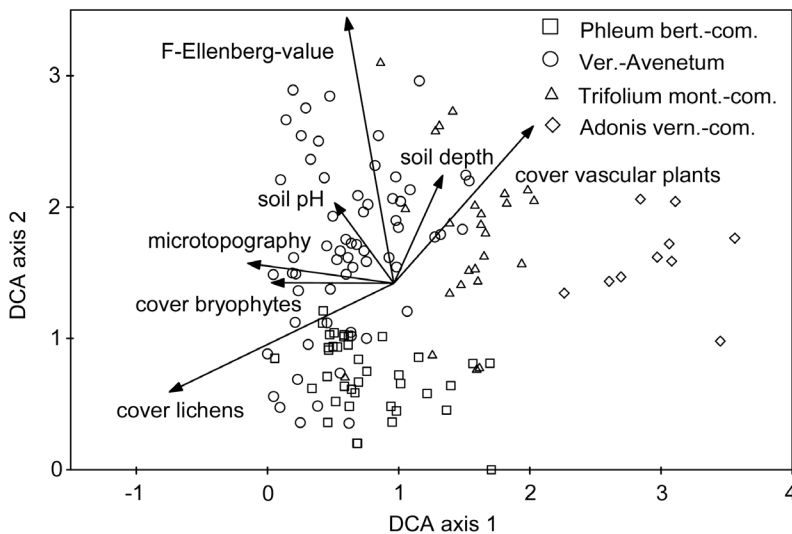


Fig. 5. Ordination diagram with axes 1 and 2 of Detrended Correspondence Analysis of the *Festuco-Brometea* relevés; eigenvalues: 0.482 and 0.353. Floristic relationships between the dry grassland communities of this class are revealed. In addition, correlations of the DCA axes with important environmental and structural variables are indicated.

Plate 1. *Sileno otitae-Festucetum brevipilae* (class *Koelerio-Corynephoretea*; subclass: *Koelerio-Corynephorenea*) at the Western Landridge with *Festuca trachy-phylla*, *Sedum acre*, and *Plantago lanceolata* (photo: J. Dengler, June 2001).



Plate 2. *Helianthemo oelandici-Galietum oelandici* (class *Koelerio-Corynephoretea*; subclass: *Sedo-Scleranthenea*) on the Great Alvar with *Helianthemum oelandicum* ssp. *oelandicum*, *Sedum album*, *Allium schoenoprasum* var. *alvarense*, *Cerastium pumilum*, *Erophila verna*, and the lichen species *Thamnolia vermicularis* (photo: J. Dengler, June 1994).



Plate 3. *Veronica spicatae-Avenetum* (class: *Festuco-Brometea*) on the Great Alvar with *Filipendula vulgaris*, *Avenula pratensis*, *Festuca ovina*, *Asperula tinctoria*, and *Dianthus deltoides* (photo: J. Dengler, June 2001).



small therophytes colonise the moss cushions. *Poa alpina* separates this community from the others.

Amongst the flowering plants of the *Helianthemum oelandici-Galietum oelandici* (Plate 2, p. 19), *Helianthemum oelandicum* ssp. *oelandicum* and *Thymus serpyllum* ssp. *serpyllum* predominate. They also occur in the following community. Floristically, this central association is poorly defined, and *Galium oelandicum* and *Sisymbrium supinum* are the only characteristic species. The ground layer contains several fruticose lichens shared with the *Gypsophila fastigiatae-Globularietum vulgaris*. This last association is characterised by *Globularia vulgaris* and *Gypsophila fastigiata*, which have their major distribution ranges in southwestern and eastern central Europe, respectively. Other typical southeastern European plants are *Vincetoxicum hirsutinaria*, *Melica ciliata*, and *Oxytropis campestris*. Species indicating moist soil conditions are missing; *Agrostis stolonifera* is replaced by *Agrostis gigantea*. Finally, the *Cladonio symphyocarpiae-Sedetum albi* lacks most of the typical alvar bryophyte and lichen species, but contains more acidophilous taxa, e.g. *Racomitrium canescens* and *Potentilla argentea* agg.

Semi-dry basiphilous grasslands: Festuco-Brometea

We distinguish four locally well-characterised communities (Fig. 5). Since it is unclear at present which of these will prove to be well-defined associations in the supraregional context, we treat them as informal units and we refrain from validating the *Veronico spicatae-Avenetum* (Plate 3, p. 19), which has been given a provisional name by Krahulec et al. (1986). Work on a synthesising study

aiming to resolve these problems in a supraregional context (Sweden, Norway, Finland, Denmark, N Germany, N Poland, Lithuania, Latvia, Estonia, NW Russia) is in preparation (see also Dengler et al. 2006b).

The syntaxonomical position of the *Phleum bertolonii-Saxifraga granulata* community is problematic since the community shows a mixture of elements from the classes *Molinio-Arrhenatheretea* Tx. 1937, *Koelerio-Coryneporetea* and *Festuco-Brometea*, although the last are most pronounced. Amongst the flowering plants *Filipendula vulgaris*, *Ranunculus bulbosus*, and *Saxifraga granulata* predominate. In depressions, relatively tall-growing grasses such as *Phleum pratense* ssp. *bertolonii*, *Anthoxanthum odoratum*, and *Avenula pubescens* ssp. *pubescens* dominate, whereas on hummocks, *Koelerio-Coryneporetea* taxa can be numerous.

The *Veronico spicatae-Avenetum* is characterised by the Öland endemic *Artemisia oelandica*, the orchids *Orchis mascula* and *O. morio* and the southeastern *Prunella grandiflora*. Other frequently occurring flowering plants are *Helianthemum nummularium* ssp. *nummularium*, *Filipendula vulgaris*, and *Veronica spicata*. The ground layer is much better developed than in the following communities. Some acidophilous species serve to differentiate the association, e.g. *Danthonia decumbens* and *Antennaria dioica*. The floristic composition varies much, and two subtypes each with two variants can be distinguished (Löbel 2002).

The *Trifolium montanum-Medicago falcata* community is characterised by *Trifolium montanum*, and differentiated by many slightly ruderal taxa, which are absent on the Great Alvar but frequently occur along roadsides, e.g. *Medicago*

Table 2. Site conditions and vegetation structure of the dry grassland communities of southern Öland. Mean values and standard deviations (in brackets) are presented. Note that soil organic matter was measured only in a subset of 130 plots, whereas all other data represent all 469 relevés of this study.

	Cover total (%)	Cover field layer (%)	Cover ground layer (%)	Cover bare rocks (%)	Soil organic matter (%)	Soil depth (cm)	Micro-topography (cm)	Soil pH (H ₂ O)	F-value Ellenberg
A – Koelerio-Coryneporetea									
A1 – <i>Corniculario-Coryneporetum</i>	37 (6)	35 (6)	2 (3)	0.0 (0.0)	1.2 (0.3)	51.7 (14.4)	0.0 (0.0)	5.0 (0.8)	2.2 (0.2)
A2 – <i>Carici-Airetum</i>	78 (6)	55 (6)	48 (3)	0.0 (0.0)	1.3 (0.0)	35.6 (17.1)	0.0 (0.0)	4.9 (0.3)	2.6 (0.3)
A3 – <i>Diantho-Armerietum</i>	92 (11)	83 (15)	43 (20)	0.0 (0.0)	7.7 (7.4)	23.2 (16.2)	0.4 (0.0)	4.6 (0.2)	3.2 (0.1)
A4 – <i>Sileno-Festucetum</i>	91 (11)	77 (14)	50 (24)	0.8 (0.0)	6.8 (4.0)	30.0 (17.3)	0.5 (1.3)	5.8 (1.0)	2.9 (0.5)
A5 – <i>Helichryso-Jasionetum</i>	75 (19)	54 (10)	50 (25)	0.0 (0.0)	3.4 (3.5)	34.3 (14.8)	0.0 (0.0)	6.0 (0.8)	2.8 (0.5)
A6 – <i>Festucetum polesicae</i>	79 (13)	56 (10)	51 (27)	0.0 (0.0)	1.4 (0.3)	50.4 (12.7)	0.0 (0.0)	5.3 (0.8)	2.8 (0.4)
B – Sedo-Scleranthenea									
B1 – <i>Cladonio-Sedetum</i>	80 (30)	55 (15)	55 (37)	9.3 (9.3)	14.7 (10.5)	5.5 (4.0)	0.0 (0.0)	7.2 (0.5)	2.6 (0.5)
B2 – <i>Crepido-Allietum</i>	68 (21)	57 (20)	32 (23)	3.9 (10.5)	17.3 (6.2)	7.1 (3.9)	5.2 (5.6)	7.4 (0.6)	4.5 (0.9)
B3 – <i>Fulgensio-Poetum</i>	43 (18)	18 (13)	35 (17)	28.4 (26.5)	20.8 (6.9)	2.4 (1.3)	1.6 (2.1)	7.4 (0.4)	3.3 (0.4)
B4 – <i>Helianthemo-Galietum</i>	68 (18)	52 (17)	38 (21)	4.6 (6.5)	13.6 (8.0)	5.7 (2.9)	0.5 (1.5)	7.4 (0.5)	3.6 (0.7)
B5 – <i>Gypsophilo-Globularietum</i>	78 (13)	60 (13)	52 (17)	8.1 (10.6)	22.7 (5.1)	5.1 (2.9)	0.3 (1.2)	7.2 (0.5)	3.5 (0.5)
C – Festuco-Brometea									
C1 – <i>Phleum bertolonii-Saxifraga granulata</i> comm.	96 (7)	83 (12)	52 (21)	0.5 (1.8)	12.0 (6.8)	18.9 (13.4)	5.6 (6.7)	5.9 (0.7)	3.1 (0.5)
C2 – <i>Veronico-Avenetum</i>	96 (5)	85 (12)	55 (19)	0.6 (1.9)	16.8 (6.3)	20.6 (13.3)	2.3 (5.4)	5.8 (0.8)	3.6 (1.1)
C3 – <i>Trifolium montanum-Medicago falcata</i> comm.	97 (11)	94 (11)	39 (15)	0.6 (1.9)	10.8 (3.4)	29.2 (19.6)	2.3 (5.4)	6.1 (1.0)	3.4 (1.0)
C4 – <i>Adonis vernalis-Ononis arvensis</i> comm.	89 (11)	89 (11)	15 (15)	3.2 (6.3)	11.6 (4.9)	19.5 (4.7)	0.5 (1.6)	6.0 (0.3)	3.5 (0.3)

sativa ssp. *falcata* and *Centaurea scabiosa*. *Knautia arvensis*, *Fragaria viridis*, and *Primula veris* are shared with the next community. Two subtypes are distinguished; the first is characterised by *Trifolium montanum*, the latter by *Carex caryophyllea* and *Potentilla cinerea*.

The *Adonis vernalis*-*Ononis arvensis* community forms a distinct group in the ordination diagram. *Adonis vernalis*, *Ononis arvensis*, and *Polygala comosa* may serve to characterise this community, at least locally.

Site conditions

The first ordination axis separating the *Sedo-Scleranthenea* from the *Festuco-Brometea* and *Koelerio-Coryneporenea* could be interpreted as mainly representing a gradient in soil depth (Fig. 2). The soil depth was negatively correlated with the soil pH and the cover of bare rocks. The second ordination axis was positively correlated with the Ellenberg F-value, and thus may indicate a gradient in soil moisture. Table 2 gives the mean values of the measured environmental and structural variables for all communities.

Dry grasslands on sandy soils

Among the *Koelerio-Coryneporenea*, the *Corniculario aculeatae-Coryneporetum canescentis* inhabits the most extreme sites in terms of water and nutrient availability. The sandy soils are very poor in organic matter. On steep slopes, the sites are fairly unstable. The *Carici arenariae-Airetum praecocis* is slightly more mesophilous. Sites are usually affected by mechanical disturbance, especially on tracks used by walkers and cyclists. The *Helichryso arenarii-Jasionetum litoralis* occurs on soils with considerably higher pH values with a mean of pH 6.0. The soil pH measured for the *Festucetum polesicae* is surprisingly low (mean: pH 5.3). The communities of the *Armerion elongatae* grow at the least extreme sites in terms of soil moisture; in addition, the organic matter content is comparatively high here (Table 2). Soils of the *Diantho deltoidis-Armerietum elongatae* are more acid than those of the *Sileno otitae-Festucetum brevipilae* (Table 2). Sites of both associations are often grazed by cows or unused, but in the latter case, some anthropogenic disturbance occurs, especially in recreation areas. The *Sileno otitae-Festucetum brevipilae* often occurs on southern or western slopes with a distinctly warmer microclimate. These sites are partly mown.

Weathered rock and outcrop communities

Within the *Sedo-Scleranthenea*, the floristic differentiation of communities can be at least partly explained by differences in soil moisture and soil depth (Table 2, Fig. 4). The soil pH is high in all alvar communities, but decreases slightly with increasing content of organic matter

(*Gypsophilo fastigiatae-Globularietum vulgaris*).

The *Crepido pumilae-Allietum alvarensis* grows at the wettest sites on loamy soils, which are poorly drained and affected by frost action, which sometimes leads to polygon structures and an often significant microtopography. The *Helianthemo oelandici-Galietum oelandici* grows in considerably drier places, which, however, still are regularly inundated in winter. The *Gypsophilo fastigiatae-Globularietum vulgaris* occurs on well-drained sites, especially in karst areas. Sites of this community are often situated close to *Juniperus communis* shrubs with a southern aspect, which leads to an especially warm microclimate. Ecologically, the sites of the *Fulgensio bracteatae-Poetum alpinae* are clearly distinguished from the other alvar communities by extremely shallow soils and a much higher coverage of bare rocks (mean: 28.4%; Table 2). This community is the first to colonise solid bedrock and gravel. In the initial stage, single moss cushions develop; during succession, fine soil rich in organic matter accumulates and the moss cushions increase in size. Later during succession, the community may be replaced by the *Helianthemo oelandici-Galietum oelandici*. However, due to wind- and water erosion as well as trampling animals, the community may persist over quite long periods.

Semi-dry basiphilous grasslands

The *Veronico spicatae-Avenetum* inhabits a broad range of both soil moisture and soil pH. The two subtypes indicate differences in soil moisture; within each subtype, it is possible to distinguish a variant occurring on more acidic and one on more base-rich soils. Sites are extensively grazed by cows, sheep, and/or horses. The floristic differences between the *Veronico spicatae-Avenetum* and the *Phleum bertolonii-Saxifraga granulata* community may be partly due to differences in the disturbance regime. Sites of the latter community are more intensively grazed, mainly by cows. Trampling animals together with rather poor drainage lead to an extreme microtopography with height differences up to 30 cm. Arising hummocks may also be caused in part by ant activities. Sites of the *Trifolium montanum-Medicago falcata* community are not or only rarely used, being either mown or grazed by cows. Sites often have a southern aspect at the margin of scrubs or forests, or they lie in larger forest gaps. The same is true for the *Adonis vernalis-Ononis arvensis* community, whose soils have a higher loam content. Sites are lightly grazed by cows, and many are visited by tourists.

Species richness

The studied dry grassland communities differed in species richness (Fig. 6), with species numbers ranging from 7 up to 80 per 4 m² plot. The mean species density was highest in *Sedo-Scleranthenea* communities, followed by

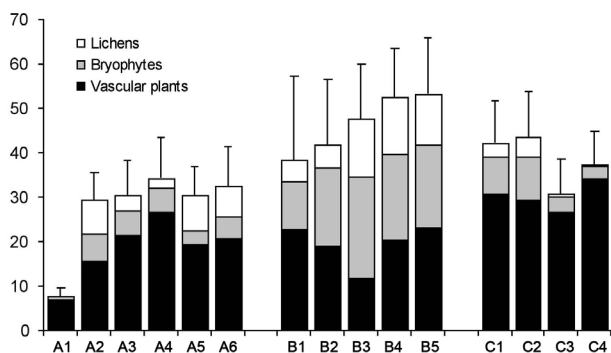


Fig. 6. Means of total and group-specific species richness on 4 m² for the dry grassland communities studied (see Table 2 for community codes). In addition, the standard deviation of the total plant species richness values is indicated. The three groups of columns correspond to the three major syntaxa, viz. from left to right *Koelerio-Corynephoronea*, *Sedo-Scleranthenea*, and *Festuco-Brometea*.

those in the *Festuco-Brometea*, and lowest in the *Koelerio-Corynephoronea*. Mean species density on 4 m² was at its maximum in the *Gypsophilo fastigiatae-Globularietum vulgaris* (53.4 species) and at its minimum in the *Corniculario aculeatae-Corynephorum canescentis* (8.0 species). The *Crepido pumilae-Allietum alvarensis* had the lowest number of species among the alvar *Sedo-Scleranthenea* communities, with a mean of 42.1 species. Among the *Koelerio-Corynephoronea*, the *Sileno otitae-Festucetum brevifoliae* showed the highest species-richness (34.5 species). With a mean of 43.9 species per 4 m², the *Veronico spicatae-Avenetum* was the most species-rich community of the Ölandic *Festuco-Brometea*.

The mean contribution of bryophytes and lichens to the total species richness at 4 m² varied between 8% and 75%. For all *Sedo-Scleranthenea* communities the number of bryophytes and lichens species exceeded on average that of vascular plants. The maximum richness values found on average for the three taxonomic groups on 4 m², were 49 vascular plants (*Veronico spicatae-Avenetum*), 40 bryophytes (*Fulgensio bracteatae-Poetum alpinae*), and 24 lichens (*Gypsophilo fastigiatae-Globularietum vulgaris*).

In the species-area analyses, we found maximum values of 4 species on 0.0001 m², 6 species on 0.0004 m², 11 species on 0.0009 m², 15 species on 0.0025 m², 25 species on 0.01 m², 33 species on 0.04 m², 43 species on 0.09 m², 54 species on 0.25 m², 63 species on 1 m², 77 species on 4 m², and 81 species on 9 m². The richest plots of the smaller sizes mostly belonged to the *Crepido pumilae-Allietum alvarensis*, those with the larger sizes mostly to the *Gypsophilo fastigiatae-Globularietum vulgaris*.

Discussion

Phytosociological classification

Even though some characteristic species of superior syntaxonomical ranks, e.g. classes and subclasses, are missing or lose their indicator value on Öland, our data showed that the three (sub-)classes are still floristically well-separated (see App. 1). Similarly, Krahulec et al. (1986) and Bengtsson et al. (1988) found a clear distinction between *Sedo-Scleranthenea* and *Festuco-Brometea* communities in their numerical analyses (they did not include *Koelerio-Corynephoronea* communities). As the *Sedo-Scleranthenea* and the *Koelerio-Corynephoronea* have both considerable numbers of specific character species, e.g. *Cerastium semidecandrum* and *Cladonia furcata* for the *Koelerio-Corynephoronea*; *Sedum album* and *Peltigera rufescens* for the *Sedo-Scleranthenea*, and of joint character species, e.g. *Sedum acre*, *Ceratodon purpureus*, *Syntrichia ruralis* var. *ruraliformis*, the concept of one class with two subclasses reflects the situation on Öland well (see App. 1). This approach had been proposed by Dengler (2001, 2003, 2004a and in Dengler et al. 2003) based on the analysis of a comprehensive dataset from large parts of Europe. It reconciles the two alternative classifications of other authors, who either distinguish these units on class level (e.g. Schaminée et al. 1996; Rivas-Martínez 2002) or accept one class with three or more orders (e.g. Mucina & Kolbek 1993; Pott 1995), which does not reflect the fact that these orders fall into two floristically and ecologically distinct groups.

The communities of the Great Alvar proved to be floristically very distinct from the others. Most associations accepted in our classification are either (largely) restricted to alvar sites or to non-alvar sites (see Fig. 1). This may be explained by differences in site conditions and history (i.e. centuries or even millennia continuity of at least semi-open conditions on the Great Alvar).

Dry grasslands on sandy soils

Within the *Koelerio-Corynephoronea*, no distinctive Fennoscandian syntaxa seem to exist. On Öland, the suboceanic *Corynephoralia canescentis* reach the northeastern limit of their range (Dierßen 1996). We observed a few stands of *Corynephorus*-dominated pioneer grasslands, which could be assigned to the central association *Corniculario aculeatae-Corynephorum canescentis*. However, compared with records of this association from other regions these are remarkably poor in cryptogams, especially lichens. This may be because the association inhabits only slightly acidic soils on Öland, whereas lichen-rich stands of the association are usually best developed as a long-lasting successional stage on more acidic soils (Dengler 2004a). The oceanic order *Thero-Airetalia* also reaches Öland, but

only with one fragmentary association.

The communities of the *Trifolium arvensis*-*Festucetalia ovinae* show the most northerly distribution within the subclass (e.g. Dierßen 1996). They are represented with two associations of the subcontinental alliance *Armerion elongatae*. Both are common within the study area, and cover huge areas.

The *Sedo acris*-*Festucetalia* have their main distribution in the subcontinental and continental parts of temperate Europe (Dengler 2001) and reach their northwestern limit on the island (Dierßen 1996). On Öland, we found typical stands of the *Festucetum polesicae*. This vegetation type has been reported from several regions and typically occurs adjacent to the southern Baltic Sea (e.g. Böcher 1947; Andersson 1950; Olsson 1974; Dolnik 2003; Dengler 2004a; Boch & Dengler 2006). Stands on the southern Swedish mainland, however, showed distinctly higher soil pH values than those that we observed on Öland. Records from Gotland (Westhoff et al. 1983) are floristically impoverished and lack *Koeleria glauca*.

Weathered rock and outcrop communities

Our comparison of *Sedo-Scleranthenea* communities from the whole of northern Europe with those of central Europe (Dengler & Löbel 2006; Dengler et al. 2006a) showed a clear distinction between the Nordic and central European basiphilous rock and outcrop communities (*Alyso alyssoidis*-*Sedetalia*). Therefore, we proposed a Nordic alliance *Tortello tortuosae*-*Sedion albi*, to be placed within the *Alyso alyssoidis*-*Sedetalia* and opposed to the central European *Alyso alyssoidis*-*Sedion* Oberd. & T. Müller in T. Müller 1961, comprising all Nordic communities on shallow, base-rich, skeletal soils (for details, see Dengler & Löbel 2006; Dengler et al. 2006a).

Since we found a close relationship between the Ölandic relevés from outside the Great Alvar and those reported from the Swedish mainland (Hallberg 1971), we suggested to assign them to the same association, called *Cladonio symphycarpiae*-*Sedetum albi*. Due to the high number of shared species, we further suggested the discrimination between the alvar communities and the other Nordic communities as two suballiances, *Tortello rigentis*-*Helianthemion oelandici* and *Tortello tortuosae*-*Sedenion albi*, respectively (Dengler & Löbel 2006; Dengler et al. 2006a).

With our classification of the alvar communities of shallow, skeletal soils we could largely confirm the units provisionally proposed by Krahulec et al. (1986), and we thus validated their names (Dengler & Löbel 2006). An exception is the differentiation of the *Fulgensio bracteatae*-*Poetum alpinae* from the *Crepido pumilae*-*Allietum alvarensis*, which, however, could be attributed to the fact that such stands were only covered to a minor extent by Krahulec et al. (1986). Albertson's (1950) *Sedum album*-

Tortella tortuosa-community is mostly identical with the *Fulgensio bracteatae*-*Poetum alpinae*.

The *Crepido pumilae*-*Allietum alvarensis* probably occurs in all extreme alvar areas of hemiboreal Europe (Dengler et al. 2006a). For example, Pärtel et al. (1999) mention alvar stands from Estonia heavily affected by frost action in which *Artemisia rupestris* is quite common, which are placed in this association by Boch & Dengler (2006) and Dengler et al. (2006a). Albertson (1946) described a periodically inundated *Tortella*-*Schistidium*-subassociation of his '*Festucetum tortellosum*' from a small alvar area on the Swedish mainland (Kinnekulle, Västergötland) which also may be included. The *Fulgensio bracteatae*-*Poetum alpinae* may similarly occur in the other Nordic alvar areas (Dengler et al. 2006a). For example, Albertson's (1946) '*Sedetum tortellosum*' may be assigned to this association. Krahulec et al. (1986) considered the *Helianthemo oelandici*-*Galietum oelandici* as endemic to Öland. However, since we classified this community as a central association of the suballiance, we suggest that it also occurs in the other alvar regions, though lacking the name-giving species (Dengler et al. 2006a). The *Gypsophilo fastigiatae*-*Globularietum vulgaris* is probably endemic to Öland and Gotland (Dengler et al. 2006a). We found one relevé originating from Stora Karlsö (Westhoff et al. 1983), a small island near Gotland's coast, which may belong to this association. However, more data from Gotland are needed.

Semi-dry basiphilous grasslands

Semi-dry basiphilous grasslands (order *Brachypodieta lia pinnati*, class *Festuco-Brometea*) in northern Europe widely lack characteristic species of the south-western and south-eastern alliances *Bromion erecti* W. Koch 1926 and *Cirsio-Brachypodion pinnati* Hadač & Klika in Klika & Hadač 1944, respectively, but are differentiated by a high number of mesophilous species (e.g. Löbel 2002; Dengler 2003; Dengler et al. 2003, 2006a). Therefore, a northern central alliance *Filipendulo vulgaris*-*Helictotrichion pratensis*, as put forward by Dengler & Löbel (in Dengler et al. 2003), seems logical, resolving most classification problems of the Ölandic *Festuco-Brometea* communities (e.g. Braun-Blanquet 1963; Krahulec et al. 1986).

The *Veronico spicatae*-*Avenetum* has been provisionally described by Krahulec et al. (1986). We confirmed it as a very distinct community of the alvar vegetation. Our data also support the authors' differentiation between a xerophilous and hygrophilous subtype of this community. These largely correspond to Albertson's (1950) '*Festucetum alvarensis* *rhacomitriosum*' and his '*Avenetum alvarensis*', respectively. *Veronica spicata*, from which the community takes its name, however, cannot serve to define the association since it also frequently occurs in the other *Festuco-Brometea* communities as well as in the *Sileno*

otitae-Festucetum brevipilae and the *Festucetum polesicae*. There are hints that the *Veronico spicatae-Avenetum* also occurs in alvar areas on Gotland (N. Ingerpuu unpubl.). However, in these relevés the characteristic Ölandic species are missing, but differential species such as *Thymus serpyllum*, *Antennaria dioica* and *Danthonia decumbens* do regularly occur. Whether the *Phleum bertolonii-Saxifraga granulata* community represents a legitimate association remains unclear. It may alternatively be considered as a subtype of the *Veronico spicatae-Avenetum*. The *Trifolium montanum-Medicago falcata* community and the *Adonis vernalis-Ononis arvensis* community are floristically well differentiated. We do not describe these communities formally here, but there are some indications that the former is widely distributed and occurs on the Swedish mainland (Hallberg 1971; Albertson 1946), Gotland and Estonia (N. Ingerpuu unpubl. data). The *Fragario-Helictotrichetum* described by Hallberg (1971) from Bohuslän, is closely related to the *Potentilla cinerea*-subtype of our *Trifolium montanum-Medicago falcata* community. The *Trifolium montanum*-rich subtype shows some similarities to the 'Avenetum' described by Albertson (1946) from Västergötland, especially his *Inula salicina*-consociation. Species such as *Adonis vernalis*, *Trifolium montanum*, *Polygala comosa*, *Ononis arvensis*, and *Medicago falcata* show some affinities to the alliance *Cirsio-Brachypodium pinnati*, which is distributed in the subcontinental parts of central Europe. However, a comprehensive supraregional study would be needed to decide upon the position of the *Trifolium montanum-Medicago falcata* and the *Adonis vernalis-Ononis arvensis* community in the syntaxonomic system (see Dengler et al. 2006b). In addition, the position of the *Brachypodietalia pinnati* communities rich in *Avenula pratensis* and *Filipendula vulgaris* from Russia (Znamenskiy et al. 2006), Estonia (Pärtel et al. 1999; Boch & Dengler 2006), and Latvia (Rūsina 2007) needs to be clarified since they are floristically somewhat floristically intermediate between the *Veronico spicatae-Avenetum* and the *Trifolium montanum-Medicago falcata* community of Öland.

Species richness

With the species densities recorded, the studied plant communities are among the most species-rich vegetation types on small spatial scales (0.0001–10 m²) documented so far. The richness values of the Ölandic dry grassland communities are significantly higher than those of the corresponding communities in central Europe (Dengler 2005), although central European dry grasslands already belong to the most diverse communities of that region (Hobohm 1998). This difference is particularly pronounced in the communities of base-rich, shallow, skeletal soils (*Alyso alyssoidis-Sedetalia*). In this order, the Öland stands are approximately twice as rich as their central European

counterparts on 4 m² are (Dengler & Löbel 2006). Although this increase is most pronounced in bryophytes and lichens, even the densities of vascular plants are significantly higher on Öland (Dengler & Löbel 2006).

If total plant species richness is considered, few other plant communities worldwide reach or exceed the maximum values achieved in stands of the *Tortello rigentis-Helianthemion oelandici* on alvar sites in Öland (and similarly on Saaremaa, Estonia, cf. Dengler et al. 2006a). Comparable are lichen-rich, basiphilous grassland and heath communities of Greenland (class *Carici rupestris-Kobresietea bellardii* Ohba 1974) with documented densities of up to 70 on 0.16 m² and 85 on 4 m² (Lünterbusch & Daniëls 2004; Sieg et al. 2006). Also some types of semi-dry basiphilous grassland (*Brachypodietalia pinnati*) are very rich. Extreme vascular plant densities (non-vascular plants are not included in the available publications but play a minor role in these communities) within stands of this order are documented from a wooded meadow on the Estonian mainland (up to 25 on 0.01 m², 42 on 0.04 m², and 76 on 1 m²; Pärtel et al. 2005), from the *Brachypodio pinnati-Molinietum arundinaceae* Klika 1939 of Czechia (up to 67 on 1 m², 88 on 4 m²; Klimeš et al. 2001), and from meadow steppes in Russia (up to 80 on 1 m², Doniță et al. 2003). Finally, Cantero et al. (1999) found up to 89 vascular plants on 1 m² in mountain pastures of Argentina.

What can explain the higher small-scale species densities in Ölandic (or more generally speaking, hemiboreal) dry grasslands compared to their phytosociological counterparts in central Europe? According to the species-pool hypothesis, the small-scale species richness of a particular ecological community is determined by the size of the local species pool, which is positively correlated to the regional species pool for this community type, whose size in turn reflects historical past processes of speciation and migration (e.g. Zobel 1992; Zobel et al. 1998). Several studies have shown that small-scale species densities are positively correlated with local and regional species pools (e.g. Pärtel et al. 1996; Pärtel & Zobel 1999; Dupré et al. 2002). When, however, species richness patterns in dry grasslands of, say, southern Sweden and Germany are compared, the results do not fit in this pattern.

Although the regional species pool for dry grasslands is undoubtedly much higher for vascular plants in Germany than in southern Sweden (most dry grassland plants of Sweden occur also in Germany but not *vice versa*) and seems to be quite similar in both regions in the case of bryophytes and lichens (due to the usually large distribution ranges of most cryptogams), the small-scale species densities nevertheless behave conversely (Dengler 2005; Dengler & Löbel 2006). This does not mean that the species-pool hypothesis is wrong but only that the effect of the different species-pool sizes here is overruled by other factors. Dengler & Löbel (2006) suggested two potential

reasons. First, interspecific competition, which is generally assumed to reduce species richness (e.g. Grime 1979; Grace 1999), could be lower in northern Europe due to a lower productivity of the stands of the same vegetation type caused by shorter vegetation period, harsher climate, and less fertile soils. In an experiment, Huber (1994) showed that competitive exclusion is practically irrelevant in the *Veronico spicatae-Avenetum*, even when the stands are either sufficiently fertilized or irrigated. Second, a 'sampling effect' might contribute to the results in so far as average plant size in Nordic dry grasslands is usually smaller than in central European ones (both individuals of the same species grow lower and small-sized taxa such as cryptogams contribute more to the total richness in northern Europe). If the plants are smaller, more individuals fit on the same area, and these more individuals simply by chance may represent more different species.

Moving from continental to regional patterns of species densities, first the differences between the three major syntaxa catch the eye. The increasing species densities from *Koelerio-Coryneporenea* over *Festuco-Brometea* towards *Sedo-Scleranthenea* nicely correspond to an increase in soil pH (Table 2). When Löbel et al. (2006) applied multiple regression models to the relevés of the present study, soil pH turned out to be the single most important factor determining species densities. This relationship was linearly increasing for total richness, bryophytes, and lichens, and unimodal for vascular plants with a maximum at about pH = 6. This is consistent with analyses throughout southern Sweden (Tyler 1996), in northern Germany (Schuster & Diekmann 2003) and in Czechia (Chytrý et al. 2003), where either monotonously increasing or unimodal relationships with maxima mainly between pH = 5 and 7 were found for dry grasslands. It is widely accepted that the reason for the positive relationship between pH and small-scale species density, which is dominating in temperate and boreal regions worldwide (Pärtel 2002), lies in the predominance of calciphilous species in these regions, and this in turn can be attributed to speciation centres and glacial refugia with dominant base-rich bedrocks (Pärtel 2002; Ewald 2003).

Second, the diversity patterns within the three subclasses may be partly explained by the intermediate disturbance hypothesis (Connell 1975), according to which both too high disturbance and too low disturbance reduce species densities (e.g. Grace 1999). The fact that we found the lowest species densities of the *Koelerio-Coryneporenea* communities in the *Corniculario aculeatae-Coryneporetum canescentis*, and of the *Sedo-Scleranthenea* in the *Crepidopumilae-Allietum alvarensis*, fits well in this hypothesis, as these two associations inhabit the most disturbed sites of the respective subclass. The *Corniculario aculeatae-Coryneporetum canescentis* on southern Öland was found on active coastal cliffs and on sites heavily disturbed by cattle trampling, whereas the *Crepidopumilae-Allietum alvarensis* grows on those alvar sites that are most heavily

exposed to cryoturbation. Within the *Festuco-Brometea*, on the other hand, the two communities of the grazed alvar sites (*Veronico spicatae-Avenetum*, *Phleum bertolonii-Saxifraga granulata* community) have significantly higher species densities than those usually growing on either abandoned or mown sites (*Trifolium montanum-Medicago falcata* community, *Adonis vernalis-Ononis arvensis* community), which could be attributed to competitive exclusion due to too low levels of disturbance. Dupré & Diekmann (2001) found similar trends for different grassland types in southern Sweden.

The specifically high species densities in the communities of the Great Alvar and the adjacent smaller alvar areas seem to be at least partly attributable to a large local species pool, which comprises nearly all basiphilous dry grassland species of the regional species pool in southern Sweden. It is well-known that the Great Alvar has a long history of centuries if not millennia of at least semi-open habitats (e.g. Königsson 1968; Rosén 1982; Sterner & Lundquist 1986) and this site continuity together with the large size may have contributed to the accumulation of a huge local species pool through migration and in the case of the endemics even through speciation. This line of reasoning is supported by Pärtel & Zobel (1999) who showed for the Estonian west coast that species density of alvar communities is positively correlated with the elevation above sea level, with the latter being a surrogate for the time since the emerging from the sea. Additionally, Helm et al. (2006) demonstrated for alvar grasslands on the island of Saaremaa that extension and connectivity of grassland habitats in the past play a crucial role in determining the present-day species densities.

For the richest communities in the present study, those of the *Sedo-Scleranthenea*, also spatio-temporal niche-separation may have contributed to the extraordinary species densities (see Dengler & Löbel 2006). The sites of this subclass often have a distinct microtopography caused by cryoturbation and/or cattle trampling leading to a high small-scale heterogeneity. This combined with the high temporal variability of the environmental conditions at these sites with very shallow soils (water logging or even flooding in winter, severe drought in summer) probably enables the co-existence of a large number of taxa that normally would not grow at the same sites (e.g. *Agrostis stolonifera* with *Sedum album*). On the one hand, the multitude of spatio-temporal micro-niches on the alvar sites provides suitable habitats for species with very divergent ecological requirements; on the other hand, the high spatio-temporal heterogeneity prevents any one species from playing off its competitive superiority. This assumption is supported by Lundholm & Larson (2003), who in a Canadian alvar site found that small-scale species densities are highly positively correlated to the within-plot variability of soil depth and microtopography as well as the number of microsite types. Additionally, van der Maarel & Sykes

(1993) demonstrated for the *Veronico spicatae-Avenetum* that even without niche separation of the adult plants high numbers of different species can co-exist when they mostly are annuals or short-lived perennials and differ in their requirements for (re-)establishment (carousel model).

Acknowledgements

We dedicate this article to Eje Rosén who tirelessly keeps on researching and teaching about the Great Alvar on Öland. We thank him and Lennart Ågren for providing useful information during the fieldwork and Bill Meek for the linguistic revision of the text. Eddy van der Maarel gave important information when we started to plan this study. Additionally, he and one anonymous referee with their constructive criticism to an earlier version, substantially contributed to the quality of this paper. Aveliina Helm, Nele Ingerpuu, and Steffen Boch provided unpublished data from Estonian and Gotlandic alvar vegetation. The fieldwork was supported by a grant of the ‘Universitäts-gesellschaft Lüneburg’.

References

- Albertson, N. 1946. Österplana hed – ett alvarområde på Kinnekulle. — Svenska Växtgeografiska Sällskapet, Uppsala, 267 pp. [In Swedish, with German summary.]
- Albertson, N. 1950. Der grosse südliche Alvar der Insel Öland – Eine pflanzensoziologische Übersicht. — Sven. Bot. Tidskr. 44: 270-331 + 4 plates.
- Ammar, M.Y. 1978. Vegetation and local environment on shore ridges at Vickleby, Öland, Sweden. An analysis. — Acta Phytogeogr. Suec. 64: 1-94.
- Andersson, O. 1950. The Scanian sand vegetation – a survey. — Bot. Not. 1950: 145-172.
- Bengtsson, K., Prentice, H. C., Rosén, E., Moberg, R. & Sjögren, E. 1988. The dry alvar grasslands of Öland: ecological amplitudes of plant species in relation to vegetation composition. In: Sjögren, E. (ed.) Plant cover on the limestone Alvar of Öland – Ecology – Sociology – Taxonomy. — Acta Phytogeogr. Suec. 76: 21-46.
- Berg, C., Dengler, J. & Abdank, A. (eds.) 2001. Die Pflanzengesellschaften Mecklenburg-Vorpommerns und ihre Gefährdung – Tabellenband. — Weissdorn, Jena, 341 pp.
- Berg, C., Dengler, J., Abdank, A. & Isermann, M. (eds.) 2004. Die Pflanzengesellschaften Mecklenburg-Vorpommerns und ihre Gefährdung – Textband — Weissdorn, Jena, 606 pp. [With English summary.]
- Bergmeier, E., Härdtle, W., Mierwald, U., Nowak, B. & Pepler, C. 1990. Vorschläge zur syntaxonomischen Arbeitsweise in der Pflanzensoziologie. — Kiel. Not. Pflanzenkd. Schleswig-Holstein Hamb. 20: 92-110.
- Boch, S. & Dengler, J. 2006. Floristische und ökologische Charakterisierung sowie Phytodiversität der Trockenrasen auf der Insel Saaremaa (Estland). In: Bültmann, H., Fartmann, T. & Hasse, T. (eds.) Trockenrasen auf unterschiedlichen Betrachtungsebenen – Berichte einer Tagung vom 26.–28. August in Münster. — Arb. Inst. Landschaftsökol. Münster 15: 55-71.
- Böcher, T.W. 1947. *Festuca polesica* Zapal., its chromosome number and occurrence in Denmark. — Bot. Not. 1947: 353-360.
- Braun-Blanquet, J. 1963. Das *Helianthemo-Globularion*, ein neuer Verband der baltischen Steppenvegetation. — Veröff. Geobot. Inst. Eidg. Tech. Hochsch. Stift. Rübél 37: 27-38.
- Cantero, J.J., Pärtel, M. & Zobel, M. 1999. Is species richness dependent on the neighbouring stands? An analysis of the community patterns of central Argentina. — Oikos 87: 346-354.
- Chytrý, M., Tichý, L. & Roleček, J. 2003. Local and regional patterns of species richness in central European vegetation types along the pH/calcium gradient. — Folia Geobot. 38: 429-442.
- Connell, J.H. 1975. Some mechanisms producing structure in natural communities: A model and evidence from field experiments. In: Cody, M. L. & Diamond, J. (eds.) Ecology and evolution of communities. — Harvard University Press, Cambridge, MA, pp. 460-490.
- Dengler, J. 2001. Erstellung und Interpretation synchorologischer Karten am Beispiel der Klasse *Koelerio-Corynephoretea*. — Ber. R.-Tüxen-Ges. 13: 223-228.
- Dengler, J. 2003. Entwicklung und Bewertung neuer Ansätze in der Pflanzensoziologie unter besonderer Berücksichtigung der Vegetationsklassifikation. — Arch. Naturwiss. Diss. 14: 1-297. — Galunder, Nümbrecht. [With English summary.]
- Dengler, J. 2004a. Klasse: *Koelerio-Corynephoretea* Klika in Klika & V. Novák 1941 – Sandtrockenrasen und Felsgrusfluren von der submeridionalen bis zur borealen Zone. In: Berg, C., Dengler, J., Abdank, A. & Isermann, M. (eds.) Die Pflanzengesellschaften Mecklenburg-Vorpommerns und ihre Gefährdung – Textband, pp. 301-326. — Weissdorn, Jena.
- Dengler, J. 2004b. Klasse: *Festuco-Brometea* Br.-Bl. & Tx. ex Klika & Hadač 1944 – Basiphile Magerrasen und Steppen im Bereich der submeridionalen und temperaten Zone. In: Berg, C., Dengler, J., Abdank, A. & Isermann, M. (eds.) Die Pflanzengesellschaften Mecklenburg-Vorpommerns und ihre Gefährdung – Textband, pp. 327-335. — Weissdorn, Jena.
- Dengler, J. 2005. Zwischen Estland und Portugal – Gemeinsamkeiten und Unterschiede der Phytodiversitätsmuster europäischer Trockenrasen. — Tuexenia 25: 387-405.
- Dengler, J. & Boch, S. 2007. Taxonomy, ecology, and distribution of six remarkable plant taxa (*Spermatophyta*, *Bryophyta*, and *Lichenes*) of the Estonian dry grassland flora. — Phytion (Horn) 47: 47-71.
- Dengler, J. & Löbel, S. 2006. The basiphilous dry grasslands of shallow, skeletal soils (*Alyso-Sedetalia*) on the island of Öland (Sweden), in the context of North and Central Europe. — Phytocoenologia 36: 343-391.
- Dengler, J., Berg, C., Eisenberg, M., Isermann, M., Jansen, F., Koska, I., Löbel, S., Manthey, M., Pätzolt, J., Spangenberg, A., Timmermann, T. & Wollert, H. 2003. New descriptions and typifications of syntaxa within the project ‘Plant communities of Mecklenburg-Vorpommern and their vulnerability’ – Part I. — Feddes Repert. 114: 587-631.
- Dengler, J., Berg, C. & Jansen, F. 2005. New ideas for modern

- phytosociological monographs. — *Ann. Bot. (Roma)* N. S. 5: 193-210.
- Dengler, J., Löbel, S. & Boch, S. 2006a. Dry grassland communities of shallow, skeletal soils (*Sedo-Scleranthenea*) in northern Europe. — *Tuexenia* 26: 159-190 + 6 tables.
- Dengler, J., Rüsina, S., Boch, S., Bruun, H.H., Diekmann, M., Dierßen, K., Dolnik, C., Dupré, C., Golub, V.B., Grytnes, J.A., Helm, A., Ingerpuu, N., Löbel, S., Pärtel, M., Rašomavičius, V., Tyler, G., Znamenskiy, S.R. & Zobel, M. 2006b. Working group on dry grasslands in the Nordic and Baltic region – Outline of the project and first results for the class *Festuco-Brometea*. — *Ann. Bot. (Roma)* N.S. 6: 1-28.
- Dengler, J., Chytrý, M. & Ewald, J. In press. Phytosociology. In: Jørgensen, S. E. (ed.) *Encyclopedia of Ecology*. — Elsevier, Oxford.
- Diekmann, M. 1995. Delimitation of syntaxa in northern Europe – A case study. — *Ann. Bot. (Roma)* 53: 65-79.
- Diekmann, M. 1997. The differentiation of alliances in South Sweden. — *Folia Geobot. Phytotaxon.* 32: 193-205.
- Dierßen, K. 1990. Einführung in die Pflanzensoziologie (Vegetationskunde). — Wissenschaftliche Buchgesellschaft, Darmstadt, 241 pp.
- Dierßen, K. 1996. *Vegetation Nordeuropas*. — Ulmer, Stuttgart, 838 pp.
- Dolnik, C. 2003. Artenzahl-Areal-Beziehungen von Wald- und Offenlandgesellschaften – Ein Beitrag zur Erfassung der botanischen Artenvielfalt unter besonderer Berücksichtigung der Flechten und Moose am Beispiel des Nationalparks Kurischen Nehrung (Russland). — *Mitt. Arbeitsgem. Geobot. Schleswig-Holstein* Hamb. 62: 1-183. [with English summary.]
- Doniță, N., Karamyševa, Z.V., Borhidi, A. & Bohn, U. 2003. Waldsteppen (Wiesensteppen im Wechsel mit sommergrünen Laubwäldern und Trockenrasen im Wechsel mit Trockengebüschen). In: Bohn, U., Gollub, G., Hettwer, C., Neuhäuslová, Z., Schlüter, H. & Weber, H. (eds.) *Karte der natürlichen Vegetation Europas – Maßstab 1 : 2 500 000 – Erläuterungstext*: pp. 426-444. — Bundesamt für Naturschutz, Bonn.
- Dupré, C. & Diekmann, M. 2001. Differences in species richness and life-history traits between grazed and abandoned grasslands in southern Sweden. — *Ecography* 24: 275-286.
- Dupré, C., Wessberg, C. & Diekmann, M. 2002. Species richness in deciduous forests: Effects of species pools and environmental variables. — *J. Veg. Sci.* 13: 505-516.
- Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W. & Paulißen, D. 1991. *Zeigerwerte von Pflanzen in Mitteleuropa*. — *Scripta Geobot.* 18: 1-248.
- Ewald, J. 2003. The calcareous riddle: Why are there so many calciphilous species in the Central European flora? — *Folia Geobot.* 38: 357-366.
- Grace, J.B. 1999. The factors controlling species density in herbaceous plant communities: an assessment. — *Perspectives Plant Ecol. Evol. Syst.* 2: 1-28.
- Grime, J.P. 1979. *Plant strategies and vegetation processes*. — Wiley, Chichester, 222 pp.
- Grolle, R. & Long, D.G. 2000. An annotated check-list of the *Hepaticae* and *Anthocerotatae* of Europe and Macaronesia. — *J. Bryol.* 22: 103-140.
- Hallberg, H.P. 1971. *Vegetation auf den Schalenablagerungen in Bohuslän, Schweden*. — *Acta Phytogeogr. Suec.* 56: 1-136 + supplement.
- Helm, A., Hanski, I. & Pärtel, M. 2006. Slow response of plant species richness to habitat loss and fragmentation. — *Ecol. Lett.* 9: 72-77.
- Hill, M.O. & Gauch, H.G. 1980. Detrended correspondence analysis: An improved ordination technique. — *Vegetatio* 42: 47-58.
- Hill, M.O., Bell, N., Bruggeman-Nannenga, M.A., Brugués, M., Cano, M.J., Enroth, J., Flatberg, K.K., Frahm, J.-P., Gallego, M.T., Garilleti, R., Guerra, J., Hedenäs, L., Hoyoak, D.T., Hyvönen, J., Ignatov, M.S., Lara, F., Mazimpaka, V., Muñoz, J. & Söderström, L. 2006. An annotated checklist of the mosses of Europe and Macaronesia. — *J. Bryol.* 28: 198-267.
- Hobohm, C. 1998. *Pflanzensoziologie und die Erforschung der Artenvielfalt – Überarbeitete und erweiterte Fassung der an der Universität Lüneburg eingereichten und angenommenen Habilitationsschrift*. *Arch. Naturwiss. Diss.* 5: 1-231. — Galunder, Wiehl.
- Huber, R. 1994. Changes in plant species richness in a calcareous grassland following changes in environmental conditions. — *Folia Geobot. Phytotax.* 29: 469-482.
- Jonsell, B. & Karlsson, T. 2004. Endemic vascular plants in Norden. In: Jonsell, B. (ed.) *Flora Nordica – General Volume*, pp. 139-159. — Royal Swedish Academy of Sciences, Stockholm.
- Klimeš, L., Danák, M., Hájek, M., Jongepierová, I. & Kučera, T. 2001. Scale-dependent biases in species counts in a grassland. — *J. Veg. Sci.* 12: 699-704.
- Königsson, L.-K. 1968. The Holocene history of the Great Alvar of Öland. — *Acta Phytogeogr. Suec.* 55: 1-172 + supplement.
- Krahulec, F., Rosén, E. & van der Maarel, E. 1986. Preliminary classification and ecology of dry grassland communities on Ölands Stora Alvar (Sweden). — *Nord. J. Bot.* 6: 797-809.
- Lawesson, J.E., Diekmann, M., Eilertsen, O., Fosaa, A.M. & Heikkilä, H. 1997. The Nordic Vegetation Survey – concepts and perspectives. — *J. Veg. Sci.* 8: 455-458.
- Löbel, S. 2002. *Trockenrasen auf Öland: Syntaxonomie – Ökologie – Biodiversität*. — Diploma thesis, Inst. für Ökologie und Umweltchemie, Univ. Lüneburg, 178 + XIV pp. + 4 tables. [Available at the university library of Lüneburg.]
- Löbel, S., Dengler, J. & Hobohm, C. 2006. Species richness of vascular plants, bryophytes and lichens in dry grasslands: The effects of environment, landscape structure and competition. — *Folia Geobot.* 41: 377-393.
- Lundholm, J.T. & Larson, D.W. 2003. Relationships between spatial environmental heterogeneity and plant species diversity on a limestone pavement. — *Ecography* 26: 715-722.
- Lünterbusch, C.H. & Daniëls, F.J.A. 2004. Phytosociological aspects of *Dryas integrifolia* vegetation on moist-wet soil in Northwest Greenland. — *Phytocoenologia* 34: 241-270.
- Mucina, L. & Kolbek, J. 1993. *Koelerio-Corynephoretea*. In: Mucina, L., Grabherr, G. & Ellmauer, T. (eds.) *Die Pflanzengesellschaften Österreichs Teil I: Anthropogene Vegetation*, pp. 493-521. — Fischer, Jena.
- Olsson, H. 1974. *Studies on South Swedish sand vegetation*. — *Acta Phytogeogr. Suec.* 60: 1-170.
- Påhlsson, L. (ed.) 1999. *Markanvändningsformer och vegetationstyper i nordiska odlingslandskap*. — *TemaNord* 555:

- 1-301. — Nordisk Ministerråd, København. [In Swedish, with English summary.]
- Pärtel, M. 2002. Local plant diversity patterns and evolutionary history at the regional scale. — *Ecology* 83: 2361-2366.
- Pärtel, M. & Zobel, M. 1999. Small-scale species richness in calcareous grasslands determined by the species pool, community age and shoot density. — *Ecography* 22: 153-159.
- Pärtel, M., Zobel, M., Zobel, K. & van der Maarel, E. 1996. The species pool and its relation to species richness: evidence from Estonian plant communities. — *Oikos* 75: 111-117.
- Pärtel, M., Kalamees, R., Zobel, M. & Rosén, E. 1999. Alvar grasslands in Estonia: variation in species composition and community structure. — *J. Veg. Sci.* 10: 561-570.
- Pärtel, M., Bruun, H.H. & Sammul, M. 2005. Biodiversity in temperate European grasslands: origin and conservation. In: Lillak, R., Viiralt, R., Linke, A. & Geherman, V. (eds.) Integrating efficient grassland farming and biodiversity – Proceedings of the 13th International Occasional Symposium of the European Grassland Federation, Tartu, Estonia, 29–31 August 2005, pp. 1-14. — Estonian Grassland Society, Tartu.
- Pott, R. 1995. Die Pflanzengesellschaften Deutschlands. 2nd. ed. — Ulmer, Stuttgart, 622 pp.
- Rivas-Martínez, S. 2002. High syntaxa of Spain and Portugal and their characteristic species. In: Rivas-Martínez, S., Díaz, T.E., Fernández-González, F., Izco, J., Loidi, J., Lousã, M. & Penas, A. (eds.) Vascular plant communities of Spain and Portugal. Addenda to the syntaxonomical checklist of 2001. — *Itinera Geobot.* 15: 434-696.
- Rosén, E. 1982. Vegetation development and sheep grazing in limestone grasslands of south Öland, Sweden. — *Acta Phytogeogr. Suec.* 72: 1-108.
- Rosén, E. & Borgegård, S.-O. 1999. The open cultural landscape. In: Rydin, H., Snoeijs, P. & Diekmann, M. (eds.) Swedish plant geography – Dedicated to Eddy van der Maarel on his 65th birthday. — *Acta Phytogeogr. Suec.* 84: 113-134.
- Rūsina, S. 2007. Diversity and contact communities of mesophytic and xerophytic grasslands in Latvia. — *Latv. Veg. (Rīga)* 12: 1-366. [In Latvian, with English summary.]
- Santesson, R., Moberg, R., Nordin, A., Tønsberg, T. & Vitikainen, O. 2004. Lichen-forming and lichenicolous fungi of Fennoscandia. — Museum of Evolution, Uppsala, 359 pp.
- Schaminée, J.H.J., Stortelder, A.H.F. & Weeda, E.J. (eds.) 1996. De Vegetatie van Nederland – Deel 3. Plantengemeenschappen van graslanden, zomen en droge heiden — *Opulus*, Uppsala, 360 pp. [In Dutch.]
- Schuster, B. & Diekmann, M. 2003. Changes in species density along the soil pH gradient – evidence from German plant communities. — *Folia Geobot.* 38: 367-379.
- Sieg, B., Drees, B. & Daniëls, F.J.A. 2006. Vegetation and altitudinal zonation in continental West Greenland. — *Medd. Grønland Biosci.* 57: 1-93.
- Sterner, R. & Lundqvist, Å. 1986. Ölands kärlväxtflora, 2nd. ed. — Förlagstjänsten, Stockholm, 400 pp. [In Swedish, with English summary.]
- ter Braak, C.J.F. & Šmilauer, P. 2002. CANOCO Reference manual and CanoDraw for Windows User's guide: Software for Canonical Community Ordination (version 4.5). — Microcomputer Power, Ithaca, NY, 500 pp.
- Tutin, T.G., Heywood, V.H., Burges, N.A., Moore, D.M., Valentine, D.H., Walters, S.M. & Webb, D.A. (eds.) 1968. Flora Europaea – Vol. 2: *Rosaceae* to *Umbelliferae*. — Cambridge University Press, Cambridge, XXVII + 455 pp. + 5 maps.
- Tutin, T.G., Heywood, V.H., Burges, N.A., Valentine, D.H., Walters, S.M. & Webb, D.A. (eds.) 1972. Flora Europaea – Vol. 3: *Diapensiaceae* to *Myoporaceae*. — Cambridge University Press, Cambridge, XXIX + 370 pp. + 5 maps.
- Tutin, T.G., Heywood, V.H., Burges, N.A., Valentine, D.H., Walters, S.M. & Webb, D.A. (eds.) 1976. Flora Europaea – Vol. 4: *Plantaginaceae* to *Compositae* (and *Rubiaceae*). — Cambridge University Press, Cambridge, XXIX + 505 pp. + 5 maps.
- Tutin, T.G., Heywood, V.H., Burges, N.A., Valentine, D.H., Walters, S.M. & Webb, D.A. (eds.) 1980. Flora Europaea – Vol. 5: *Alismataceae* to *Orchidaceae* (*Monocotyledones*). — Cambridge University Press, Cambridge, XXXVI + 452 pp. + 5 maps.
- Tutin, T.G., Burges, N.A., Chater, A.O., Edmondson, J.R., Heywood, V.H., Moore, D.M., Valentine, D.H., Walters, S.M. & Webb, D.A. (eds.) 1993. Flora Europaea – Vol. 1: *Psilotaceae* to *Platanaceae*. 2nd. ed. — Cambridge University Press, Cambridge, 2nd ed., XLVI + 581 pp.
- Tyler, G. 1996. Soil chemistry and plant distributions in rock habitats of southern Sweden. — *Nord. J. Bot.* 16: 609-635.
- van der Maarel, E. 2005. Vegetation ecology – an overview. In: Maarel, E. van der (ed.) *Vegetation ecology*, pp. 1–51. — Blackwell Publishing, Oxford.
- van der Maarel, E. & Sykes, M.T. 1993. Small-scale plant species turnover in a limestone grassland: the carousel model and some comments on the niche concept. — *J. Veg. Sci.* 4: 179-188.
- Weber, H. E., Moravec, J. & Theurillat, J.-P. 2000. International Code of Phytosociological Nomenclature. 3rd. ed. — *J. Veg. Sci.* 11: 739-768.
- Westhoff, V., Schaminée, J. & Sýkora, K.V. 1983. Aufzeichnungen zur Vegetation der schwedischen Inseln Öland, Gotland und Stora Karlsö. — *Tuexenia* 3: 179-198.
- Williamson, M. 2003. Species-area relationships at small scales in continuum vegetation. — *J. Ecol.* 91: 904-907.
- Wilmanns, O. 1998. Ökologische Pflanzensoziologie, 6th ed. — Quelle & Meyer, Wiesbaden, 405 pp.
- Znamenskiy, S., Helm, A. & Pärtel, M. 2006. Threatened alvar grasslands in NW Russia and their relationship to alvars in Estonia. — *Biodiv. Conserv.* 15: 1797-1809.
- Zobel, M. 1992. Plant species coexistence – the role of historical, evolutionary and ecological factors. — *Oikos* 65: 314-320.
- Zobel, M., van der Maarel, E. & Dupré, C. 1998. Species pool: the concept, its determination and significance for community restoration. — *Appl. Veg. Sci.* 1: 55-66.

App. 1. Synoptic table of the dry grassland communities on southern Öland. Taxa are labelled as vascular plants (V), bryophytes (B), lichens (L), and 'algae' (A). Percentage constancy values are given per taxon and per associations. Columns based on less than 10 relevés (and therefore less reliable) are printed in italics. The columns to the left refer to all relevés and to the three major syntaxa. In the first case, constancy was calculated based on individual relevés, whereas for in the columns A to C mean constancy values of the included associations are given. The diagnostic value of the taxa is indicated by shading and frames and refers to the situation in southern Öland.

Legend																										
 	= character taxon																									
 	= transgressive character taxon on the superior hierarchical level																									
		 = differential taxon																								
		 = negatively differentiating taxon within a 'species block'																								
Class		Koelerio-Coryneporetea															C - Festuco-Brometea									
Subclass		A - Koelerio-Coryneporenea										B - Sedo-Scleranthenea					C.a									
Order, alliance, or suballiance												B.a1					B.a2									
Association (or equivalent unit)												B1		B2			B3		B4		B5					
	Group	All relevés (mean rel.)	Subcl. A (mean ass.)	Subcl. B (mean ass.)	Class C (mean ass.)	A1	A2	A3	A4	A5	A6	B1	B2	B3	B4	B5	C1	C2	C3	C4						
Number of relevés or associations		469	6 ass.	5 ass.	4 ass.	3	4	60	66	7	12	3	74	25	41	39	39	61	25	10						
Mean number of plant taxa (total)		41	27	47	39	8	29	30	34	30	33	39	43	48	53	54	42	44	31	37						
Mean number of vascular plants		24	19	19	31	7,3	16	22	27	20	21	23	19	12	20	23	31	30	27	34						
Mean number of bryophytes		11	4,3	18	6,0	0,7	6,3	5,5	5,5	2,9	5,1	11	18	23	19	19	8,1	9,7	3,4	2,8						
Mean number of lichens		5,5	4,5	9,4	2,1	0,0	7,3	2,8	2,0	7,9	6,9	5,0	5,1	13	13	11	3,2	4,4	0,6	0,2						
Class Koelerio-Coryneporetea																										
Order C - Sedum acre																										
V	46	50	54	22	67	100	52	82	57	83	100	35	40	41	56	64	16	8	.	.						
V	27	70	27	11	67	100	55	18	86	92	67	14	16	24	13	33	3	8	.	.						
B	31	50	44	9	100	75	5	.	86	58	3						
L	21	42	44	4	75	12	3	86	75	67	4	8	66	74	5	10	5	10	.	.						
V	31	50	29	10	75	45	50	86	42	.	11	20	44	69	15	5	20	.	.	.						
L	19	26	38	5	50	23	7	33	33	34	14	20	66	59	5	13						
V	4	12	18	1	2	3	57	8	67	1	8	15	.	.	5						
V	28	39	36	11	25	5	23	100	83	.	.	9	16	66	90	10	30	4	.	.						
Subclass A - Koelerio-Coryneporenea																										
Order C - Cerastium semidecandrum																										
V	22	65	10	11	33	75	33	47	100	100	33	3	15	.	.	31	8	4	.	.						
L	30	62	14	24	100	47	44	86	92	33	5	4	20	10	44	41	12	.	.	.						
V	5	54	.	.	100	75	5	.	86	58						
V	9	51	.	1	67	75	22	14	43	83	3						
V	22	47	6	8	33	75	62	35	29	50	23	.	5	.	21	7	4	.	.							
B	25	47	8	8	75	80	67	.	58	.	33	4	5	.	.	15	5	12	.	.						
V	8	38	.	2	33	25	20	12	71	67	8						
V	8	30	1	4	50	12	14	29	75	.	.	.	5	.	.	8	8	.	.	.						
V	10	24	.	6	50	30	27	29	8	3	12	10	.						
L	8	20	4	5	50	18	.	29	25	.	.	4	10	5	.	3	16	.	.	.						
V	6	20	0	3	33	50	25	5	8	.	.	.	2	.	.	10	2	.	.	.						
V	10	44	0	1	67	75	38	17	14	50	.	1	.	.	.	5						
V	8	42	.	1	33	75	23	6	29	83	3	2	.	.	.						
L	16	30	6	15	25	17	12	43	83	.	3	.	10	18	.	18	36	4	.	.						
Order A.b - Thero-Airetalia																										
Order C - Aira praecox																										
V	4	21	.	5	100	18	5	8	8	4	.	.					
B	8	19	0	5	75	37	3	2	.	.	.	8	8	4	.	.					
Order A.c - Trifolium arvensis-Festucetalia ovinae																										
Order C - Trifolium campestre																										
V	19	18	8	16	.	.	43	42	14	8	33	9	.	.	.	31	11	20	.	.						
V	18	25	2	16	25	52	26	29	17	.	4	4	.	.	.	36	13	16	.	.						
L	8	12	7	4	25	32	15	.	.	.	33	1	2	.	.	5	2	8	.	.						
Order D - Rhytidadelphus squarrosus																										
B	16	15	.	22	60	21	.	8	31	11	16	30	.	.					
V	26	21	17	25	33	38	29	25	.	.	7	4	32	41	.	8	34	56	.	.						
V	13	14	5	9	43	24	14	10	15	5	2	28	.	.	.						
V	15	14	12	19	25	23	33	.	.	.	33	1	.	10	15	21	3	40	10	.						
Alliance Armerion elongatae																										
Order C - Festuca trachyphylla																										
V	0	13	1	2	25	20	30	3	.	.	.	3	.	4	.	.						
D	16	19	24	17	25	35	38	14	.	100	5	.	10	3	.	31	2	4	30	.						
Association A3 - Diantho deltoideis-Armerietum elongatae																										
Order C - Armeria maritima ssp. elongata																										
V	10	24	.	4	50	52	12	29	3	.	12	.	.					
Order A.d - Sedo acris-Festucetalia																										
Order C - Carex ligerica																										
V	3	10	.	1	.	8	3	14	33	3					
V	1	7	14	25					
Alliance Koelerion glaucae																										
Order D - Cetraria ericetorum ssp. ericetorum																										
L	16	30	21	7	25	10	3	86	58	.	1	4	46	54	8	15	4	.	.	.						
L	9	18	16	1	.	.	2	71	33	.	.	.	29	49	2						
Association A5 - Helichryso arenarii-Jasionetum litoralis																										
Order D - Festuca rubra ssp. rubra																										
V	8	19	8	8	25	7	9	71	.	33	8	18	13	.	.	.						
L	7	10	10	3	.	.	.	57	.	1	4	17	28	.	.	3	10	.	.	.						
B	10	15	19	10	25	5	8	43	8	67	4	8	7	10	.	18	20	.	.	.						
Association A6 - Festucetum polesicae																										
Order C - Koeleria glauca																										
V	3	15	.	1	.	.	3	14	75	3						
V	1	10						
L	10	12	8	9	.	.	2	5	14	50	.	.	24	18	.	5	31	.	.	.						
L	14	17	6	15	25	12	8	14	42	.	4	.	15	13	.	21	36	4	.	.						
Subclass B - Sedo-Scleranthenea																										
Order C - Sedum album																										
V	35	5	86	3	.	2	12	17	.	100	70	96	83	82	.	5	8	.	.	.						
V	30	18	50	19	50	20	20	17	.	67	38	72	39	36	.	59	15	.	.	.						
L	16	3	32	8	.	.	15	.	.	33	27	40	34	26	.	31						
B	15	.	32	3	33	46	36	22	21	.	.	13	.	.	.						
B	13	1	26	6	.	3	3	.	.	33	19	32	27	21	3	20						
L	6	1	24	1	.	2	2	.	.	67	11	24	17	3	.	3						
Order B.a - Alysso alyssoides-Sedetalia																										
Order V - Acinos arvensis																										
V	34	5	55	19	.	20	.	8	.	33	58	48	63	74	.	46	21	8	.	.						
V	33	15	54	23	22	45	.	25	.	100	22	32	73	44	.	67	13	12	.	.						
B	21	.	49	2	34	88	61	62	3	.	3						
L	20	.	48	35	92	63	51						
V	21	4	48	12	.	.	.	25	.	67	35	56	49	31	.	41	7	.	.	.						
V	18	4	47	5	2	12	.	8	.	67	27	80	27	33	.	15	5	.	.	.						
V	15	2	40	2	.	.	11	.	.	33	8	56	54	49	.	8						
L	11	.	27	1	16	56	39	23	.	.	2						
Alliance Tortello tortuosae-Sedion albi																										
Order C - Ditrichum flexicaule																										
B	37	1	75	11	.	.	6	.	.	33	77	88	83	92	21	18	4	.	.	.						
L	14	1	35	1	.	.	3	.	.	33	18	24	4													

Class Subclass Order, alliance, or suballiance Association (or equivalent unit) Number of relevés or associations	Group	All relevés (mean rel.)	Subcl. A (mean ass.)	Subcl. B (mean ass.)	Subcl. C (mean ass.)	Koelerio-Corynephoretea												C - Festuco-Brometea			
						A - Koelerio-Corynephoretea						B - Sedo-Scleranthea						C.a			
						A.a	A.b	A.c	A.d	A5	A6	B.a1	B.a2	B.a3	B.a4	B.a5	B1	B2	B3	B4	B5
		469	6 ass.	5 ass.	4 ass.	3	4	60	66	7	12	3	74	25	41	39	39	61	25	10	
Suballiance B.a2 – Tortello riqentis-Helianthemion oelandici																					
C	<i>Cladonia subrangiformis</i>	V	25	8	47	10	25	3	5	14			14	48	85	87	21	20			
	<i>Encalypta vulgaris</i>	B	22	1	43	5			5				39	64	49	62	10	8			
	<i>Allium schoenoprasum</i> var. <i>alvarense</i>	V	19		36	3							69	68	24	21	3	7			
	<i>Helianthemum oelandicum</i> ssp. <i>oelandicum</i>	V	19	0	36	7			2				7	12	76	85	3	23			
	<i>Trichostomum crispulum</i>	B	18		36	3							39	44	54	41		11			
	<i>Distichium capillaceum</i>	B	18	0	41	3						33	38	52	51	31	5	8			
	<i>Tortella rigens</i>	B	16		32	1							46	48	34	31		5			
	<i>Didymodon ferrugineus</i>	B	14		33	4						33	35	56	27	13	3	11			
	<i>Didymodon rigidulus</i>	B	11		25	1							26	68	20	13		5			
	<i>Athalamia hyalina</i>	B	10		25	3						33	26	16	29	21	3	7			
	<i>Festuca oelandica</i>	V	9		22							33	39	24	10	3					
	<i>Gymnostomum aeruginosum</i>	B	7		13	2							23	20	10	13		7			
	<i>Leptogium schraderei</i>	L	6		13	1							11	24	20	8		3			
	<i>Silene uniflora</i> ssp. <i>petraea</i>	V	1		4								8	5	5						
	<i>Hieracium x dichotomum</i>	V	1	0	2		2						5	2	3						
D	<i>Didymodon fallax</i>	B	24	1	54	5	2	2				33	51	76	63	46	8	11			
	<i>Weissia brachycarpa</i>	B	23	1	42	6		3					47	52	49	64	8	15			
	<i>Agrostis stolonifera</i>	V	26		42	6							97	44	56	13	13	10			
	<i>Pseudocalliergon turgescens</i>	B	21		42	6						33	62	56	41	18	8	15			
	<i>Pleurodium acuminatum</i>	B	16		32	3							35	60	41	26		10			
	<i>Campyladiellus chrysophyllus</i>	B	22	0	31	11		2					55	20	46	33	8	30	4		
	<i>Grimmia pulvinata</i>	B	10	1	23	1	8						4	28	27	54			4		
	<i>Myurella julacea</i>	B	12		22	4							34	32	22	21	5	10			
	<i>Collema tenax</i>	L	8		17	1							19	32	24	10		5			
	<i>Ctenidium molluscum</i>	B	11		17	5							27	24	24	10	3	15			
	<i>Pseudocrossidium hornschiuanum</i>	B	7	0	17	1	2						12	36	27	10		2			
D Associations B2 and B3 (against B4 and B5)																					
	<i>Nostoc</i> sp.	A	13		32							33	49	56	15	5					
Association B2 – Crepido pumilae-Allietum alvarensis																					
C	<i>Crepis tectorum</i> ssp. <i>pumila</i>	V	14		23	1							62	28	27		3	2			
	<i>Artemisia rupestris</i>	V	4		5	1							18		2	5		3			
D	<i>Prunella vulgaris</i>	V	19		25	17						33	72	4	12	3	13	33	20		
	<i>Sagina nodosa</i>	V	13		17	5							58	20	5		8	10			
	<i>Leontodon autumnalis</i>	V	9	2	13				14				42	12	7	5					
	<i>Scorpidium cossonii</i>	B	7		9								36		7	3					
	<i>Calliergonella cuspidata</i>	B	8		6	6							30		2		8	16			
	<i>Eucladium verticillatum</i>	B	7		12	1							26	12	12	8		5			
Association B3 – Fulgensio bracteatae-Poetum alpinae																					
C	<i>Fulgensia bracteata</i>	L	13		32	1							22	84	34	21		2			
	<i>Toninia sedifolia</i>	L	9		25								15	76	24	8					
	<i>Syntrichia calcicola</i>	B	10	1	31	1	2	2				33	9	76	17	21		3			
	<i>Mycobilimia lurida</i>	L	10		25	1							19	68	27	10		5			
	<i>Schistidium atrofusum</i>	B	8		19	1							16	60	7	13	3	2			
	<i>Fulgensia fulgens</i>	L	4		11								7	40	7	3					
	<i>Tortella inclinata</i> var. <i>densa</i>	B	6		14	1							12	40	15	5		2			
	<i>Ceratodon conicus</i>	B	3		9	1							5	28	7	3		2			
	<i>Leptogium gelatinosum</i>	L	3		7	1							8	24	2			2			
	<i>Squamarina cartilaginea</i>	L	1		3									16							
	<i>Squamarina lentigera</i>	L	1		4								1	16	2						
D	<i>Poa alpina</i>	V	8	0	27	1	2					33	14	76	7	3	3	2			
	<i>Collema cristatum</i>	L	7		19	1							9	76		8		3			
	<i>Collema crispum</i>	L	8		20	1							14	56	20	8		2			
	<i>Bryum argenteum</i>	B	6	1	15	1	3	2					4	48	10	13		2			
	<i>Schistidium apocarpum</i>	B	6	1	14	1	3						15	40	7	8			4		
D Associations B2 and B3 (against B4 and B5)																					
	<i>Hieracium pilosella</i>	V	40	30	25	50	25	48	52	14	42		18	4	46	59	18	51	60	70	
	<i>Potentilla tabernaemontani</i>	V	39	21	27	44		25	56	43			8	12	51	62	49	72	44	10	
	<i>Thamnolia vermicularis</i> var. <i>subuliformis</i>	L	10		26									20	49	59					
	<i>Cephalozella divaricata</i>	B	16	10	25	6	25	7			25		19	4	49	51	15	7			
	<i>Taraxacum erythrospermum</i> aqq.	V	32	17	39	32		13	44	14	33	67	20	8	46	54	59	34	4	30	
	<i>Scapania calcicola</i>	B	9		18	1							9	8	34	41		3			
	<i>Hypogymnia physodes</i>	L	11	11	16	6		7	57				1	4	37	38		13	12		
	<i>Sedum rupestre</i>	V	17	6	20	22			2	14	17	33	8		29	28	31	56			
Association B4 – Helianthemo oelandici-Galietum oelandici																					
C	<i>Galium oelandicum</i>	V	7	1	11	2	2	2					9		39	5		7			
	<i>Sisymbrium supinum</i>	V	3		5								5	4	17						
Association B5 – Gypsophilo fastigiatæ-Globularietum vulgaris																					
C	<i>Globularia vulgaris</i>	V	7		15	1									2	72		3			
	<i>Gypsophila fastigiata</i>	V	6		15										8	7	62				
	<i>Cladonia convoluta</i>	L	3		7	1							3	4	7	23		2			
D	<i>Vincetoxicum hirsutinaria</i> ssp. <i>hirsutinaria</i>	V	7		15	1							1		12	64		2			
	<i>Rhytidium rugosum</i>	B	12		17	9							8	8	17	51	8	26			
	<i>Melica ciliata</i>	V	4		9	1									10	36		3			
	<i>Oxytropis campestris</i> ssp. <i>campestris</i>	V	10	6	13	9		21	14			33			2	31	5	21	8		
	<i>Arabis hirsuta</i> var. <i>glaberrima</i>	V	8	1	9	8	2	3					4	4	7	28	5	16	12		
	<i>Agrostis qiqantea</i> ssp. <i>qiqantea</i>	V	4		8	1							3	4	7	26	3				
Class Festuco-Brometea																					
C	<i>Homalothecium lutescens</i>	B	46	13	44	73		7	55		17	67	36	24	44	51	79	70	84	60	
	<i>Veronica spicata</i> ssp. <i>spicata</i>	V	35	19	10	50		22	42	14	33		26		10	13	74	79	48		
	<i>Helianthemum nummularium</i> ssp. <i>numm.</i>	V	19	8	3	45			41		8		1		2	10	10	41	80	50	
	<i>Asperula tinctoria</i>	V	20	2	13	34			6		8		1		17	49	28	64	4		

Class Subclass Order, alliance, or suballiance Association (or equivalent unit)	Group	All relevés (mean rel.)	Subcl. A (mean ass.)	Subcl. B (mean ass.)	Class C (mean ass.)	Koelerio-Corynephoretea											C - Festuco-Brometea				
						A - Koelerio-Corynephorenea						B - Sedo-Scleranthenea					C a				
						A.a	A.b	A.c		A.d		B.a1	B.a2				C1	C2	C3	C4	
						A1	A2	A3	A4	A5	A6	B1	B2	B3	B4	B5	C1	C2	C3	C4	
Number of relevés or associations		469	6 ass.	5 ass.	4 ass.	3	4	60	66	7	12	3	74	25	41	39	39	61	25	10	
<i>Lotus corniculatus</i>	V	21	8	14	49	15	9	25	33	30	5	3	26	44	36	90	
<i>Carex caryophylla</i>	V	13	5	1	28	8	21	8	34	48	20	
<i>Cirsium acaule</i> ssp. <i>acaule</i>	V	13	1	10	29	3	9	22	3	31	52	30	
D <i>Achillea millefolium</i> ssp. <i>millefolium</i>	V	43	31	13	70	80	64	43	33	23	7	64	57	80	80	
<i>Avenula pubescens</i> ssp. <i>pubescens</i>	V	15	6	7	33	25	11	33	1	3	18	36	56	20	
<i>Cerastium fontanum</i> ssp. <i>vulgare</i>	V	31	15	12	33	33	44	14	30	4	12	15	44	66	12	10	
<i>Poa pratensis</i>	V	18	13	8	32	38	39	33	7	2	31	8	20	70	
<i>Plagiominium affine</i>	B	17	8	1	31	20	27	3	33	43	28	20	
<i>Trifolium pratense</i>	V	7	3	1	28	2	14	3	20	28	60	
<i>Trifolium repens</i> ssp. <i>repens</i>	V	15	11	10	25	18	20	29	33	16	38	15	16	30	
Alliance – Filipendulo vulgaris-Helictotrichion pratensis																					
D <i>Galium boreale</i>	V	12	1	5	29	3	5	1	5	21	18	28	60	10	
<i>Sesleria caerulea</i>	V	10	2	25	1	5	3	5	54	32	10	
<i>Hylcomium splendens</i>	B	9	3	1	21	7	8	4	10	43	12	20	
D Association C1 and C2 (against C3 and C4)																					
<i>Dicranum scoparium</i>	B	33	13	18	41	25	35	11	8	16	34	38	64	90	8
<i>Stellaria graminea</i>	V	16	11	1	20	23	32	8	5	2	49	23	8	
Association C1 – Phleum bertolonii-Saxifraga granulata community																					
C <i>Saxifraga granulata</i>	V	13	7	3	26	25	7	11	14	2	79	11	4	10	
<i>Phleum pratense</i> ssp. <i>bertolonii</i>	V	11	3	13	15	2	5	8	33	23	4	5	46	13	
D <i>Veronica arvensis</i>	V	13	9	8	19	15	24	17	33	7	54	7	4	10	
<i>Myosotis ramosissima</i> ssp. <i>ramosissima</i>	V	7	1	2	13	3	5	8	46	5	
<i>Myosotis stricta</i>	V	7	2	8	13	2	8	33	8	44	8	
<i>Rhinanthus minor</i>	V	10	6	3	18	25	13	14	2	44	16	10	10	
<i>Climacium dendroides</i>	B	10	6	9	10	18	15	33	11	28	10	
Association C2 – Veronica spicatae-Avenetum																					
C <i>Prunella grandiflora</i> ssp. <i>grandiflora</i>	V	5	1	10	2	3	31	8	
<i>Orchis mascula</i> ssp. <i>mascula</i>	V	4	1	8	2	5	3	26	4	
<i>Orchis morio</i> ssp. <i>morio</i>	V	3	1	6	5	18	
<i>Artemisia oelandica</i>	V	1	3	10	
D <i>Carex flacca</i> ssp. <i>flacca</i>	V	12	9	20	11	17	15	49	12	20	
<i>Danthonia decumbens</i>	V	6	1	13	3	43	8	
<i>Antennaria dioica</i>	V	6	2	10	1	5	3	3	36	
D Association C3 and C4 (against C1 and C2)																					
<i>Knautia arvensis</i>	V	9	6	38	13	12	8	8	60	90	
<i>Primula veris</i> ssp. <i>veris</i>	V	4	0	25	2	8	32	60	
Association C3 – Trifolium montanum-Medicago falcata community																					
C <i>Pimpinella saxifraga</i>	V	7	7	1	15	15	11	17	3	3	7	48	10	
<i>Trifolium montanum</i>	V	3	0	11	2	7	28	10	
D <i>Carex ericetorum</i>	V	14	6	6	25	7	9	14	8	1	28	3	44	52	
<i>Centaurea scabiosa</i>	V	7	6	4	9	3	24	8	4	5	10	2	32	
Association C4 – Adonis vernalis-Ononis arvensis community																					
C <i>Adonis vernalis</i>	V	2	23	3	2	4	90	
<i>Polygala comosa</i>	V	5	2	4	15	11	18	3	2	4	50	
<i>Ononis arvensis</i>	V	1	10	40	
D <i>Dactylis glomerata</i> ssp. <i>glomerata</i>	V	9	5	2	30	8	23	2	8	3	3	12	100	
<i>Agrimonia eupatoria</i> ssp. <i>eupatoria</i>	V	2	23	2	90	
<i>Leucanthemum vulgare</i>	V	2	0	23	2	2	90	
<i>Veronica chamaedrys</i> ssp. <i>chamaedrys</i>	V	6	7	24	15	5	14	8	15	2	8	70	
<i>Clinopodium vulgare</i> ssp. <i>vulgare</i>	V	1	13	50	
<i>Festuca pratensis</i> ssp. <i>pratensis</i>	V	1	13	50	
D Festuco-Brometea and Koelerio-Corynephorenea (against Sedo-Scleranthenea)																					
<i>Anthoxanthum odoratum</i>	V	31	32	8	53	50	32	20	57	33	9	22	10	85	67	28	30
<i>Pulsatilla pratensis</i> ssp. <i>pratensis</i>	V	28	55	6	27	33	47	58	100	92	7	21	18	21	68
<i>Agrostis capillaris</i>	V	25	32	2	23	25	73	38	14	42	3	8	23	26	32	10
<i>Luzula campestris</i>	V	25	23	53	25	37	30	29	17	49	56	36	70
<i>Phleum phleoides</i>	V	24	28	3	31	22	67	29	50	4	5	5	33	20	60	10	
D Festuco-Brometea and Sedo-Scleranthenea (against Koelerio-Corynephorenea)																					
<i>Anthyllus vulneraria</i> ssp. <i>vulneraria</i>	V	39	16	40	49	25	7	27	29	8	33	34	4	41	87	69	66	32
<i>Abietinella abietina</i>	B	37	14	40	39	13	56	17	67	41	32	27	31	56	51	40
<i>Medicago lupulina</i>	V	36	8	59	48	8	38	100	30	40	63	62	69	25	
<i>Fissidens dubius</i>	B																				