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Changes in structure and function in response to changing diversity within Mediterranean grassland communities

Changements de structure et de fonction en réponse à des modifications de diversité dans des communautés de pelouses méditerranéennes

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Abstract

The effects of species richness, functional group richness and functional composition upon structural traits of vegetation (cover, canopy height, LAI and PAR) and ecosystem processes (above- and below-ground biomass production and short- and long-term decomposition) have been monitored in constructed Mediterranean mixed grasslands. The experiment is part of the european-wide BIODEPTH project.

The main findings are:

- 1. Ecosystem processes and structural traits of constructed grasslands showed different responses to the variation of the various community diversity components. For instance, biomass production varied in a non-significant way across manipulated diversity levels. On the contrary, short-term decomposition has showed a strong curvilinear response to species richness. Strong significance was also observed for plant cover and leaf area index.*
- 2. Since the various descriptors of productivity (plant cover, Leaf Area Index, and standing biomass) can respond differently to the variation of diversity, a direct measurement of productivity would offer a more robust evidence on the diversity- productivity relationship in these ecosystems.*
- 3. Species composition has significant effects on above- and below-ground biomass production, plant cover, canopy height and decomposition. Identity of species is of primary importance in determining the overall performance of ecosystem processes in grasslands.*

Key-words

Mediterranean grassland, diversity, productivity, decomposition, BIODEPTH

Résumé

Cet article présente les résultats d'une étude expérimentale concernant les effets de la richesse spécifique et fonctionnelle ainsi que de la composition fonctionnelle sur les traits structurels et les processus écosystémiques de pelouses méditerranéennes synthétiques. L'étude fait partie du projet multinational BIODEPTH.

- 1. Les processus écosystémiques et les traits structuraux de la végétation des pelouses manipulées répondent de manière différente à la variation des composantes de la diversité de ces communautés. La production de biomasse ne répond pas de façon significative à la variation de la diversité. Au contraire, la décomposition rapide, le pourcentage de recouvrement végétal et l'index de surface foliaire (LAI) montrent une réponse puissante et curvi-linéaire aux variations de la richesse spécifique.*
- 2. Les différents descripteurs de la productivité (pourcentage de recouvrement végétal, LAI et biomasse) répondent de façon différente aux variations de la diversité. Ainsi, des mesures directes de la productivité semblent plus appropriées afin d'acquérir des données robustes sur la relation diversité-productivité dans ces écosystèmes.*
- 3. La composition spécifique engendre des effets importants sur la variation de la production épigée et souterraine de biomasse, la hauteur de la végétation et la décomposition. L'identité des espèces semble ainsi avoir une importance significative dans la détermination de la performance globale des processus écosystémiques de ces pelouses.*

Mots-clés

Pelouses méditerranéennes, diversité, productivité, décomposition, BIODEPTH

INTRODUCTION

The understanding of patterns and mechanisms of association between the biotic characteristics of the community (such as species numbers, identity of species and assemblages and community structure), the ecosystem functions (such as production and decomposition), and abiotic factors (such as climate and soil) is fundamental to the preservation of biodiversity and the sustainable use of ecosystems. Ecosystem processes determine the levels of diversity, while they are in turn the consequences of diversity. For example, although local productivity can be strongly influenced by species richness, the limits of its variation are determined by abiotic factors such as nutrient availability or climatic parameters (e.g. Hector *et al.*, 1999). The loss of biodiversity, at local, regional and global scales, impairs the integrity of ecosystems and at least some aspects of ecosystem functioning. At the species level, the generic question on the association between diversity and ecosystem functioning is: '*Will depauperate, but nevertheless functionally intact (containing primary producers, consumers, and decomposers) ecosystems perform differently from the more species-rich systems from which they are derived?*' (BIODEPTH project 1999).

This question is particularly important for hot spot areas, where the severity of species extinction is expected to reach its maximum. Within the 2.3 million km² of the Mediterranean Basin occur at least 30,000 plant taxa; in other words, 1.6% of Earth's land surface contains *ca* 10% of all plant species (e.g. Médail & Quézel, 1999). Roughly half of these species are endemic to the area, and *ca* 4,800 are endemic to individual countries (Greuter, 1991). Approximately 14-15% of this flora is threatened with extinction (Greuter, 1994). Mediterranean-type ecosystems (MTE) are species-rich, nutrient-poor and seasonally-stressed ecosystems; there is a well documented need for research specifically designed to address the question of the role of diversity on ecosystem function in these systems (e.g. Keeley & Swift, 1995), which offer both good biological models and ideal sites for testing the diversity-function hypotheses at all scales (e.g. Richardson & Cowling, 1993).

Ecosystem processes, such as primary productivity, decomposition and nutrient cycling, are traditionally viewed in MTE literature as determinants of local diversity rather than as an ecosystem process potentially affected by species diversity (see reviews in Dávis & Richardson, 1995). These processes are well studied, mostly in mediterranean-type shrublands and grasslands, especially in relation to soil fertility, summer drought and perturba-

tion, mostly fire and grazing (see reviews in e.g. Di Castri & Mooney, 1973; Kruger *et al.*, 1983; Di Castri *et al.*, 1981). It has already been suggested that Mediterranean-type grasslands would be ideal experimental systems (R. Hobbs cited in Richardson & Cowling, 1993), because ecosystems with short-lived species provide fastest responses, especially under experimentally controlled conditions.

The response curve of ecosystem processes to diversity variation has been investigated in many current experiments which manipulate -directly or indirectly- species diversity and monitor the responses of the biogeochemical processes that drive ecosystem functioning. Laboratory (e.g. Naeem *et al.*, 1994) and field experimental studies (e.g. Tilman *et al.*, 1996; Tilman & Downing, 1994; Hooper & Vitousek, 1997; Tilman *et al.*, 1997; Hector *et al.*, 1999) provide evidence in favour of the hypothesis that biodiversity influences various ecosystem processes, e.g. primary productivity or nutrient retention. The conclusions drawn from them remain contentious as to their experimental design, analysis and interpretation (Givnish, 1994; Aarssen, 1997; Grime, 1997; Huston, 1997; Hodgson *et al.* 1998; Wardle, 1999; Loreau, 2000). Observational or correlational field studies have also addressed the same question (e.g., McNaughton, 1993; Wardle *et al.*, 1997b; Troumbis & Memtsas, 2000), without having however the potential to investigate the underlying mechanisms for the observed patterns.

The purpose of this paper is to provide evidence on the diversity-ecosystem function relationship from eastern Mediterranean grasslands, where experimental plots with controlled levels of plant diversity (species richness, functional groups and composition) have been established. Two major questions will be addressed, (i) does there exist a genuine effect of diversity on functional and structural features of these experimental grasslands? and (ii) if any, is it expressed by a consistent overall pattern?

MATERIALS AND METHODS

The research reported here has been carried out within the framework of the BIODEPTH (Biodiversity and Ecological Processes in Terrestrial Herbaceous Communities) experiment, which is an experimental investigation of the effects of the reduction of plant species diversity on ecosystem processes, such as biomass production, decomposition, nutrient cycling, water retention etc. BIODEPTH used manipulated grassland commu-

nities, situated along two crossing transects in eight sites across Europe (Sweden, United Kingdom, Ireland, Germany, Switzerland, Portugal and Greece) during a three year period (1996-1998) (Hector *et al.*, 1999). The experimental grasslands in the Greek site, representing the south-eastern end of the European gradient, were dominated by annual species, in contrast to the rest of experimental sites where perennial grasslands were used as models for the study.

Experimental design

Sixty 4 m² plots have been established by sowing specific combinations of seeds in a > 15 year-old abandoned arable field. Annuals dominate the floristic cohort of the grassland (on average 27±1 species/m²); however, in terms of aboveground phytomass, the grassland is dominated by *Phalaris coerulescens* Desf., a perennial grass.

The plots are located in the island of Lesbos (39° 08' 35" N, 26° 31' 23" E). The mean annual temperature in the area is 17.6 °C, the warmest month is July (mean 26.5 °C) and the coolest month is January (mean 9.6 °C). The average annual rainfall is 682 mm. The clayish soil (71.4% clay, 15.9% silt, 12.7% sand) has a neutral pH (average 7.12) and typical nutrient content values (mean ± 1 SE) are organic C (%) = 1.03 ± 0.04, total N (%) = 0.05 ± 0.00 and available P = 16.46 ± 0.13 (mg/kg).

Before sowing, natural vegetation was mechanically and manually removed and the seed bank was killed by using methyl-bromide, during early winter 1996. A pool of 18 annual plant species, to which the perennials *Phalaris coerulescens* Desf., *Bellevalia trifoliata* (Ten) Kunth, *Gladiolus italicus* Miller, *Hordeum bulbosum* L., and *Bituminaria bituminosa* (L.) Stirton were added on purpose, was selected from the natural grassland communities in the surrounding area (appendix I); seeds were collected during spring and summer 1995.

Five levels of species diversity – the diversity treatments –, from monocultures to 18-species mixtures, were established; the number of replicates per diversity treatment is presented in Table 1. Species were allocated randomly in each mixture; the species composition of each mixture is given in Appendix II. Monocultures were sowed at a density of 2,000 viable seeds per m². In polycultures, seeding densities were reduced according to the total number of species in the community. For instance, in four-species communities the density of each species was reduced to one-quarter its density in monoculture. The maintenance of the experimental gradient was achieved by continuous weeding in order to control invasions (weeding was

more intensive in low diversity communities; special effort to minimise eventual disturbance was paid in them). The replicates in each diversity treatment had a different species composition in order to avoid the dependence of results on the individual traits of a particular species more than on the diversity level *per se* (Naaem *et al.*, 1994; Givnish, 1994; Tilman *et al.*, 1997). The number of replicates per diversity treatment decreased as the richness of the mixture increased, assuming that variability in ecosystem response variables would be lower between high-diversity mixtures in comparison to low-diversity ones, as far as the species specific effects are concerned.

The 2 x 2 m plots were grouped into two 30-plot blocks, of which 26 received pre-determined mixtures of seeds in order to establish the gradient of species diversity, while the remaining four were used as reference plots, to monitor soil conditions in the absence of vegetation and to survey the intensity of invasions from the surrounding natural vegetation. Plots were randomly allocated in the two blocks.

Functional diversity was manipulated by controlling the composition of each plot in terms of the combination of three plant functional groups (table 1): (i) legumes, (ii) grasses, and (iii) non-legume forbs, including geophytes. Although *a priori* simplistic, this PFT classification allows for comparisons with similar experimental investigations of the diversity/ecosystem function relationship in Cedar Creek (e.g. Tilman *et al.*, 1996), Nash's Field (Crawley *et al.*, 1999) and Camp Redon (Prieur-Richard *et al.*, 2000). To increase the similarity of the mixtures with the natural grassland of the field the majority of the combinations included grasses. The manipulation of functional diversity therefore produced mixtures with one, two or three functional groups.

The processes and structural traits measured were: plant species richness, total plant cover, species

Functional groups	Species richness				
	1	2	4	8	18
Grasses	3	1	0	0	0
Legumes	1	0	0	0	0
Forbs	3	0	0	0	0
Grasses + legumes		2	1	0	0
Grasses + forbs		2	2	0	0
Legumes + forbs		1	0	0	0
Grasses + legumes + forbs			2	4	4

Table 1. The experimental design in the Greek site of BIODEPTH: number of replicates for species richness and functional group richness

abundance, maximum canopy height, leaf area index, aboveground biomass, belowground biomass, short- and long-term decomposition rate (Table 2).

The experimental treatment is the number of plant species per plot, subdivided into five classes for ANOVA or used as continuous variable in regression analysis. Biomass production, vegetation structure traits and decomposition were the response variables examined for significant difference between treatments. Regression analysis was performed on productivity descriptors (biomass and LAI) and decomposition to investigate for the type (if any) of dependence of the examined variable on diver-

sity treatment. Several diversity components were used: species diversity (*i.e.* number of species, *S*), $\log S$, functional diversity and Shannon diversity index H' . The linear – and the power – model were used to determine whether (i) the efficiency of ecosystem processes will increase as the number of species in the system increases, *i.e.* the linear rivet hypothesis or (ii) the changes in ecosystem functioning are initially weak, but accelerate as more species are lost – non-linear version of the rivet hypothesis (Johnson *et al.*, 1996). All analyses were performed using the SPSS 9.0 software on the data of the third establishment year (1998).

Ecosystem function	Method	Frequency and details
A. Productivity		
1. Aboveground biomass	Harvesting ¹	A sample taken from one 0.5x0.2m portion of the permanent quadrat 0.5x1m located in the centre of each plot at the time of peak standing crop. The vegetation was cut in canopy layers at different heights (<5, 5-20, 20-35,35-50 and >50cm) and separated by species. Harvested material was dried at 80 °C for 24h and weighed.
2. Belowground community biomass		Two soil cores (4cm diameter and 20cm depth) for each plot, taken at the same time as aboveground biomass, outside the central area. Roots were extracted by washing and sieving.
B. Decomposition		
3. Short-term	Cotton strip assay ³	Mean weight loss of four 50x122mm strips per plot placed vertically into the soil at a depth of 10cm for 6 week during the spring.
4. Long-term	Birch sticks ⁴	Mean differences in dry mass of the central stick of each bundle. Four bundles of sticks were used per plot for 7 months.
C. Vegetation structure		
5. Canopy height	HFRO sward stick ²	10 random readings per plot of the height of the first uppermost lamina. Once per month till the end of the growing season
6. Leaf Area Index	Delta T Sunscan ceptometer ¹	Five measurements taken at ground level and one above the canopy during the middle of the day facing roughly into the sun and along the same edge of each plot at the end of the growing season. A constant leaf angle distribution of 0.55 was assumed for all species compositions.
7. Total plant cover	Visual inspection ¹	At the end of the growing season
8. Plant species richness	Visual inspection ¹	At the time of the peak aboveground biomass
9. Pseudo-frequency	Quadrat ¹	One measurement per plot at the time of the peak aboveground biomass. All rooted plant species were recorded in 50 10x10cm cells of the permanent quadrat.

1. Diemer *et al.*, 1997; 2. Bircham, 1981; 3. Harisson *et al.*, 1988; 4. Nacem *et al.*, 1994.

Table 2. Ecosystem processes and vegetation structure monitored in communities

RESULTS

All experimental communities were successfully established. At the end of the second growing season, the plots – independently of the diversity treatment – had reached the originally planned species numbers, as well as a very satisfactory horizontal plant cover. Total plant cover excee-

ded 70% in the majority of the plant communities (46 out of 52), and reached 100% in the higher-diversity communities (Figure 1a): a linear model fits better ($R^2=0.14$, $F=7.97$, $p=0.007$) than the power one ($R^2=0.12$, $F=6.40$, $p=0.01$) but both models produce significant results. The average canopy height reaches a plateau at a rather low diversity level (4 species mixtures), and then remains

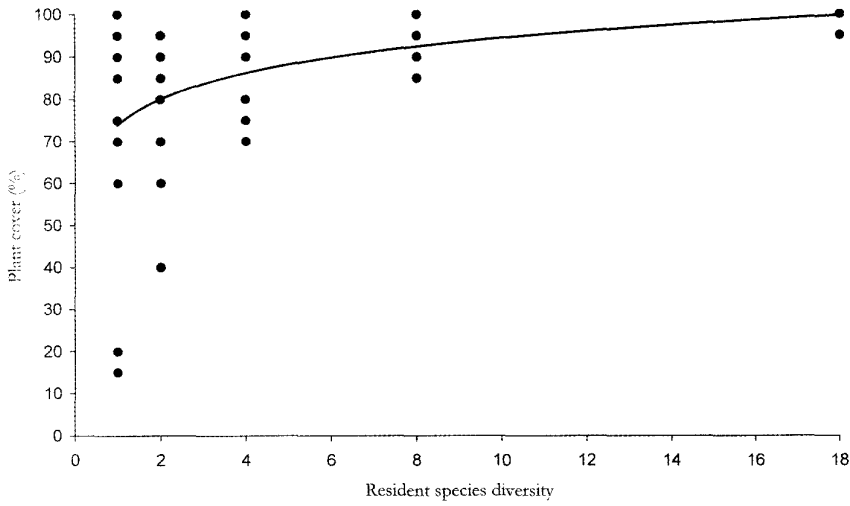


Fig. 1a. Variation of total plant cover along the species richness gradient in the Greek site of BIODDEPTH. Data and best-fit model refer to the 3rd-year of establishment of the experimental communities.

Fig. 1b. Variation of canopy height cover along the species richness gradient in the Greek site of BIODDEPTH.

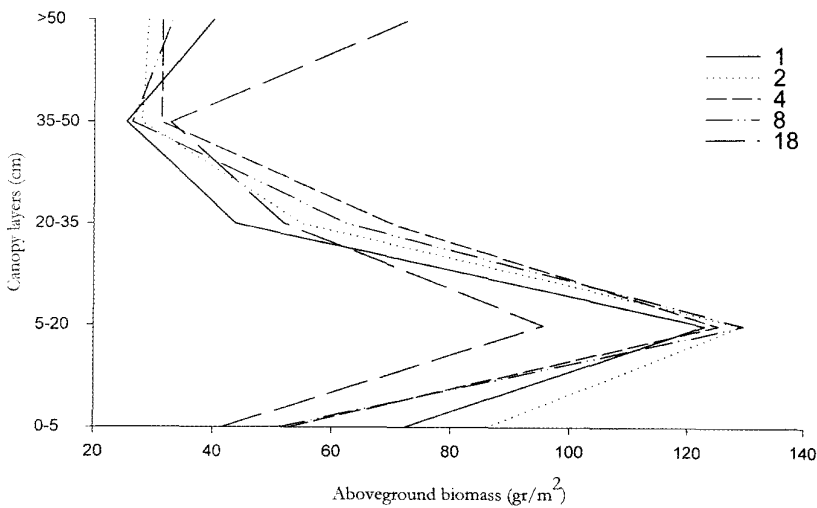
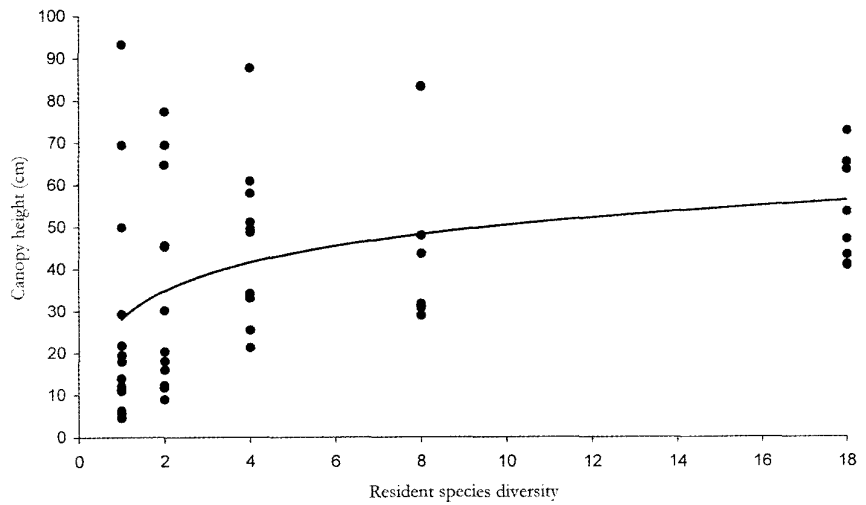


Fig. 1c. Variation of vertical stratification of aboveground biomass (mean values) in the Greek site of BIODDEPTH.

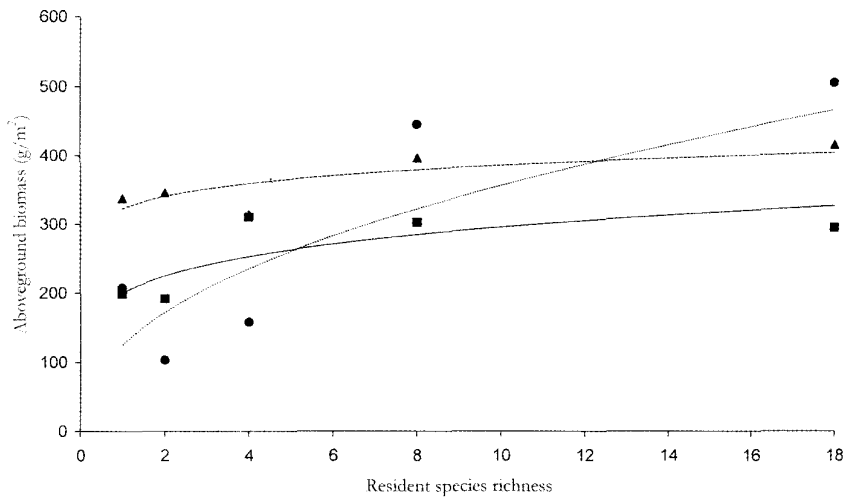


Fig. 1d. Inter-annual changes of the diversity – aboveground biomass production relationship: the solid line represents this relationship for the third experimental year, the broken line for the second year and dot line for the first year. Squares show the average biomass produced the third year, triangles the second year and circles the first year.

Fig. 1e. Variation of Leaf Area Index along the species richness gradient in the Greek site of BIODEPTH.

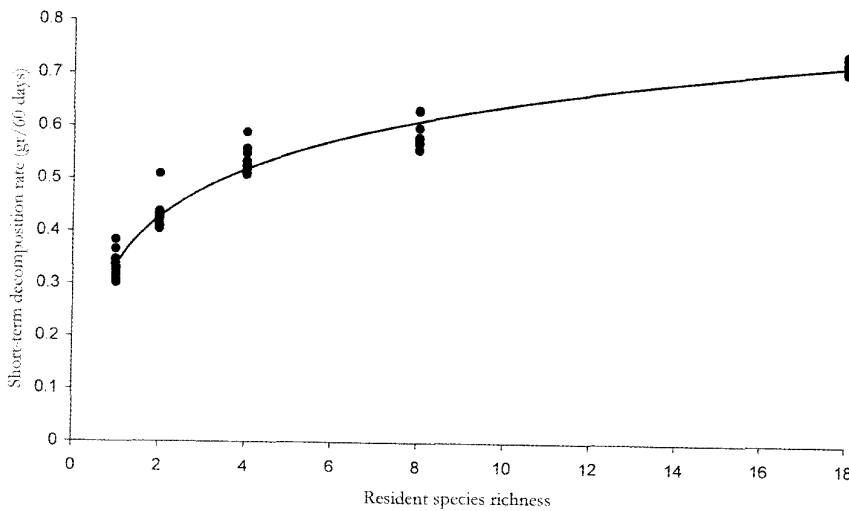
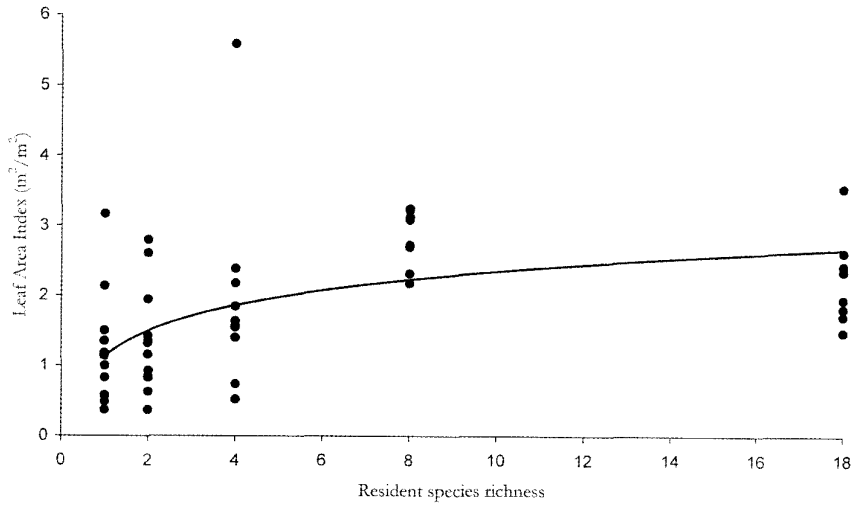


Fig. 1f. Short-term decomposition rate (measured as the loss of dry weight of cotton strips inserted into the soil in a two months period).

practically constant (Fig. 1b). A simple power model describes significantly the canopy height variation ($R^2=0.27$, $F=18.42$, $p<0.001$). The vertical partitioning of biomass among vegetation strata showed a significant peak in the lower canopy layers (especially between 5-20cm above ground); no significant difference among diversity treatments has appeared in the third year of establishment (Fig. 1c).

Figure 1d presents the evolution of the relationship between species diversity and aboveground biomass production during the three years period of plot establishment. The first year's relationship presents noticeable differentiation in comparison with the other two years, while the comparison between second and third year's relationship suggests that, although quantitatively different, a common pattern appears. Figure 1e shows the variation

of LAI with the number of species in 1998 data. A power model gave a better fit and produced significant results ($R^2=0.33$, $F=24.78$, $p<0.001$) than a linear one ($R^2=0.16$, $F=9.65$, $p=0.003$). The variation of short-term decomposition rate across diversity treatments is presented in Figure 1f. Short-term decomposition rates differed among treatments increasing from monocultures to higher-diversity communities. Both power ($R^2=0.94$, $F=821.8$, $p<0.001$) and linear ($R^2=0.83$, $F=237.37$, $p<0.001$) models gave significant results on mean values of decomposition per diversity level but the power model fitted better than the linear one.

The summary of the ANOVA on the 1998 data set for: (1) above- and below-ground biomass production, (2) decomposition, and (3) vegetation structure (LAI, height, % cover) is presented in Table 3. The experiment has a nes-

Dependent variable	Source of variation	Type I sum of squares	df	Mean square	F value	P
A. Productivity						
Aboveground biomass	S	6255.087	4	1563.722	0.016	0.999 (NS)
	FG	7388.871	2	3694.436	0.039	0.962 (NS)
	MIX	1822710.610	19	95932.137	5.829	< 0.001
Belowground biomass	S	0.6060	4	0.1520	0.521	0.904 (NS)
	FG	0.0381	2	0.0190	0.032	0.969 (NS)
	MIX	11.355	19	0.5890	2.289	0.025
B. Vegetation structure						
LAI	S	19.582	4	4.896	6.259	0.002
	FG	17.109	2	8.555	10.937	0.001
	MIX	14.861	19	0.782	0.968	0.521 (NS)
PAR	S	617310.558	4	154327.64	5.587	0.003
	FG	443347.609	2	22167.804	8.025	0.003
	MIX	524839.210	19	27623.116	1.041	0.454 (NS)
Plant Cover	S	2688.3880	4	672.097	1.162	0.359 (NS)
	FG	2746.3940	2	1373.197	2.374	0.120 (NS)
	MIX	10989.464	19	578.393	3.702	0.001
Canopy Height	S	5380.8380	4	1345.210	1.479	0.248 (NS)
	FG	4021.4060	2	2010.703	2.210	0.137 (NS)
	MIX	17286.411	19	909.811	3.521	0.002
C. Decomposition						
Cotton strips	S	0.941	4	0.235	373.406	< 0.001
	FG	0.780	2	0.390	619.541	< 0.001
	MIX	0.012	19	0.001	1.110	0.395 (NS)
Birch sticks	S	0.035	4	0.009	0.979	0.442 (NS)
	FG	0.038	2	0.019	2.099	0.150 (NS)
	MIX	0.171	19	0.009	0.658	0.825 (NS)

Note : F -values and their corresponding p- values for the FGR (functional groups) factor was emerged when it was entered first in the model. All analyses were performed by the use of TYPE I Sum of Squares.

Table 3. ANOVA results for 1998 data. All dependent variables were examined for the factors: Species richness (S), functional group richness (FG), and plant assemblage (MIX). The term 'plant assemblage' (MIX) was defined as RANDOM and Mixture Mean Square Error was the error term for the determination of the F statistics.

ted design with multiple error terms: species diversity (S) and functional diversity (FG) are tested against the species mixture term (MIX). Species diversity influences differently the various response variables studied, *i.e.* vegetation characteristics and ecosystem processes. Significance of the various ANOVA terms supports the hypothesis that different levels of biodiversity are associated with different levels of ecosystem functioning, and especially productivity. Although, there is no consistent overall pattern of variation for the studied vegetation structure characteristics and ecosystem processes, higher diversity mixtures (for the various diversity terms) showed significant differences in

comparison to low diversity mixtures for LAI which can be interpreted either as productivity or vegetation structure descriptor. Short-term decomposition variation was significantly dependent on the majority of the examined factors (species diversity, functional diversity and mixture). Species composition had significant effects on above- and below-ground biomass production, plant cover and canopy height. ANOVA results for the mixture term indicate that the taxonomic identity of the mixtures has significant effects on most of the studied variables.

Table 4 presents summary results on the comparison of the two versions of the rivet hypothesis (linear and non-

Y	X	Model R ²	Overall F-value	Overall	Model parameters a	B		
BIOMASS								
Species richness	Y = aX + b	0.001	0.052	NS	-1.165	NS	315.43	***
	Y = aX ^b	0.023	1.20	NS	211.213	***	0.114	NS
Functional group richness	Y = aX + b	0.001	0.046	NS	-7.655	NS	324.92	***
	Y = aX ^b	0.017	0.889	NS	210.80	***	0.216	NS
Log.(Diversity)	Y = aX + b	0.001	0.029	NS	-3.50	NS	315.04	***
	Y = aX ^b	0.032	1.69	NS	256.87	***	0.030	NS
Shannon Index	Y = aX + b	0.001	0.06	NS	-5.73	NS	317.48	***
	Y = aX ^b	0.032	1.70	NS	258.168	***	0.03	NS
LAI								
Species richness	Y = aX + b	0.161	9.65	***	0.071	**	1.363	***
	Y = aX ^b	0.331	24.78	***	0.928	***	0.375	***
Functional group richness	Y = aX + b	0.2978	21.20	***	0.681	***	0.342	NS
	Y = aX ^b	0.320	23.63	***	0.864	***	0.815	***
Log. (Diversity)	Y = aX + b	0.268	18.34	***	0.369	***	1.123	***
	Y = aX ^b	0.241	15.911	***	1.673	***	0.072	***
Shannon Index	Y = aX + b	0.272	18.76	***	0.428	***	1.124	***
	Y = aX ^b	0.245	16.24	***	1.69	***	0.074	***
DECOMPOSITION								
Species richness	Y = aX + b	0.826	237.37	***	0.021	***	0.375	***
	Y = aX ^b	0.942	821.87	***	0.344	***	0.269	***
Functional group richness	Y = aX + b	0.800	200.23	***	0.147	***	0.186	***
	Y = aX ^b	0.819	227.56	***	0.333	***	0.555	***
Log. (Diversity)	Y = aX + b	0.963	1320.68	***	0.092	***	0.334	***
	Y = aX ^b	0.715	126.04	***	0.526	***	0.053	***
Shannon Index	Y = aX + b	0.943	830.18	***	0.105	***	0.337	***
	Y = aX ^b	0.722	130.45	***	0.531	***	0.054	***

Table 4. Dependence of 1998 biomass, LAI, and decomposition on species richness, functional group richness, Log.(diversity) and Shannon index respectively. Linear and power fit statistic results are presented. Significance of differences of parameter value from 0: NS for p≥0.05; * for 0.05>p≥0.01; ** for 0.01>p≥0.001; and *** for p<0.001.

linear). Biomass production, decomposition and LAI were used as the dependent variables and the various components of diversity as the independent variables to test for the fit of linear and power models (field data of 1998). No significant relationship was found between above-ground biomass and all components of diversity, for both models. On the contrary, LAI and short-term decomposition rate were significantly dependent on all components of diversity for both models. However, a discrimination was possible between the two alternative models: power models fitted better than linear models, showing higher R^2 values, when F values were significant.

DISCUSSION

Methodological considerations

Our study has tested directly the effects of variation in different components of community diversity upon primary ecosystem functions in synthesised Mediterranean grasslands. It sought to investigate the short-term effects of the loss of species *within* a site; at that scale, no significant differentiation in environmental conditions, soil nutrients, management and disturbance exists – as preliminary measurements have shown – that could produce variation in ecosystem processes and structures. In that sense, this study treats diversity as the independent variable driving variation in ecosystem functions such as productivity or decomposition, that are considered as the dependent variables. Similar approach has been used in field diversity – function experiments in both temperate grasslands (e.g. Tilman *et al.*, 1997; Crawley *et al.*, 1999) and Mediterranean grasslands (e.g. Hooper & Vitousek, 1997; Lavorel *et al.*, 1999). To our best knowledge, the present study is the only published experiment in Mediterranean-type grasslands which tests the effect of all biodiversity components, i.e. species richness, functional composition and taxonomic diversity, since Hooper & Vitousek (1997) have focused on the effect of functional diversity upon ecosystem function(s). Unavoidably, our approach and results enter into the so-called ‘diversity debate’ (for a summary see Wardle *et al.*, 2000; Naeem, 2000). Much of the controversy in the analysis of the diversity – ecosystem function relationship(s) is related to differences in appreciation of the methodological context within which diversity experiments are conceived.

Under average or relatively constant environmental conditions, literature describes several hypothetical rela-

tionships between *within-site* changes in diversity and the performance of an ecosystem process, i.e. the null hypothesis, the linear and non-linear versions of the rivet hypothesis and the redundancy hypothesis, the idiosyncratic hypothesis (see review by Johnson *et al.*, 1996). When diversity is not considered as a potential determinant of function, but on the contrary as an ‘ecosystem property’ driven by the variation in abiotic and biotic variables such as productivity or soil nutrient content, then a unimodal or hump-back relationship between them is considered as widely valid (e.g. Huston & De Angelis, 1994). Observational studies have addressed the problem of determinants and controls of diversity in Mediterranean grasslands in relation to natural gradients (elevation, e.g. Montalvo *et al.*, 1993; or soil fertility, e.g. Puerto *et al.*, 1990) and disturbances (mainly fire and grazing, e.g. Perevolotsky & Seligman, 1998). In correlational studies across such gradients, the relationship between production descriptors (cover or biomass) and diversity has been shown to follow a unimodal curve, as predicted in theory (Puerto *et al.*, 1990). It should be noticed however, that the hump-back model addresses *between-site* variation in the diversity – ecosystem function relationship. In an observational study of *within-site* variation of diversity in *Cistus* dominated shrublands, Troumbis & Memtsas (2000) have shown that variation in diversity is strongly correlated with variation in productivity. The implications of these supposed ‘divergent’ approaches have been discussed by Hodgson *et al.* (1998) and Lawton *et al.* (1998). Loreau (2000) has shown how locally defined diversity-ecosystem function relationship(s) can generate different patterns at larger scales or across ecological gradients, one of which is the hump-back model.

Ecosystem responses to variation of diversity

The results of the ANOVA and the regression analysis may have ambiguous interpretations as to which type of diversity – ecosystem function (especially productivity) actually exists in the studied communities. At first, there is no unique pattern of influence of species richness or functional group richness upon the ensemble of ecosystem processes and structural traits of the synthesised communities. Biomass production varies in a non-significant way across the gradient of these diversity component terms. On the contrary, the variation of short-term decomposition rate with species richness has showed a strong curvilinear trend. Strong significance was also observed for plant cover and leaf area index: it should be borne in

mind that these parameters can be considered as descriptors of both production and vegetation structure. Regression analysis has shown significant dependence of LAI and decomposition rate upon species – and functional group richness, best described by a simple power model. This model supports a non-linear version of the rivet hypothesis. The same variables were linearly related to other expressions of diversity, *i.e.* Shannon diversity and the logarithmic transformation of species diversity, supporting the linear version of the same hypothesis.

The third component of diversity, *i.e.* species composition or in other terms the taxonomic identity of the mixture, has significant effects on above – and below – ground biomass production, plant cover, canopy height and decomposition. Hooper & Vitousek (1997) have reported similar diversity – productivity patterns in experimental Californian serpentine grasslands: although they focused on the effects of functional group diversity, they found that the *number* of functional groups had no effect on productivity, whereas the *composition of functional groups* affected productivity significantly.

The lack of a common pattern for the different ecosystem processes observed in our study supports earlier findings from laboratory mesocosms. Naeem *et al.* (1994) have reported that the decrease of species richness in Ecotron communities affected the studied ecosystem processes differently: community respiration and productivity differed significantly among treatments, though for short-term decomposition rate, nutrient retention and water retention no clear pattern of association with species richness appeared; long-term decomposition rate did not present significant treatment effects.

A rather few published studies have examined the effects of diversity on decomposition rates. Both negative (Naeem *et al.*, 1994) or weak effects (Hector *et al.*, 2000; Knops *et al.*, 2001) have been reported. Wardle *et al.* (1997a) manipulated diversity of plant litter on decomposition processes and found that there was no relationship between litter species richness and ecosystem processes such as plant litter decomposition and litter nitrogen loss. Our results demonstrate a clear pattern of increasing short decomposition rate along the species- and functional group richness terms of the diversity gradient.

Experimental design and descriptors of change(s) in ecosystem processes

The ambiguity of the results on the diversity – productivity relationship refers to the differential perception of our statistical findings: (i) the significance of the ‘com-

position’ term of the diversity treatment in the ANOVA, which supports the *idiosyncratic hypothesis*; and, (ii) the selection of a constant model, where productivity equals to grand mean across the diversity gradient, as best regression model for this relationship. This model describes the *null hypothesis*. This apparent contradiction can be reconciled by noticing that these two hypotheses do not constitute an *a priori* mutually exclusive pair of diversity – productivity patterns. By definition, an idiosyncratic response of an ecosystem process to changes in community diversity depends on its composition but it is unpredictable as to its form. Statistically it is feasible to have a collection of data where an ANOVA is significant and the overall response trend is constant across the treatments. In the present case, it is only *a posteriori* that the compatibility of the two hypotheses can be accepted, when the null hypothesis is shown to be a special case of the idiosyncratic hypothesis. The selection of species and the way they are sequentially introduced into the mixtures of increasing richness may affect strongly the final perception of the diversity – function relationship. This result supports Allison’s (1999) assumption on the critical role of the experimental design as to the identification of the diversity term responsible for the productivity response.

Experimental design in diversity-function studies is strongly driven by the necessity to replicate properly for species- and or functional group- richness as well as for composition. The need for a suite of diversity classes increases much further the number of mixtures that should be established and maintained. Given the large number of mixtures where ecosystem processes should be monitored under the usual constraints for time and man effort, investigators would look for a sub-optimal trade-off between replication of diversity terms and increase of diversity levels and would ‘spontaneously’ simplify their monitoring techniques. They would use rather easy-to-measure ‘descriptors’ than ‘actual measures’ of processes: our results suggest that there is here a source of potential errors, and that there is a need to introduce this aspect too in the search for overall optimality in the experimental design.

In several diversity experiments, productivity was measured or estimated indirectly. For instance, Tilman *et al.* (1996) used total plant cover, a 2-dimension parameter, as a descriptor of production or productivity, which is a 3-dimension property of vegetation. In the Ecotron experiment (Naeem *et al.*, 1994) the productivity was estimated by comparing the percent transmittance of photosynthetic active radiation (PAR) through the canopy assuming no significant differences in individual leaf transmittance among plant species. Our results suggest that

productivity descriptors are not equivalent or neutral as to their influence upon the identification of a diversity - productivity pattern. As mentioned above, LAI, a widely used descriptor of productivity varied significantly with species richness, but the actual measurement of above-ground biomass produced yearly, i.e. productivity, did not differ across this gradient. Differential response of descriptors was previously reported by McNaughton (1993): the author reporting on a series of studies on successional old fields encompassing a soil properties scalar, indicated that productivity measured as peak community biomass was negatively related to diversity, but was not related to diversity when the sum of species biomass peaks was the measurement of productivity, because the temporal seasonal dispersion of species peaks is part of the mechanism of diversification.

Key-stone species and variation in productivity

Ecosystem function can be critically affected by the presence of a key-stone species. In diversity experiments, this corresponds to the so-called sampling effect (e.g. Aarsen, 1997; Huston, 1997). The sampling effect hypothesis assumes that the increase in productivity in species-rich mixtures is caused by the probable inclusion of highly performant species. This is predicted by the law of constant yield (Crawley, 1986) assuming that a polyculture is less productive than a monoculture of the most productive species; biomass is controlled by abiotic factors and the species-specific growth rate under these factors. It is implied that dominant species maintains the same biomass independently of the richness of the mixture. In our case, the perennial grass *Phalaris coerulescens* was the most productive species of the pool. A simple regression of its biomass across the diversity gradient has showed a significantly reduced biomass in the high-diversity mixtures in comparison to the monoculture (power model: Productivity = 1088.3* (diversity)^{-1.07}, F = 68.962, p = 0.004). Similar patterns were obtained for the sub-set of species from the pool grown in monocultures (Troumbis *et al.*, 2000). This result, especially for the dominant *Phalaris*, is an indication that the sampling effect does not occur in the synthesised communities. This was expected to some extent because of the absence of a significant relationship between species richness and aboveground biomass. It is, however, worth reporting because other descriptors of productivity were positively correlated with diversity.

Furthermore, the same conclusion was proposed by Spehn *et al.* (1999) for the temperate grassland of the Swiss BIODEPTH site, where a clear curvilinear increase of productivity with diversity was observed.

CONCLUSIONS

In summary, our results support : (i) the feasibility of a 'diversity experiment' in the Mediterranean free from secondary treatments and weaknesses in the experimental design ; (ii) a non-linear relationship between diversity and certain ecosystem functions and quantitative structural traits, and (iii) the need for direct measurement of an ecosystem process, especially productivity, because its various descriptors can respond differently to the variation of diversity.

Our results provide evidence that the variation of diversity affects important ecosystem processes and structural traits of Mediterranean grasslands. This finding offers additional support to conservation arguments focusing on the relationship between biodiversity maintenance, ecosystem integrity and perpetuation of the life-support services. This is particularly important for conservation in an area like the Mediterranean, where biodiversity is severely threatened by invasions, landscape fragmentation and habitat alteration.

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APPENDIX I. The species pool used to assemble the experimental mixtures in the greek site of BIODEPTH: growth forms and classification into functional groups.

Species	Life form	
	Growth form	Functional group
<i>Anthemis cotula</i> L.	annual	nonlegume forb
<i>Avena barbata</i> Link subsp. <i>barbata</i>	annual	grass
<i>Bellevaia trifoliata</i> (Ten) Kunth	perennial/geophyte	nonlegume forb
<i>Bituminaria bituminosa</i> (L.) Stirton	perennial	legume
<i>Bromus intermedius</i> Guss.	annual	grass
<i>Catananche lutea</i> L.	annual	nonlegume forb
<i>Crepis foetida</i> (Spreng.) Babcock subsp. <i>commutata</i>	annual	nonlegume forb
<i>Daucus carota</i> L. s.l.	annual	nonlegume forb
<i>Gladiolus italicus</i> Miller	perennial/geophyte	nonlegume forb
<i>Helminthotheca echioides</i> (L.) Holub	annual	nonlegume forb
<i>Hirschfeldia incana</i> (L.) Lagreze-Fossat	annual	nonlegume forb
<i>Hordeum bulbosum</i> L.	perennial	grass
<i>Hordeum geniculatum</i> All.	annual	grass
<i>Lagoecia cuminoides</i> L.	annual	nonlegume forb
<i>Lotus tetragonolobus</i> L.	annual	legume
<i>Malva sylvestris</i> L.	perennial	nonlegume forb
<i>Medicago lupulina</i> L.	annual	legume
<i>Phalaris coerulescens</i> Desf.	perennial	grass
<i>Plantago lagopus</i> L.	annual	nonlegume forb
<i>Scorpiurus muricatus</i> L.	annual	legume
<i>Securigera parviflora</i> (Desv.) Lassen	annual	legume
<i>Tragopogon hybridus</i> L.	annual	nonlegume forb
<i>Trifolium lappaceum</i> L.	annual	legume

APPENDIX II. List of the mixtures utilized in the five levels of diversity treatment.

Monocultures	2-species mixtures	4-species mixtures	8-species mixtures		18-species mixtures
<i>Phalaris coeruleascens</i>	<i>Phalaris coeruleascens</i> <i>Hordeum geniculatum</i>	<i>Phalaris coeruleascens</i> <i>Bromus intermedius</i> <i>Hordeum geniculatum</i> <i>Bituminaria bituminosa</i>	<i>Bromus intermedius</i> <i>Hordeum geniculatum</i> <i>Avena barbata ssp. barbata</i> <i>Hordeum bulbosum</i> <i>Medicago lupulina</i> <i>Securigera parviflora</i> <i>Malva sylvestris</i> <i>Crepis foetida ssp. commutata</i>	<i>Phalaris coeruleascens</i> <i>Bromus intermedius</i> <i>Hordeum geniculatum</i> <i>Avena barbata ssp. barbata</i> <i>Hordeum bulbosum</i> <i>Trifolium lappaceum</i> <i>Bituminaria bituminosa</i> <i>Scorpiurus muricatus</i> <i>Daucus carota</i> <i>Malva sylvestris</i> <i>Anthemis cotula</i> <i>Hirschfeldia incana</i>	<i>Bromus intermedius</i> <i>Avena barbata ssp. barbata</i> <i>Hordeum bulbosum</i> <i>Medicago lupulina</i> <i>Trifolium lappaceum</i> <i>Bituminaria bituminosa</i> <i>Securigera parviflora</i> <i>Lotus tetragonolobus</i> <i>Daucus carota</i> <i>Malva sylvestris</i> <i>Anthemis cotula</i> <i>Hirschfeldia incana</i>
<i>Bromus intermedius</i>	<i>Phalaris coeruleascens</i> <i>Bituminaria bituminosa</i>	<i>Bromus intermedius</i> <i>Hordeum geniculatum</i> <i>Avena barbata ssp. barbata</i> <i>Hirschfeldia incana</i>	<i>Phalaris coeruleascens</i> <i>Bromus intermedius</i> <i>Hordeum geniculatum</i>	<i>Daucus carota</i> <i>Malva sylvestris</i> <i>Anthemis cotula</i> <i>Hirschfeldia incana</i>	<i>Medicago lupulina</i> <i>Trifolium lappaceum</i> <i>Bituminaria bituminosa</i> <i>Securigera parviflora</i> <i>Lotus tetragonolobus</i> <i>Daucus carota</i> <i>Malva sylvestris</i> <i>Anthemis cotula</i> <i>Hirschfeldia incana</i>
<i>Hordeum geniculatum</i>	<i>Phalaris coeruleascens</i> <i>Bituminaria bituminosa</i>	<i>Bromus intermedius</i> <i>Hordeum geniculatum</i> <i>Avena barbata ssp. barbata</i> <i>Hirschfeldia incana</i>	<i>Phalaris coeruleascens</i> <i>Bromus intermedius</i> <i>Hordeum geniculatum</i>	<i>Daucus carota</i> <i>Malva sylvestris</i> <i>Anthemis cotula</i> <i>Hirschfeldia incana</i>	<i>Medicago lupulina</i> <i>Trifolium lappaceum</i> <i>Bituminaria bituminosa</i> <i>Securigera parviflora</i> <i>Lotus tetragonolobus</i> <i>Daucus carota</i> <i>Malva sylvestris</i> <i>Anthemis cotula</i> <i>Hirschfeldia incana</i>
<i>Trifolium lappaceum</i>	<i>Bromus intermedius</i> <i>Trifolium lappaceum</i>	<i>Phalaris coeruleascens</i> <i>Bromus intermedius</i>	<i>Phalaris coeruleascens</i> <i>Bromus intermedius</i> <i>Hordeum geniculatum</i>	<i>Daucus carota</i> <i>Malva sylvestris</i> <i>Anthemis cotula</i> <i>Hirschfeldia incana</i>	<i>Medicago lupulina</i> <i>Trifolium lappaceum</i> <i>Bituminaria bituminosa</i> <i>Securigera parviflora</i> <i>Lotus tetragonolobus</i> <i>Daucus carota</i> <i>Malva sylvestris</i> <i>Anthemis cotula</i> <i>Hirschfeldia incana</i>
<i>Daucus carota</i>	<i>Bromus intermedius</i> <i>Gladiolus italicus</i>	<i>Phalaris coeruleascens</i> <i>Bromus intermedius</i>	<i>Phalaris coeruleascens</i> <i>Bromus intermedius</i> <i>Hordeum geniculatum</i>	<i>Daucus carota</i> <i>Malva sylvestris</i> <i>Anthemis cotula</i> <i>Hirschfeldia incana</i>	<i>Medicago lupulina</i> <i>Trifolium lappaceum</i> <i>Bituminaria bituminosa</i> <i>Securigera parviflora</i> <i>Lotus tetragonolobus</i> <i>Daucus carota</i> <i>Malva sylvestris</i> <i>Anthemis cotula</i> <i>Hirschfeldia incana</i>
<i>Hirschfeldia incana</i>	<i>Bromus intermedius</i> <i>Gladiolus italicus</i>	<i>Phalaris coeruleascens</i> <i>Bromus intermedius</i>	<i>Phalaris coeruleascens</i> <i>Bromus intermedius</i> <i>Hordeum geniculatum</i>	<i>Daucus carota</i> <i>Malva sylvestris</i> <i>Anthemis cotula</i> <i>Hirschfeldia incana</i>	<i>Medicago lupulina</i> <i>Trifolium lappaceum</i> <i>Bituminaria bituminosa</i> <i>Securigera parviflora</i> <i>Lotus tetragonolobus</i> <i>Daucus carota</i> <i>Malva sylvestris</i> <i>Anthemis cotula</i> <i>Hirschfeldia incana</i>
<i>Crepis foetida ssp. commutata</i>	<i>Phalaris coeruleascens</i> <i>Hirschfeldia incana</i>	<i>Hordeum geniculatum</i> <i>Gladiolus italicus</i>	<i>Trifolium lappaceum</i> <i>Securigera parviflora</i> <i>Hirschfeldia incana</i> <i>Catananche lutea</i> <i>Gladiolus italicus</i>	<i>Crepis foetida ssp. commutata</i> <i>Catananche lutea</i> <i>Plantago lagopus</i> <i>Helminthotheca echioides</i> <i>Tragopogon hybridus</i> <i>Gladiolus italicus</i>	<i>Crepis foetida ssp. commutata</i> <i>Lagoecia cuminoides</i> <i>Catananche lutea</i> <i>Plantago lagopus</i> <i>Tragopogon hybridus</i> <i>Gladiolus italicus</i>
	<i>Bituminaria bituminosa</i> <i>Lagoecia cuminoides</i>	<i>Phalaris coeruleascens</i> <i>Hordeum geniculatum</i> <i>Securigera parviflora</i> <i>Hirschfeldia incana</i>	<i>Phalaris coeruleascens</i> <i>Hordeum geniculatum</i> <i>Securigera parviflora</i> <i>Bituminaria bituminosa</i> <i>Anthemis cotula</i> <i>Hirschfeldia incana</i> <i>Catananche lutea</i> <i>Gladiolus italicus</i>	<i>Bromus intermedius</i> <i>Hordeum geniculatum</i> <i>Avena barbata ssp. barbata</i> <i>Hordeum bulbosum</i> <i>Trifolium lappaceum</i> <i>Bituminaria bituminosa</i> <i>Securigera parviflora</i> <i>Scorpiurus muricatus</i> <i>Daucus carota</i> <i>Malva sylvestris</i> <i>Anthemis cotula</i> <i>Hirschfeldia incana</i> <i>Crepis foetida ssp. commutata</i>	<i>Phalaris coeruleascens</i> <i>Bromus intermedius</i> <i>Hordeum geniculatum</i> <i>Medicago lupulina</i> <i>Trifolium lappaceum</i> <i>Bituminaria bituminosa</i> <i>Securigera parviflora</i> <i>Scorpiurus muricatus</i> <i>Daucus carota</i> <i>Malva sylvestris</i> <i>Anthemis cotula</i> <i>Hirschfeldia incana</i> <i>Crepis foetida ssp. commutata</i>
		<i>Bromus intermedius</i> <i>Trifolium lappaceum</i> <i>Crepis foetida ssp. commutata</i> <i>Gladiolus italicus</i>	<i>Bromus intermedius</i> <i>Trifolium lappaceum</i> <i>Securigera parviflora</i> <i>Daucus carota</i> <i>Malva sylvestris</i>	<i>Daucus carota</i> <i>Malva sylvestris</i> <i>Anthemis cotula</i> <i>Hirschfeldia incana</i> <i>Crepis foetida ssp. commutata</i>	<i>Phalaris coeruleascens</i> <i>Bromus intermedius</i> <i>Hordeum geniculatum</i> <i>Medicago lupulina</i> <i>Trifolium lappaceum</i> <i>Bituminaria bituminosa</i> <i>Securigera parviflora</i> <i>Scorpiurus muricatus</i> <i>Daucus carota</i> <i>Malva sylvestris</i> <i>Anthemis cotula</i> <i>Hirschfeldia incana</i> <i>Crepis foetida ssp. commutata</i>
			<i>Anthemis cotula</i> <i>Tragopogon hybridus</i> <i>Gladiolus italicus</i>	<i>Lagoecia cuminoides</i> <i>Plantago lagopus</i> <i>Helminthotheca echioides</i> <i>Tragopogon hybridus</i> <i>Gladiolus italicus</i>	<i>Catananche lutea</i> <i>Plantago lagopus</i> <i>Helminthotheca echioides</i> <i>Tragopogon hybridus</i> <i>Bellevalia trifoliata</i>

Biomasse aérienne du cytise de Battandier (*Argyrocytismus battandieri* Maire) dans les parcours du Moyen Atlas tabulaire marocain

Prédiction et effet de la pression pastorale

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Résumé

Dans le Moyen Atlas central, la biomasse épigée du cytise de Battandier (*Argyrocytismus battandieri* Maire), arbuste fourrager très apprécié par le bétail, a été appréhendée à partir de données dendrométriques et pondérales de 251 arbustes. Sur la base de ces données, des régressions simples et multiples ont été développées pour estimer les biomasses ligneuse et foliaire de cette espèce.

De ces analyses il ressort que :

- l'estimation des biomasses sèches des brins peut être réalisée à partir de leur diamètre à la souche ;
- la combinaison entre le nombre de brins, la hauteur maximale et le diamètre moyen de l'arbuste constitue le meilleur estimateur des biomasses sèches ;
- les meilleurs modèles obtenus pour les brins et les arbustes sont allométriques, s'ajustant le mieux aux données de biomasses ;
- la production totale estimée d'*Argyrocytismus battandieri* est de 2.2 t/ha, répartie à raison de 2.0 t/ha de biomasse de bois et 0.2 t/ha de poids secs des feuilles.

Une pression de pâturage intense contribue à la destruction du cytise de Battandier. Une pression pastorale moyenne sur substrat basaltique est significativement favorable à la production de l'arbuste, comparée à celle des stations protégées.

Mots-clés

Arbuste fourrager, action anthropique, régression multiple, pression pastorale, Maroc

Summary

Above-ground biomass of *Argyrocytismus battandieri* Maire in the range lands of the Moroccan tabular Middle Atlas. Prediction and effect of the grazing pressure. In the central Middle Atlas, epigeal biomass of the livestock-appreciated forage shrub *Argyrocytismus battandieri* Maire was assessed, based on dendrometric and weight data of 251 shrub individuals. Simple and multiple regressions were applied to the data in order to estimate wood and leaves biomass in this species.

The data analysis allows us to conclude that:

- it's possible to estimate the dry biomass of the stems based on basal diameter;
- the combination of stems count, maximal height and mean diameter of the shrub, is the best estimate of its dry biomasses;
- allometric models for the stems and the shrubs fit better the biomass data;
- average laburnum total dry biomass is 2.2 t/ha, and was composed of 2.0 t/ha of wood and 0.2 t/ha of leaves.

An intensive grazing pressure lead to the species' destruction. A medium grazing pressure on a basaltic substratum is significantly propitious to the production of the shrub, in comparison with stations protected by enclosure.

Key-words

Forager shrub, Anthropic action, Multiple regression, Browsing intensity, Morocco

Abridged english version

This work on *battandieri laburnum* (*Argyrocytismus battandieri* Maire), a Moroccan endemic shrub, is the first one in the Moroccan central Middle Atlas. This perennial fodder species, associated with cedar in the tabular Middle Atlas, belongs to association *Argyrocytiso battandieri-Cedretum atlanticae*. This association, which represents the ecological optimum of the cedar forest, is relatively frequent on causses and volcanic zones of the Middle Atlas. Like all the range lands under the Mediterranean climate, the Middle Atlas shows degradation signs resulting from range resources overuse. The woody forage *Argyrocytismus battandieri*, which is very appreciated by sheep and goats, is undergoing a high anthropic stress trying to provide for livestock needs.

In order to assess this impact on the shrub and to know the survival conditions of this range resource, we propose in this work :

– some models allowing to estimate aerial biomass of the stems and the shrubs,

– then a study of effect of the grazing pressure on above-ground biomass of *Argyrocytismus battandieri*.

The study site is located in the tabular Middle Atlas, particularly in Azrou and Sidi M'guild forests. Prospecting the two forests has allowed us to choose 8 parcels which have different combinations of the four variables: spontaneous or planted *laburnum*, browsing intensity, tree cover and soil substrate types.

In each parcel, we have distinguished two planting types: tree covered and uncovered. Four 100 m² (10 m x 10 m) plots, representing four repetitions, were randomly delimited in each parcel.

Before cutting, the following measurements were taken from 251 shrubs: maximal diameter, orthogonal diameter, maximal height, stems count and stems basal diameters. The shrub volume (phyto-

volume) was calculated by multiplying the shrub projection area by its average height. In each plot, shrubs were divided among 6 volume classes; and 3 shrubs (when available) per volume class were cut. Different shrub forms and sizes were, therefore, represented in this sample.

In order to avoid cutting down the shrubs, stems were sorted by their basal diameter and foliage density. Only two stems of each class of similar ones were then cut. This has increased the sample size and representativeness. Cutting was performed in mid-July at the end of *laburnum* development cycle. The two stems of each class were simultaneously cut. Their average dry weights were used to calculate the total dry weight of the shrub whose classes and stems counts were determined prior to cutting.

Simple and multiple regressions were applied to the dendrometric and weight data of the 251 shrubs in order to estimate wood and leaves biomasses of the stems and the shrubs.

From these analyses, it came out that :

– the estimate for the dry biomass of the stems was realized based on basal diameter.

– the combination of stems count, maximal height and average diameter of the shrub, is the best estimate of its dry biomasses.

– allometric models of the stems and the shrubs fit better the biomass data.

– the estimated *laburnum* total dry biomass was 2.2 t/ha, and was composed of 2.0 t/ha of wood and 0.2 t/ha of leaves.

An intensive grazing pressure lead to the species' destruction. A medium grazing pressure on a basaltic substratum was significantly propitious to the production of the shrub, in comparison with stations protected by enclosure.



Argyrocytismus battandieri Maire (photos F. Médail)

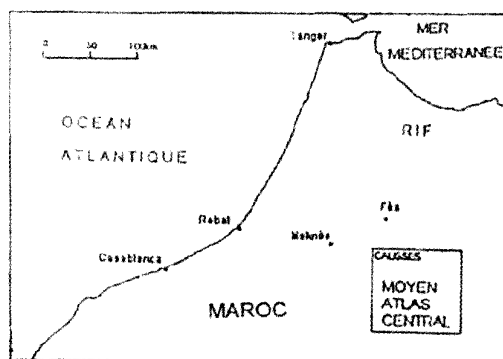
INTRODUCTION

Comme tous les parcours sous climat méditerranéen (Étienne, 1996), le Moyen Atlas présente des signes de dégradation liés à une surexploitation des ressources pastorales (Sauvage, 1950). Les travaux d'évaluation fourragère quantitative de la strate herbacée et arborescente (Qarro, 1985 ; Benabid *et al.*, 1987) dans cette zone concluent à une pression anthropique plus ou moins intense sur les faciès pastoraux, et les plantations d'arbustes fourragers (IAV : Institut agronomique et vétérinaire Hassan II, 1988) pour l'amélioration sylvo-pastorale n'ont pas été poursuivies durant la période prévue de 1979 à 1990. Depuis, les potentialités des écosystèmes sylvo-pastoraux dans le Moyen Atlas sont en continuelle décroissance (Projet sylvo-pastoralisme, 1995).

Ce travail sur le cytise de Battandier, endémique marocaine (Raynaud, 1975) et arbuste fourragère très apprécié par le bétail, est le premier pour le Moyen Atlas central. Cette espèce pastorale vivace associée au cèdre dans le Moyen Atlas tabulaire (Bouri & Qarro, 1978) appartient à l'association *Argyrocytiso battandieri-Cedretum atlanticae* caractérisée par Barbero *et al.* (1981). Ce groupement

qui représente l'optimum écologique de la cédraie est relativement fréquent sur les causses (figure 1A) et les zones volcaniques du Moyen Atlas (Pujos, 1966 ; Lecompte, 1969 ; Barbero *et al.*, 1981). Selon les témoignages des populations riveraines, dans un passé récent, le cytise de Battandier constituait dans la cédraie un couvert arbustif très élevé en hauteur (7 m), surtout dans la région de Boujirt, entre Ifrane et Azrou, et la région de Seheb, entre Azrou et Aïn-Leuh (figure 1B). Ce couvert constituait dans certaines localités des broussailles denses telles que le bétail n'y accédait pas. Actuellement, suite au développement de l'élevage surtout dépendant du parcours pour satisfaire les besoins du bétail, un appauvrissement considérable du cortège sylvatique initial est facilement observable sur le terrain (Benabid *et al.*, 1987 ; Ezzahiri, 1989).

Afin d'évaluer cette action anthropique sur le cytise de Battandier et de connaître les conditions de survie de cette ressource pastorale, cette étude se propose 1) d'établir des modèles permettant d'estimer la biomasse aérienne des brins et des arbustes par des mesures indirectes non destructives et 2) d'étudier l'effet de la pression pastorale sur la production du cytise de Battandier.



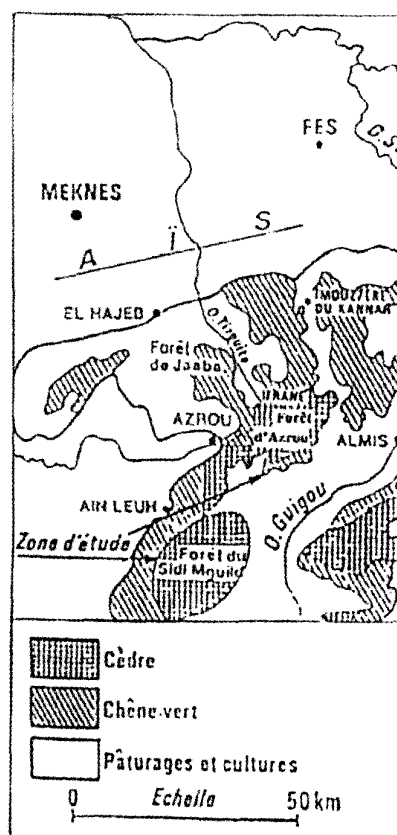
A

Figure 1A. Position géographique de la zone d'étude au Maroc, d'après Lecompte (1969).

Figure 1A. Geographic position of the study zone in Morocco, refer to Lecompte (1969).

Figure 1B. Situation des forêts d'Azrou et de Sidi M'guild dans le Moyen Atlas central au Maroc, d'après Martin *et al.* (1964) dans Martin (1977).

Figure 1B. Situation of the Azrou and Sidi M'guild forests in the central Middle Atlas in Morocco, refer to Martin *et al.* (1964) in Martin (1977).



B

MATÉRIEL ET MÉTHODES

Présentation de la zone d'étude

La zone d'étude est située dans le Moyen Atlas central (fig. 1), dans la forêt d'Azrou et la forêt de Sidi M'guild qui font partie du Moyen Atlas tabulaire. Les précipitations varient d'une station à une autre entre 1 122 et 1 497 mm/an. La couche de neige peut atteindre en janvier jusqu'à 110 cm (Qarro, 1980). Les températures moyennes minimales mensuelles varient de -5° à 2,6 °C. Les températures moyennes maximales mensuelles varient de 29,5° à 32,8 °C. Le climat est typiquement à sécheresse estivale prononcée (Daget, 1980) et l'ambiance bioclimatique subhumide ou humide à variante fraîche à froide (Emberger, 1955 ; Sauvage, 1963). Le substrat est calcaire, dolomitique ou basaltique (Martin, 1977 ; CREA : Centre régional des études et des aménagements des forêts, 1979 ; CREA, 1995a).

La végétation forestière est dominée par le cèdre de l'Atlas (*Cedrus atlantica* Manetti) sur différents substrats : cédraie presque pure sur basalte et cédraie mixte en mélange avec le chêne vert (*Quercus rotundifolia* Lamk.) en altitude (Boudy, 1950) et sur substrat carbonaté. Le chêne vert se développe aussi en peuplement pur, en futaie sur souche ou en taillis. Le chêne zeen (*Quercus canariensis* Willd.) est la troisième essence dans la forêt d'Azrou

tandis que dans la forêt de Sidi M'guild, le genévrier thurifère (*Juniperus thurifera* L.) constitue la troisième essence majeure et succède au chêne vert en haute altitude, dans des stations froides moins favorables au cèdre. D'autres essences accompagnent ces peuplements dans les deux forêts : l'érable de Montpellier (*Acer monspessulanum* L.), l'if (*Taxus baccata* L.), les aubépines (*Crataegus laciniata* Ucria, *Crataegus monogyna* Jacq.), le houx (*Ilex aquifolium* L.), le cytise de Battandier (*Argyrocytisus battandieri* Maire) et le viorne tin (*Viburnum tinus* L.).

Stratégie d'échantillonnage et taille de l'échantillon

La prospection des deux forêts, avec l'aide du Centre régional des études et des aménagements des forêts (CREA) de Meknès, a permis d'identifier 8 types de stations (tableau 1), combinaisons des quatre variables : peuplements spontanés ou plantés du cytise de Battandier, intensité de la pression pastorale, type de végétation arborée et nature du substrat (roche mère).

Dans chaque type de station ont été discriminés les peuplements de cytise de Battandier en sous-bois de ceux situés à découvert. Dans chacune des huit stations étudiées, quatre placettes carrées (correspondant à 4 répétitions) de 100 m² chacune ont été installées d'une manière aléatoire selon un dispositif en bloc.

Station*	Cytise de Battandier spontané ou planté*	Pression pastorale*	Végétation arborée*	Substrat*	Surface (ha)	Nbr d'arbustes pour mesures dendrométriques	Nbr d'arbustes pour coupe de biomasses	Nbr de brins coupés	Nbr d'arbuste par ha		
									Total	sous couvert	à découvert
90	S	PP0	C	Ba	149	149	50	157	709	581	128
44	S	PP0	B	Bd	157	31	25	144	156	0	156
116	S	PP0	B	Ca	108	35	28	134	144	0	144
35	P	PP0	C	Do	334	44	33	67	0,7	0,7	0
4	S	PP2	A	Ba	106	19	16	57	0,2	0,2	0
119	S	PP2	B	Ba	70	38	32	117	225	0	225
75	S	PP1	B	Ba	281	28	26	122	643	99	544
7	S	PP1	B	Ba	90	58	41	177	963	0	963

* Station : les numéros des stations sont extraits des cartes de description parcellaire (CREA, 1979 ; CREA, 1995b)
 Cytise de Battandier spontané : S, planté : P
 Pression pastorale intense : 2, moyenne : 1, faible : 0
 Végétation arborée : A : chêne vert + chêne zeen, B : cèdre de l'Atlas + chêne vert, C : cèdre de l'Atlas + chêne vert + chêne zeen
 Substrat : Ba : basaltique, Bd : épandages volcaniques basaltiques sur dolomie, Ca : calcaire, Do : dolomitique

Tableau 1. Caractérisation des stations d'étude et des arbustes échantillonnés.
 Table 1. Characteristics of the study sites and sampled shrubs.

Détermination de la charge animale

La charge des parcours est déterminée selon la méthode de Sarson et Salmon (1976) (cités dans Projet Parcours, 1978).

Deux types de charge animale sont déterminés :

– la charge d'équilibre déterminée en fonction de la production fourragère de toutes les ressources détectées et les besoins du cheptel. Cette charge est égale à l'effectif du bétail (UPB) pouvant pâturer par hectare sans endommager le potentiel pastoral de la zone concernée et assurant ainsi sa continuité.

– la charge réelle (CR) déterminée en fonction de la charge apparente (CA) et le temps de séjour (TS = nombre de journées de pâturage effectif) est égale à $(CA \times TS) / 365$. La charge apparente est obtenue en divisant l'effectif du bétail (UPB) observé sur terrain à un instant t , par la superficie pâturée (ha).

Pour un parcours non surchargé, la charge réelle est inférieure à la charge d'équilibre. En cas de surcharge des parcours, la charge réelle est supérieure à la charge d'équilibre.

Choix de la méthode d'étude de la biomasse

La méthode d'évaluation de la biomasse par stratification non destructive (Étienne, 1989) a été retenue. Elle est suivie d'une estimation indirecte de la biomasse à partir des régressions établies sur les brins échantillons coupés.

Les mesures des paramètres morphométriques de l'arbuste (diamètre maximum, diamètre orthogonal, hauteur maximale, nombre de brins et leur diamètre basal) et les mesures de la phytomasse aérienne totale ont été effectuées sur 251 arbustes.

Au niveau des placettes, les individus sont agencés en classes de volume. Le phytovolume ou volume d'encombrement (Étienne *et al.*, 1991) a été calculé en multipliant la surface de la projection de l'arbuste par sa hauteur maximale ou la hauteur du maître-brin selon Cabanettes (1989).

Le phytovolume de l'arbuste égal à $V = \pi R^2 h_m$, R ou rayon moyen de l'arbuste, est obtenu en faisant la moyenne arithmétique (Étienne, 1989) du diamètre maximum avec le diamètre orthogonal et en divisant cette moyenne (égale au diamètre moyen de l'arbuste) par deux.

Six classes de volume sont calculées dans chaque placette tenant compte du volume moyen (V_m) des arbustes et de l'écart-type (σ) (Ludwig *et al.*, 1975 ; Molinero, 1983) :

Classe 1 : volume $< V_m - \sigma$

Classe 2 : $V_m - \sigma < \text{volume} < V_m - (\sigma/2)$

Classe 3 : $V_m - (\sigma/2) < \text{volume} < V_m$

Classe 4 : $V_m < \text{volume} < V_m + (\sigma/2)$

Classe 5 : $V_m + (\sigma/2) < \text{volume} < V_m + \sigma$

Classe 6 : volume $> V_m + \sigma$

Trois individus au plus par classe de volume ont été choisis pour effectuer les coupes de biomasse. La représentativité vis-à-vis de la forme et de la taille de l'arbuste est ainsi intégrée (Cabral & West, 1986). Pour éviter l'abatage des individus, on a eu recours à une stratification de l'arbuste (Étienne, 1989) et seule une partie de la touffe a été échantillonnée : pour chaque souche, les différents brins ont été regroupés en strates composées chacune de brins semblables par leur diamètre basal et la densité de leur feuillage. Dans chacune des strates, deux brins au plus ont été prélevés.

La coupe est réalisée vers mi-juillet, à la fin du cycle de développement du cytise de Battandier. Les deux brins de la même classe de brins similaires sont coupés simultanément.

Détermination de la masse sèche

Les pesées sont effectuées avec une précision de 1/10 (g) près. Après avoir coupé les brins, les différentes composantes de chaque brin sont séparées et chaque composante a fait l'objet d'une étude particulière :

– brins : avec diamètre $< 1,5$ cm (bois tendre)

Ces brins sont mesurés à l'état frais et un échantillon est prélevé, pesé puis étuvé jusqu'à poids constant.

– brins : avec diamètre $> 1,5$ cm (bois dur)

Cette partie du brin est débitée en billons et pesée sur place pour déterminer le poids frais. Trois rondelles ont été prélevées à différents niveaux : à la base, à mi-longueur et à la découpe 1,5 cm (Auclair & Métayer, 1980). Celles-ci sont pesées puis mises en sachet afin d'être étuvées au laboratoire pour déterminer la masse sèche.

– feuilles : après avoir coupé les brins, les feuilles sont pesées en totalité à l'état frais. Un échantillon de 50 grammes mesuré précisément à l'aide d'une balance électrique de terrain est retenu pour séchage.

Les échantillons prélevés sur le terrain ont été placés dans une étuve jusqu'à poids constant. Les températures de séchage ont été maintenues à 105 °C pour la composante ligneuse et 70 °C pour les feuilles afin d'éviter les pertes d'azote qui se volatilise à des températures supérieures (Reidacker, 1968). La masse sèche moyenne des deux brins de la même strate de brins similaires est utilisée pour calculer la masse sèche totale

de l'arbuste dont on connaît le nombre de strates et le nombre de leurs brins.

Analyse de l'information

Estimation de la biomasse et précision des modèles

Dans la littérature forestière, il existe un grand nombre de modèles expliquant la relation entre le poids et les caractéristiques de l'arbre.

Dans cette étude, les deux catégories de modèles exprimées ci-après ont été ajustées :

— modèles polynomiaux :

$$MS_i = a_0 + a_1 p$$

$$MS_i = a_0 + a_1 p + a_2 p^2$$

$$MS_i = a_0 + a_1 p + a_2 p^2 + a_3 p^3$$

— modèles allométriques :

$$MS_i = a_0 p^{a_1}$$

où

MS : masse sèche ; i désigne la nature de l'organe : bois (B), feuilles (F) ou les deux (T)

p : paramètre dendrométrique mesurable

a_0, a_1, a_2, a_3 : coefficients de régression

Le choix du meilleur modèle a été fondé sur une analyse statistique rigoureuse, basée sur les valeurs du coefficient de détermination (r^2), de l'écart-type résiduel (σ_{res}), des tests de signification des coefficients de régression et de l'indice de Furnival (IF).

Modélisation de la biomasse des brins et des arbustes

Avant d'effectuer l'estimation de la biomasse aérienne au niveau de l'arbuste, différents modèles ont été préalablement testés sur les brins pour établir des régressions utilisant le diamètre basal comme paramètre dendrométrique.

Traitement des données et analyse des effets de la pression pastorale

L'effet de la pression pastorale ne peut être comparé qu'en conservant l'égalité entre les substrats. Pour les trois

types de substrat Bd, Ca et Do (tableau 1) la comparaison n'est pas possible puisque les trois sont à pression pastorale faible. Il faut donc limiter l'analyse au basalte (Ba) où les trois types de pression pastorale sont présentes. Par conséquent, le dispositif permettrait la réalisation de plusieurs analyses de variance pour étudier l'effet "pression de pâturage" sur substrat basaltique.

Pour ces classements établis à partir de la méthode de contraste et du test de Duncan, deux moyennes n'ayant aucune lettre commune sont significativement différentes ($P < 0,05$).

RÉSULTATS

Prédiction de la biomasse aérienne

Tarifs biomasses des brins

MSB : masse sèche du bois

MSF : masse sèche des feuilles

MST : masse sèche totale

Ces tarifs concernent respectivement le bois, les feuilles et le brin entier. Ils consistent à fournir la masse sèche de chaque composante en fonction du diamètre basal (D) du brin. L'ajustement des observations aux divers modèles et l'analyse statistique des résultats, permettent de retenir les équations consignées dans le tableau 2. Le meilleur modèle obtenu est allométrique démontré graphiquement par les résidus de la figure 2.

Tarifs biomasses des arbustes

Ces tarifs consistent à fournir la masse sèche de chaque composante en fonction des paramètres dendrométriques de l'arbuste suivants : le diamètre moyen (d_m), la hauteur maximale (h_m) et le nombre de brins (N). Les divers modèles obtenus sont représentés par les équations consignées dans les tableaux 3, 4 et 5 suivants :

Composante	Nombre de brins	Modèles	r^2	σ_{res}	IF	d	F	Résidus
Bois	975	MSB = 0,097 D ^{2,514}	0,87	0,61	0,10	1,29	6 696	Figure 2A
Feuille	975	MSF = 0,175 D ^{1,673}	0,65	0,76	0,02	1,68	1 774	Figure 2B
Total	975	MST = 0,167 D ^{2,391}	0,87	0,59	0,12	1,36	6 478	Figure 2C

r^2 : coefficient de détermination, σ_{res} : écart-type résiduel, IF : indice de Furnival, d : test de Durbin-Watson, F : test de Fisher

Tableau 2. Modèle à une seule entrée.
Table 2. One-entry model.

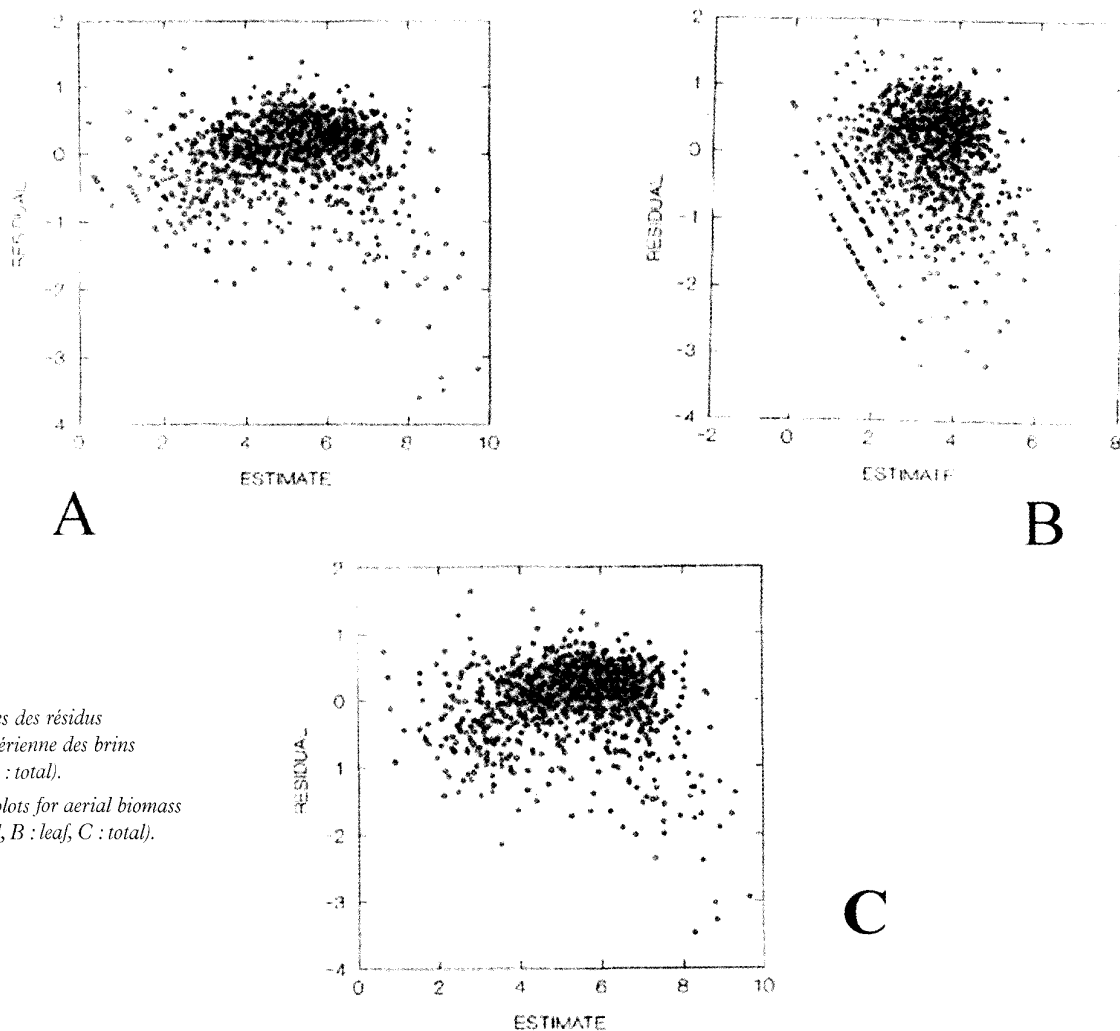


Figure 2. Graphiques des résidus pour la phytomasse aérienne des brins (A : bois, B : feuille, C : total).

Figure 2. Residual plots for aerial biomass of the stems (A : wood, B : leaf, C : total).

Composante	Nombre d'individus	Modèles	r ²	σ _{xx}	IF	d	F
Bois	251	MSB = 0,422 d _m ^{2,268}	0,85	0,71	0,68	2,06	1487
Feuille	251	MSF = 0,026 + 0,063 d _m ²	0,61	0,22	0,22	2,02	393
Total	251	MST = 0,5 d _m ^{2,206}	0,85	0,71	0,80	2,09	1429

Tableau 3. Modèle à une seule entrée.
Table 3. One-entry model.

Composante	Nombre d'individus	Modèles	r ²	σ _{xx}	IF	d	F
Bois	251	MSB = 0,276 d _m ^{1,734} h _m ^{0,847}	0,88	0,66	0,63	2,10	902
Feuille	251	MSF = 0,06 d _m ^{1,55} h _m ^{0,338}	0,76	0,73	0,11	2,24	387
Total	251	MST = 0,338 d _m ^{1,717} h _m ^{0,776}	0,87	0,66	0,75	2,14	841

Tableau 4. Modèle à deux entrées.
Table 4. Two-entry model.

À l'exception du modèle polynomial concernant la composante foliaire pour le modèle à une seule entrée (tableau 3), tous les autres sont allométriques. Pour la biomasse foliaire arbustive, le coefficient de détermination (r^2) est inférieur à celui des biomasses ligneuse et totale. Les équations retenues pour les tarifs biomasses sont meilleures pour le modèle à 3 entrées (tableau 5, figure 3), qui explique jusqu'à concurrence de 90 % de la variabilité pour le bois et 83 % pour les feuilles.

Production moyenne en biomasse

L'application des tarifs de biomasses individuels à l'ensemble des arbustes de toutes les placettes, permet de déterminer la biomasse sèche par placette. La biomasse sèche à l'hectare est obtenue par une extrapolation linéaire des résultats obtenus par placette. Dans chaque placette, la phytomasse aérienne de chaque arbuste est calculée à partir des tarifs de biomasses. La phytomasse moyenne

Composante	Nombre d'individus	Modèles	r^2	σ_{ϵ}	IF	d	F	Résidus
Bois	251	MSB=0,14 $d_m^{1,224} h_m^{1,088} N^{0,449}$	0,90	0,59	0,56	2,03	777	Figure 3A
Feuille	251	MSF=0,024 $d_m^{0,88} h_m^{0,653} N^{0,588}$	0,83	0,62	0,09	2,38	395	Figure 3B
Total	251	MST=0,167 $d_m^{1,183} h_m^{1,029} N^{0,470}$	0,90	0,58	0,66	2,09	745,00	Figure 3C

Tableau 5. Modèle à trois entrées.
Table 5. Three-entry model.

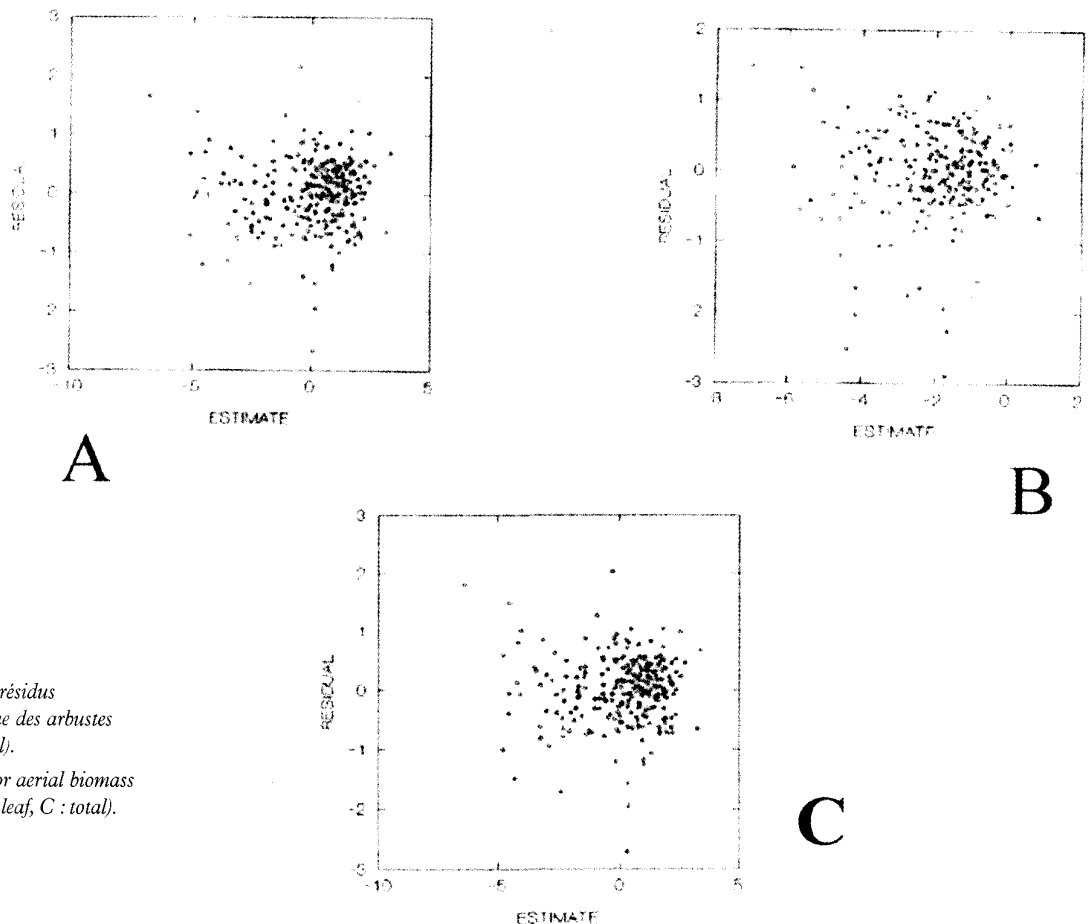


Figure 3. Graphiques des résidus pour la phytomasse aérienne des arbustes (A : bois, B : feuille, C : total).

Figure 3. Residual plots for aerial biomass of the shrubs (A : wood, B : leaf, C : total).

de la placette est ensuite obtenue. Pour les 32 placettes des 8 stations étudiées la valeur moyenne de la phytomasse est calculée. Cette dernière correspondant à la superficie d'une placette (100 m²) est ensuite rapportée à l'hectare.

Ainsi, la production moyenne en biomasse du cytise de Battandier dans le Moyen Atlas tabulaire marocain est de l'ordre de 2196 kg de matière sèche (MS) à l'hectare. Par catégorie de composante aérienne, la masse sèche moyenne du bois est de 1979 kg/ha, celle des feuilles de 217 kg/ha.

Effets de la pression pastorale sur la biomasse aérienne du cytise de Battandier

La charge animale correspondant à un pâturage d'équilibre dans la zone étudiée nous a été communiquée par le Centre régional des études et des aménagements des forêts (CREA, 1995a) de Meknès. Cette charge est de 1,42 Unité Petit Bétail par hectare (UPB/ha). Toute charge

supérieure à ce seuil correspond à une pression pastorale intense (notée PP2). Toute charge inférieure à ce seuil correspond à une pression pastorale moyenne (PP1). Dans les sites protégés, la pression pastorale est faible (PP0) à cause des pâturages occasionnels et non autorisés réalisés par les bergers qui amènent leurs troupeaux dans ces endroits, surtout en période de disette. Durant cette saison, la maîtrise du pâturage est délicate à réaliser. Les biomasses correspondant à ces différentes intensités pastorales sont mentionnées dans la deuxième partie du tableau 6.

Dans les sites à pression pastorale moyenne, la biomasse du cytise de Battandier est plus élevée (mais non significativement) que celle des stations à pression pastorale faible. Dans les sites à pression pastorale intense, la biomasse est plus faible que celle des stations à pression pastorale faible.

Sous pression pastorale intense, la biomasse du cytise de Battandier est significativement ($P < 0,05$) plus faible que celle des stations à pressions pastorales faible et moyenne.

Station*	Pression pastorale	Végétation arborée	Substrat	Nbr d'arbustes échantillonnés	Phytomasse* (kg MS/ha)				
					Total	foliaire	total du bois	bois dur	bois tendre
75 + 7	PP1	B	Ba	26 + 41	2 785 A	277 A	2 508 A	1 746 A	762 A
90	PP0	C	Ba	50	1 988 A	174 A	1 814 A	1 122 AC	692 A
4 + 119	PP2	A + B	Ba	16 + 32	488 B	45 B	443 B	319 BC	124 B

* Deux moyennes n'ayant aucune lettre commune sont significativement différentes ($P < 0,05$)

Tableau 6. Phytomasses de feuilles et de bois (dur et tendre) en fonction de la pression pastorale.
Table 6. Biomass of leaves and of wood (soft and hard) as influenced by grazing pressure.

DISCUSSION

Modélisation de la biomasse aérienne

L'introduction dans le modèle à une seule entrée, de l'estimateur "diamètre moyen" de l'arbuste n'amène pas à une meilleure estimation. Le diamètre moyen de l'arbuste est une dimension "synthétique" introduite après les tentatives d'estimation d'Uresk *et al.* (1977) à partir du diamètre maximum de l'arbuste et celles de Kittredge (1945), Medin (1960) et Rittenhouse & Sneva (1977) à partir du grand diamètre et du petit diamètre.

Cabanettes (1989) qualifiant le paramètre "diamètre moyen" d'estimateur représentant la dimension latérale pour l'estimation de la biomasse ligneuse aérienne dans les jeunes taillis, trouve que l'utilisation de cette variable explicative seule dans son modèle n'aboutit pas comme dans notre cas à une bonne estimation.

Le modèle incorporant les deux estimateurs "diamètre moyen et hauteur maximale" de l'arbuste nous a permis d'améliorer l'estimation comme celle de Frandsen (1983) et de Cabanettes (1989). En effet, le paramètre "hauteur" utilisé seul (Fitzgerald, 1983) fournit des estimations de biomasse bonnes mais qui restent insuffisantes. Haase & Haase (1995) pour estimer la biomasse aérienne arbustive

de quelques espèces au Brésil, aboutissent en combinant les deux estimateurs "diamètre et hauteur" à un modèle allométrique comme celui de nos équations à deux entrées.

À l'aide de notre modèle allométrique à trois entrées, introduisant dans les équations un troisième paramètre dimensionnel, le "nombre de brins" constituant la touffe de l'arbuste, nous améliorons d'avantage l'estimation de la biomasse, surtout pour la biomasse foliaire ($r^2 = 83,0\%$) qui reste meilleure que celle estimée par les modèles de Haase & Haase ($r^2 = 76,2\%$).

Dans nos trois modèles et comme ceux des derniers auteurs, l'estimation de la biomasse ligneuse et totale est dans tous les cas meilleure que celle de la biomasse foliaire.

La biomasse aérienne (2,2 t/ha) du cytise de Battandier soumis au climat méditerranéen dans le Moyen

Atlas, comparée aux valeurs de biomasses obtenues sur des légumineuses arbustives se développant sous le même type de climat dans d'autres écosystèmes méditerranéens (tableau 7), est faible, bien que ces écosystèmes présentent déjà des valeurs peu élevées. En effet, selon Étienne *et al.* (1991), le faciès à cytise triflore étudié est à faible phytomasse (2,7 t/ha), et les maquis à cytise et à calycotome constituent un groupe à faible indice de phytomasse (Baudin, 1985). Un impact intensif sur les peuplements à cytise accélérerait ainsi leur dégradation, car vis-à-vis de la vitesse d'accumulation de biomasse, ces peuplements démarrent très vite la première année puis diminuent leur vitesse de production progressivement (Rousseau & Loiseau, 1982 ; Étienne *et al.*, 1991).

Auteurs	Légumineuse arbustive	Site	Age (ans)	Biomasse aérienne (t/ha)
Hamrouni, 1983	<i>Acacia cyanophylla</i>	Tunisie	3	5,5
Etienne <i>et al.</i> , 1991	<i>Cytisus triflorus</i>	Massif de l'Esterel	2	2,7
Etienne <i>et al.</i> , 1991	<i>Calycotome spinosa</i>	Massif de l'Esterel	3	2,7

Tableau 7. Biomasse aérienne de quelques légumineuses arbustives.
Table 7. Aerial biomass of some legume shrubs.

Effet de la pression pastorale sur la biomasse aérienne du cytise de Battandier

Dans les sites à pression pastorale faible, la phytomasse du cytise de Battandier est inférieure à celle des stations à pression pastorale moyenne. L'application de la mise en défens pour une régénération efficace est par conséquent délicate car elle requiert une connaissance précise de la dynamique de la végétation que l'on veut transformer (Le Houérou, 1980).

Dans les sites à pression pastorale faible, la biomasse est supérieure à celle des parcelles à pression pastorale intense. Le Moyen Atlas représente un refuge pour les troupeaux pendant la période estivale (Ezzahiri, 1989). La plupart des espèces ligneuses méditerranéennes sont consommées par le bétail ; le cytise est parmi les espèces particulièrement appréciées (Bourbouze, 1980 ; Le Houérou, 1980). Dans les zones protégées et suite au pâturage occasionnel ou accidentel, le bétail consomme sans modération le cytise au cours de la période estivale.

La pression pastorale moyenne n'est pas destructrice pour le cytise de Battandier ; elle favorise la production du cytise, sans gêner sa régénération. La pression pastorale intense a un effet dépressif sur la biomasse du cytise de Battandier.

CONCLUSION

La biomasse épigée du cytise de Battandier du Moyen Atlas tabulaire marocain a été appréhendée à partir de données dendrométriques et pondérales de 251 arbustes. Sur la base de ces données, des régressions simples et multiples ont été développées pour estimer la biomasse ligneuse et foliaire de cet arbuste.

De ces analyses il ressort que :

- l'estimation des biomasses sèches des brins peut être réalisée à partir de leur diamètre à la souche.
- la combinaison entre le nombre de brins, la hauteur maximale et le diamètre moyen de l'arbuste, constitue le meilleur estimateur des biomasses sèches.

– les modèles allométriques sont ceux qui s'ajustent le mieux aux données de biomasses des brins et des arbustes.

– la production totale estimée d'*Argyrocytisus battandieri* est de 2,2 tonnes à l'hectare, répartie à raison de 2,0 t/ha de biomasse de bois et 0,2 t/ha de biomasse de feuilles.

Comme outil d'aide à un aménagement sylvo-pastoral plus étendu, notre modèle est ainsi conçu pour un domaine d'application plus vaste non limité à une végétation stationnelle. En effet, il a été établi à partir d'un échantillonnage plus important qui tient compte à la fois de toute la gamme potentielle de volumes d'arbustes que l'on rencontre habituellement dans nos peuplements forestiers de cytise de Battandier, ainsi que de la diversité de leurs conditions de croissance.

La pression pastorale intense contribue à la destruction de l'arbuste. La forte dégradation du peuplement du cytise de Battandier est essentiellement due au surpâturage et à la surexploitation de cet arbuste par la population en réponse aux besoins des troupeaux, et dans une moindre mesure aux conditions climatiques aléatoires.

Devant cette situation alarmante, les recommandations ci-dessous s'imposent d'urgence pour la gestion conservatoire de cet écosystème sylvo-pastoral :

– diminuer la charge pastorale en forêt dans les stations à parcours intensif, en réduisant le nombre de têtes du bétail au profit d'un revenu compensatoire (développement de l'artisanat,...) ;

– réorganiser le parcours en laissant un accès contrôlé aux secteurs actuellement protégés afin de diminuer la pression sur les secteurs fortement pâturés ;

– créer des prairies artificielles dans les zones dépourvues de formations forestières basses ;

– semer d'une manière intensive le cytise de Battandier avec des graines scarifiées ou abrasées, sur substrat volcanique basaltique dans les stations à forte dégradation de l'arbuste. La protection et le suivi des arbustes après semis doivent être réalisés au moins pour une période de 10 ans.

Toutefois, ces recommandations, comme les autres, ne peuvent aboutir que s'il y a mise en place des bases d'un système d'entente social s'appuyant sur l'encadrement et l'organisation des éleveurs pour une utilisation commune de l'espace pastoral. L'aboutissement de cet aménagement sylvo-pastoral reste conditionné par l'adhésion des éleveurs au principe organisationnel et par la mobilisation de l'ensemble des acteurs concernés par le développement des forêts et de l'élevage.

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Fast regeneration of the tussock grass *Ampelodesmos mauritanica* after clearing

Régénération rapide de la graminée *Ampelodesmos mauritanica* après débroussaillage

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Résumé

Les perturbations par débroussaillage sont une pratique commune dans les formations arbustives méditerranéennes du nord-est de l'Espagne comme technique de prévention contre les incendies afin de réduire la quantité de combustible disponible. Dans cette étude, nous avons comparé la régénération de communautés végétales dominées par des graminées dans des placettes débroussaillées voisines de placettes non débroussaillées. Nous nous sommes particulièrement intéressés à la réponse de la graminée pérenne couvrante *Ampelodesmos mauritanica* dans des placettes débroussaillées depuis 6 mois (récemment débroussaillée), depuis 2 ans (débroussaillée une fois) et dans une placette âgée d'une année mais débroussaillée pendant deux années consécutives (débroussaillée deux fois). Les placettes débroussaillées ont retrouvé rapidement leur couverture végétale après le débroussaillage en liaison avec la dominance dans la communauté d'espèces qui rejettent à partir d'organes souterrains suite à la perturbation. La richesse spécifique n'est pas significativement différente entre les placettes débroussaillées et les placettes non débroussaillées adjacentes. De même, le recouvrement végétal total est plus faible dans les placettes récemment débroussaillées par rapport aux placettes adjacentes non débroussaillées, mais il n'y a pas de différence significative entre les placettes débroussaillées une fois et deux fois. Les individus d'*Ampelodesmos mauritanica* tondu ont de nombreux rejets survivants et vigoureux après le débroussaillage. Bien que dans les placettes débroussaillées, les individus d'*Ampelodesmos mauritanica* soient plus petits que dans les placettes adjacentes non débroussaillées, le recouvrement végétal n'y est pas significativement différent. La reprise des plantules est supérieure dans les placettes récemment débroussaillées par rapport aux placettes non débroussaillées adjacentes. Nos résultats suggèrent donc que le débroussaillage n'est pas vraiment un outil de gestion efficace pour réduire l'abondance d'*Ampelodesmos mauritanica*. Il n'est donc pas une technique de prévention efficace contre le feu parce que cette graminée dominante ne montre pas de mortalité après le débroussaillage et accumule du combustible très rapidement après la destruction de sa biomasse épigée.

Abstract

Disturbance by clearing is common in Mediterranean shrublands of NE Spain as a fire prevention technique to reduce fuel loads. We compared the regeneration of the vegetation in grass-dominated communities in cleared stands with adjacent non-cleared stands. We especially focussed on the response of the expansive perennial grass *Ampelodesmos mauritanica* in a 6 month (recently cleared), two year old (once cleared) stands and in a one-year-old stand cleared in two consecutive years (twice cleared). Cleared plots recovered quickly from clearing due to the dominance in the community of species that resprout from belowground organs after disturbance. The number of species was not significantly different between cleared and adjacent non-cleared plots. Total plant cover was lower in recently cleared plots than in adjacent non-cleared plots, but not significantly different in once and twice cleared plots. Clipped *Ampelodesmos mauritanica* plants had high survival and vigorous resprouting after clearing. Although in cleared plots *Ampelodesmos mauritanica* plants were smaller than in adjacent non-cleared plots, cover was not significantly different. Seedling recruitment was higher in recently cleared plots than in adjacent non-cleared plots. Our results suggest that clearing is not a very effective management tool for reducing *Ampelodesmos mauritanica* abundance and as a fire-prevention technique because this dominant grass shows no mortality after clearing and accumulates fuel loads very fast after aboveground biomass removal.

Key-words

Disturbance, fire prevention, grass expansion, Mediterranean vegetation, resprouting, seedling establishment.

Mots-clés

Perturbation, prévention contre l'incendie, extension des graminées, végétation méditerranéenne, rejets, installation des plantules.

INTRODUCTION

Beside wildfires, Mediterranean Basin plant communities are subjected to other man-induced disturbances such as clearing and selective thinning for increasing tree wood productivity or for fire prevention (Rico *et al.*, 1981). These disturbances are, more frequent and usually restricted to smaller patch sizes than fire, and thus may have different effects on community structure and dynamics (Malanson, 1984). However, despite the great amount of information regarding resprouting and seeding regeneration of Mediterranean species after fire (Trabaud, 1981; 1994), few studies have addressed these regeneration mechanisms after aerial biomass removal by clearing. Some studies have described patterns of regeneration in communities dominated by shrub or woody species (Retana *et al.*, 1991; Giovannini *et al.*, 1992; Perevolotsky & Haimov, 1992; Herrera, 1997; Lloret & Vilà, 1997; Riba, 1997), but there is no information on regeneration after clearing in stands dominated by grass species.

In Spain, prevention of fire risk is one of the main goals to avoid catastrophic wildfires with large ecologic and ecologic costs (ICONA, 1988). Preventive techniques are mostly designed to decrease fuel loads and highly flammable species while enhancing protected species performance. In Catalonia (NE Spain) there is a great investment to prevent fire risk by manual or mechanical clearing of the vegetation in selected areas such as belts beside roads and tracks, below power lines or next to urbanized areas (Rico *et al.*, 1981; Terradas, 1996). Although this technique is fairly expensive (900 € = 1500 US\$ per ha approximately) depending on the method used, vegetation density and ground heterogeneity, (TRAGSA, pers. com.) few studies have investigated vegetation responses after clearing in order to quantify the effectiveness of this fire prevention technique to build belts of low fire risk.

Ampelodesmos mauritanica is a perennial tussock grass that has been suggested to be expanding (sensu Pyšek, 1995) in coastal shrubland communities of northeastern Spain (ORCA, 1985) and the Balearic Islands (Castelló & Mayol, 1987). In Mallorca it forms extensive and thick tall prairies known as “carritxeres” which are believed to be favoured by repeated fire (Castelló & Mayol, 1987). Managers are interested in reducing dominance of *A. mauritanica* for two reasons: 1) because of its high flammability due to its high accumulation of fuel loads and standing dead material (Vilà *et al.*, 2001), and 2) because stands dominated by this grass have low plant species diversity perhaps due to the inhibitory effects of the grass

on the recruitment of other species (Castelló & Mayol, 1987). In this study we investigate the effect of mechanical clearing on vegetation regeneration of communities dominated by *A. mauritanica* by comparing cleared stands with adjacent non-cleared stands in a protected area south of Barcelona (Spain). The main objective was to determine if clearing is effective in controlling *A. mauritanica* abundance and reducing fire risk.

METHODS

Study species and study sites

Ampelodesmos mauritanica (Poiret) T. Durand et Schinz (Poaceae) is a large, C₃, tussock grass patchily distributed in coastal, usually karstic areas of the western Mediterranean Basin, eastwards to western Greece. Plants may attain 100 cm in diameter and produce up to 25 large inflorescences at the top of 2-3.5 m high reproductive stalks during the spring (Bolòs *et al.*, 1990). Seeds are wind dispersed in late summer and fall. *Ampelodesmos mauritanica* (*Ampelodesmos* hereafter) vigorously regrows after aerial biomass removal from rhizomes situated at the crown. *Ampelodesmos* could have been introduced in Catalonia and could have been introduced from the Balearic Islands in the XVIII century as horse fodder (Montserrat, 1989). *Ampelodesmos* may be expanding in Catalonia (ORCA, 1985) and Mallorca due to its fast regeneration after fire (Castelló & Mayol, 1987; Salvador, 1987; Vilà *et al.*, 2000).

The study site was at the Garraf Natural Park (Garraf hereafter) located about 30 Km south of Barcelona. The area (almost 10000 ha) is a karstic massif ranging from sea level to 600 m altitude. The climate is typically Mediterranean. At the nearest weather station (Viladecans), mean annual rainfall is 550 mm, with a pronounced summer drought. Mean annual temperature is 17 °C. Mean maximum and minimum temperatures are reached in July (28 °C) and January (0.5 °C), respectively. Wildfires deliberately and undeliverately produced by man are frequent in Garraf (Papió 1994). The survey was conducted in a 4800 ha area that had been burned in July 1982 and again in April 1994.

In this area a vegetation management program conducted by park managers was started two years after the 1994 fire with the goal of reducing fuel loads in belts along track and roadsides. Mechanical selective clearing of the aboveground biomass except for protected (e.g. *Chamaerops*

humilis), slow growing (e.g. *Juniperus oxycedrus*) and low flammable (e.g. *Arbutus unedo*) species was conducted in three sites at different times. In fall 1996 a 4.8 km long belt ("once cleared") and an 8.3 km long belt were cleared. In fall 1997 the 8.3 km long belt was cleared again ("twice cleared"). In spring 1998 a new 2.8 km long belt was cleared at another site ("recently cleared"). On average, the belts were 20 m wide. Minimum and maximum distance between cleared belts were 1 and 4 km. There are no records of stands cleared in Garraf before 1996.

Field survey

From September to November 1998 a survey was conducted to compare vegetation structure in the 3 cleared and adjacent control stands. We mainly focussed on *Ampelodesmos* regeneration. Twenty randomised paired plots that were at least 100 m apart were selected along each cleared belt. Each paired plot consisted of a 10 x 5 m plot in the cleared belt and a 10 x 5 m plot in the adjacent non-cleared area (control plot). Cleared plots were placed 5 m from the adjacent cleared stand to avoid edge effects. This distance would be enough taking into account the size and density of the species. Aerial photographs from 1994 show that canopy structure was similar in the cleared belts as compared to the adjacent non-cleared areas before the treatments.

Vegetation cover of perennial species in each plot was estimated by the point intercept sampling procedure by detecting the presence of species every 0.5 m along the four sides of the plot quadrat. Thus, in each stand a total of 60 points were used to estimate plant cover. The number of perennial species within the plot was also counted.

All regrowing and non-regrowing *Ampelodesmos* plants per plot were counted and the number of plants with reproductive stalks was noted. The percentage of *Ampelodesmos* mortality after clearing was estimated by counting clipped rhizomes that had not regrown. The size of *Ampelodesmos* plants was estimated as the cylinder volume calculated from the height of the plant vegetative part and the crown area calculated from the mean value of the longest canopy diameter and the perpendicular to it. Previous allometric analysis (Vilà *et al.*, 2001) demonstrated that the cylinder volume (V) of the plant was a good prediction of plant aerial biomass (W) ($\ln W = -5.67 + 828 \ln V$, $r^2 = 0.914$, $n = 51$). Because of the small size of seedlings (less than 2 cm in height) and because they tend to be more numerous than mature plants, seedling abundance was recorded in three 40 x 40 cm subplots randomly selected within each plot.

Statistical analysis

We compared differences between cleared and control plots within a site in species richness (number of species per plot), species cover, average *Ampelodesmos* volume and height, percentage of reproductive *Ampelodesmos* plants and *Ampelodesmos* seedling density (averaged among the three subplots within each plot) by paired t-tests. Data were $\log(x + 1)$ transformed before analysis to normalize data. We could not compare differences among clearing treatments because they were not randomly assigned among areas.

RESULTS

Species richness per plot ranged from 4 to 12 species (average 6 or 7 species per plot). There was no significant effect of clearing on species richness (once cleared: t-value = -0.55, $p = 0.59$; twice cleared: t-value = 1.21, $p = 0.24$; recently cleared: t-value = 0.65, $p = 0.53$).

Total plant cover was not significantly different between cleared and control plots except in recently cleared plots where cleared plots had significantly lower cover than controls (table 1). In recently cleared plots, only *Rosmarinus officinalis*, *Ulex parviflorus* and *Globularia alypum* had significantly lower cover than in adjacent control plots. In twice cleared plots, only *Erica multiflora* cover was lower than in adjacent control plots (table 1).

All clipped *Ampelodesmos* plant survived. All of the 769 *Ampelodesmos* plants measured that had been cleared resprouted quickly. *Ampelodesmos* were significantly larger (fig. 1A) and taller (fig. 1B) in control plots than in cleared plots. However, *Ampelodesmos* cover was not significantly different between control and cleared plots (table 1). All cleared plots had lower percentage of reproductive *Ampelodesmos* plants than in adjacent control plots (fig. 1C). However, density of seedlings was higher in recently cleared plots than in adjacent control plots (fig. 1D).

DISCUSSION

All the studied species that resprout after fire in Mediterranean garrigues (Trabaud & Lepart, 1980) were also found to resprout after clearing. Six months after clearing the vegetation in our study site already covered 65 %

Species	Once cleared	Control	t-value (p)
<i>Ampelodesmos mauritanica</i> (R)	41.17 ± 4.57	35.86 ± 3.87	1.45 (0.16)
<i>Quercus coccifera</i> (R)	38.75 ± 3.55	36.58 ± 3.58	0.73 (0.47)
<i>Pistacia lentiscus</i> (R)	4.10 ± 0.77	3.75 ± 0.70	0.40 (0.69)
<i>Coronilla minima</i>	6.00 ± 2.07	5.42 ± 1.58	1.42 (0.59)
<i>Brachypodium retusum</i> (R)	15.58 ± 2.60	14.00 ± 2.65	0.56 (0.58)
<i>Erica multiflora</i> (R)	1.25 ± 0.34	5.47 ± 1.77	2.10 (0.08)
<i>Phillyrea latifolia</i> (R)	1.58 ± 1.06	0.17 ± 0.17	1.31 (0.21)
<i>Cistus albidus</i>	1.33 ± 0.71	0.17 ± 0.17	1.56 (0.13)
<i>Cistus salvifolius</i>	0.67 ± 0.28	1.08 ± 0.49	1.04 (0.31)
<i>Globularia alypum</i> (R)	3.66 ± 2.55	0.50 ± 0.34	1.24 (0.23)
Total	98.83 ± 5.15	92.25 ± 2.77	1.26 (0.22)

Species	Twice cleared	Control	t-value (p)
<i>Ampelodesmos mauritanica</i> (R)	16.50 ± 2.52	22.08 ± 2.85	1.66 (0.11)
<i>Quercus coccifera</i> (R)	20.17 ± 5.14	20.50 ± 4.45	0.09 (0.92)
<i>Pistacia lentiscus</i> (R)	6.50 ± 1.24	7.50 ± 1.30	0.61 (0.55)
<i>Coronilla minima</i>	1.43 ± 0.59	0.57 ± 0.41	1.16 (0.26)
<i>Brachypodium retusum</i> (R)	25.67 ± 4.97	26.25 ± 5.22	0.14 (0.89)
<i>Erica multiflora</i> (R)	0.42 ± 0.34	1.00 ± 0.39	2.33 (0.03)
<i>Phillyrea latifolia</i> (R)	1.17 ± 0.63	11.00 ± 0.42	0.33 (0.75)
<i>Cistus albidus</i>	1.00 ± 0.49	1.92 ± 0.91	0.38 (0.71)
<i>Cistus salvifolius</i>	1.92 ± 1.12	0.80 ± 0.68	1.05 (0.31)
<i>Globularia alypum</i> (R)	3.83 ± 0.41	3.83 ± 2.20	0.18 (0.86)
Total	86.08 ± 6.81	93.08 ± 6.05	0.79 (0.44)

Species	Recently cleared	Control	t-value (p)
<i>Ampelodesmos mauritanica</i> (R)	7.84 ± 1.83	11.74 ± 3.24	0.32 (0.75)
<i>Quercus coccifera</i> (R)	12.17 ± 2.73	17.75 ± 4.8	1.30 (0.18)
<i>Pistacia lentiscus</i> (R)	4.42 ± 1.34	4.58 ± 1	0.14 (0.89)
<i>Coronilla minima</i>	6.58 ± 1.05	4.67 ± 0.97	1.39 (0.18)
<i>Brachypodium retusum</i> (R)	21.5 ± 3.25	16.58 ± 2.21	1.47 (0.16)
<i>Erica multiflora</i> (R)	2.25 ± 0.73	3.75 ± 1.19	1.48 (0.13)
<i>Phillyrea latifolia</i> (R)	1.25 ± 0.58	2.50 ± 1.15	1.56 (0.13)
<i>Rosmarinus officinalis</i>	0	6.33 ± 1.73	3.07 (0.006)
<i>Ulex parviflorus</i>	0	4.02 ± 0.9	2.13 (0.05)
<i>Globularia alypum</i> (R)	2.08 ± 0.63	4.75 ± 1.19	2.75 (0.02)
Total	65.33 ± 2.59	86.83 ± 5.03	3.95 (0.0009)

Table 1. Plant cover of the 10 most dominant species in cleared and adjacent non-cleared plots. (R = species that resprout from belowground structures).

of the soil surface with *Ampelodesmos*, *Quercus coccifera* and *Brachypodium retusum* as the dominant species, just as in control plots. *Quercus coccifera* sprouted vigorously from stolons after clearing as it does after fire (Malanson & Trabaud, 1988). However, most species (e.g. *Pistacia lentiscus*, *Erica multiflora*, *Globularia alypum*) resprouted from

a well-formed burl or the root system that stores nutrient resources and a bud bank (James, 1984). Differences in plant cover between recently cleared plots and control plots were due to mortality of non-resprouting species (e.g. *Rosmarinus officinalis*, *Ulex parviflorus*) that rely on their seed bank for regeneration after disturbance.

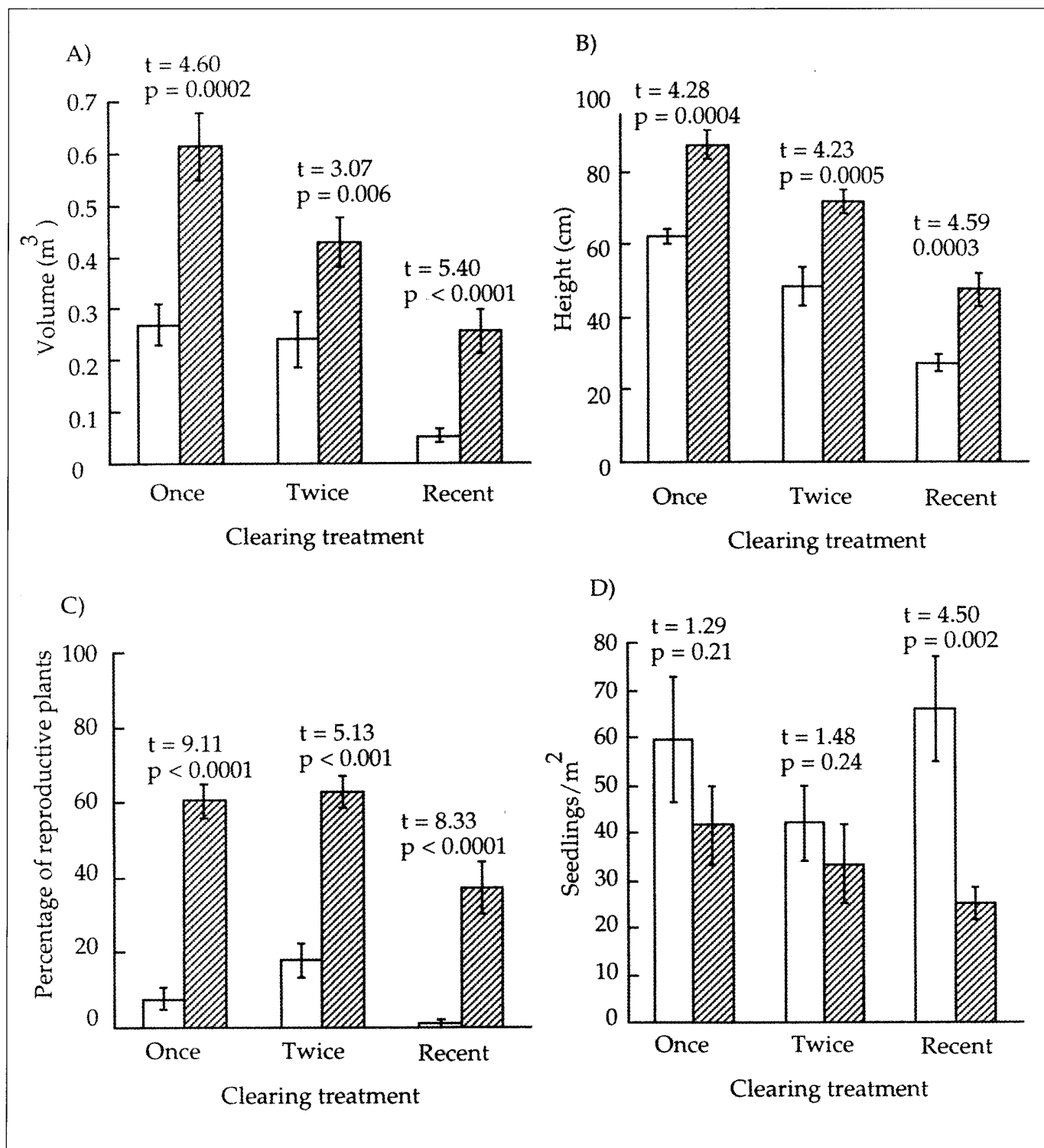


Figure 1. *Ampelodesmos mauritanica* volume (A), height per plant (B), percentage of reproductive plants (C) and seedling density (D) in cleared (open bars) and in adjacent control (shaded bars) plots in Garraf. Results of paired t-test comparisons are indicated (n = 20).

As for resprouting species, the grass *Ampelodesmos* displayed a spectacular response to clearing. New tillers were quickly formed from tussocks contributing to plant survival. *Ampelodesmos* resprouting is also very vigorous after fire (Vilà *et al.*, 2001). Fast regrowth of perennial grasses regardless of the cause of disturbance has been described in species subjected to fire, clearing and herbivory (Westoby, 1980; Caldwell *et al.*, 1981; Van der Toorn & Mook, 1982). Regrowth of tillers is stimulated by intrinsic factors (hormonal stimulation after release from apical dominance inhibition) and also by the temporary decrease of competition by neighbors after clearing. The positive response of *Ampelodesmos* to clearing matches other studies conducted in temperate grasslands (Malanson, 1984; Mueggler, 1972). For example, *Agropyron spicatum* recovered from the adverse effects of clipping if neighbors were also clipped (Mueggler, 1972). Similarly, defoliated *Andropogon gerardii* plants had higher leaf biomass under reduced competition than plants in full competition conditions (Archer & Detling, 1984).

Ampelodesmos plants produced seeds fast, too. Plants produced reproductive stalks one year after aboveground biomass removal and seedling recruitment was stimulated shortly after clearing. *Ampelodesmos* seedling recruitment was higher in recently cleared plots than in adjacent control plots. Since very few 6 month-old *Ampelodesmos* plants produced reproductive stalks but seedling recruitment was very high, two causes could explain this pattern. After clearing seeds from the seed bank could be stimulated or seedling mortality could be reduced due to vegetation and litter removal. Open areas could have more seedlings because plant competition is reduced when vegetation is removed or absent (Herrera, 1997; Vilà & Lloret, 2000). Several studies have also demonstrated that litter reduces seed germination and seedling establishment (Xiong & Nilsson, 1999). The removal of *Ampelodesmos* implies the removal of a large amount of standing dead material that can interfere with seedling recruitment. Both hypothesis seems plausible.

In the last three decades the study of regeneration of Mediterranean sclerophyllous shrublands has concentrated on the regeneration of woody species after fire (Naveh, 1974; Trabaud, 1981; 1994). However, clearing is also a very common disturbance especially in NE Spain and SE France that deserves further research. Land abandonment in this region has caused an increase in vegetation cover that increases fire risk (Debusche *et al.*, 1999). From the management point of view, clearing is not a very effective management tool for fire-prevention in the studied vegetation type because *Ampelodesmos* is very dominant, and shows no mortality after clearing; this grass is one of

most flammable species in the community (Vilà *et al.*, 2001) and accumulates fuel loads very fast after aboveground biomass removal.

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Numerical revision of syntaxonomy and ecological characteristics of vegetation on gypsum substrates in Spain (C. and SE.)

Révision syntaxonomique numérique et caractéristiques écologiques de la végétation gypsophile de l'Espagne (C. et SE.)

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Abstract

Scrub vegetation growing on gypsiferous soils of the sedimentary watersheds in the central and southeast regions of the Iberian Peninsula constitutes discontinuous plant formations with both common and differential species. A syntaxonomic revision at the alliance and suballiance level is conducted according to the new groupings and the differential species extracted from TWINSPAN analysis. Order Gypsophiletalia includes both Thymo-Teucrion verticillati, characterising the Alicantino and Murciano Sectors of the Murciano-Almeriense biogeographic province and Lepidion subulati alliances. The largest floristic and ecological diversity of latter alliance allows for the establishment of three suballiances: Lepidienion subulati, in the Castellano-Maestrazgo-Manchega province, Sector Manchego, Gypsophilo-Santolinenion viscosae in both the Bética and Murciano-Almeriense provinces and Gypsophilenion hispanicae in the Valenciano-Catalano-Provenzal province, Sector Setabense. Floristic affinities between biogeographical provinces and their relationships with bioclimatic and edaphic factors are established.

Key-words

Phytosociology, Gypsaceous scrubland, TWINSPAN, Edaphic factors, Biogeography, Bioclimatic factors; Spain.

Résumé

La végétation gypseuse, dans la péninsule ibérique est irrégulièrement distribuée dans toute sa moitié orientale.

Une révision phytosociologique a été réalisée moyennant l'application de méthodes numériques (TWINSPAN, ACP). Nous établis-

sons des modifications syntaxonomiques au niveau des alliances et suballiances, et les relations de celles-ci avec les unités biogéographiques et les facteurs tant climatiques qu'édaphiques plus significatifs. Après la modification syntaxonomique on propose l'alliance Thymo-Teucrion verticillati dans le domaine de la province biogéographique Murciano-Almeriense (secteurs Alicantino et Murciano). D'ailleurs l'alliance Lepidion subulati présente une diversité floristique et écologique plus grande pour laquelle on propose trois suballiances: Lepidienion subulati, dans la province Castellano-Maestrazgo-Manchega, (Secteur Manchego); Gypsophilo-Santolinenion viscosae dans les provinces Bética et Murciano-Almeriense et Gypsophilenion hispanicae dans la province Valenciano-Catalano-Provençal, (Secteur Setabense).

De même, on a établi les affinités floristiques parmi les différents unités biogéographiques.

Mots-clés

Phytosociologie, matorrals gypsicoles, TWINSPAN, facteurs édaphiques, biogéographie, facteurs bioclimatiques, Espagne.

Nomenclature

Flora Europaea. Vols. 1-5 (Tutin, T.G. et al. (ed.). 1964-1980). Others taxa not included in the former: Launaea fragilis (Asso) Pau var. fragilis, Helianthemum syriacum (Jacq.) Dum. Cors. subsp. thibaudii Pers., Ononis tridentata L. var. edentula Weeb, Thymus gypsicola R. God., Lithodora fruticosa (L.) Griseb., Helianthemum alypoides Losa & R. Goday, Asteriscus spinosus (L.) Schultz and Diplotaxis harra (Forsk.) Boiss. subsp. lagascana (D.C.) Bolós & Vigo 1984-1995. Rivas-Martínez et al. (1987) for syntaxa.

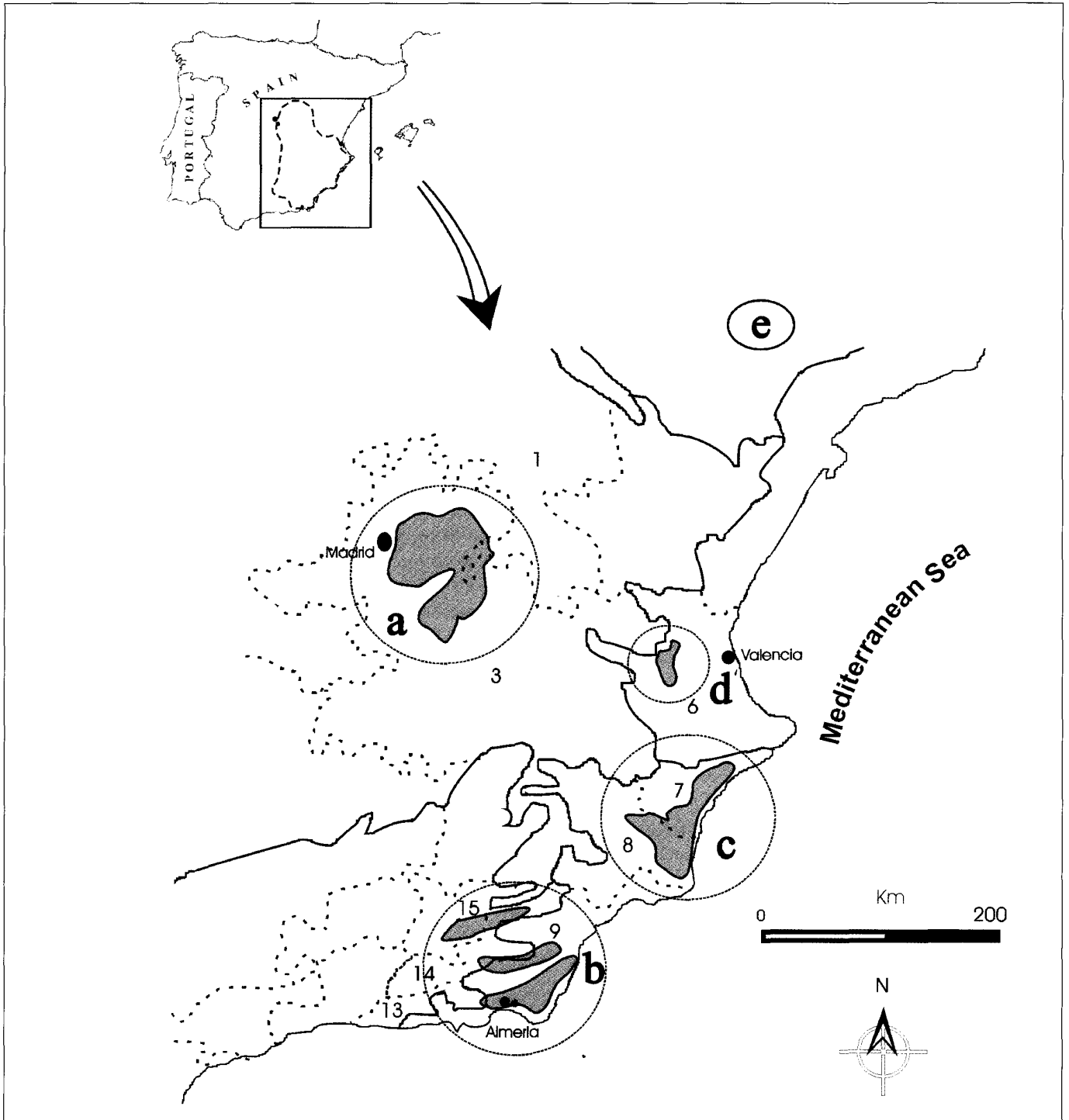


Fig. 1. Distribution of gypsiferous soils (black stains) in the eastern areas of the Iberian Peninsula adapted from Riba and Macau (1962), and biogeographic references of the studied areas. Castellano-Maestrazgo-Manchega Province (a) with Celtibérico-Alcarreño (1) and Manchego (3) Sectors; Bética and Murciano-Almeriense Provinces (b) with Alpujarreño-Gadoreño (13), Nevadense (14), Guadiciano-Bacense (15) and Almeriense (9) Sectors; Murciano Almariense Province (c) with Alicantino (7), and Murciano (8) Sectors; Valenciano-Catalano-Provenzal Province (d), with Setabense Sector (6). Aragonese Province (e), Monegrino Sector. Dotted lines: sectorial division. Continuous lines: provincial division.

INTRODUCTION

European countries with significant areas of gypsiferous soils include Spain (with 1.650 km²) and Turkey (with 650 km²). In Spain those areas extend for the eastern half (Riba & Macau 1962), and has been a subject of detailed studies (Gumuzzio & Alvarez 1984; Porta & Herrero 1988). Geographically, gypsiferous soils occur in discontinuous areas (fig. 1). When they are not subject to agricultural practices, they give rise to ecosystems with severe growing conditions for plants and are thus composed of a set of plants tolerant to them. In these areas, original phytocenosis with a large proportion of exclusive Ibero-Mediterranean endemisms occur.

The majority of gypsiferous soils in the study area have been developed from geological formations belonging to several sedimentary watersheds and originated throughout the Tertiary period (Riba & Macau 1962). In the Tajo Valley (biogeographic province Castellano-Maestrazgo-Manchega, fig. 1a) soils are constituted by Oligocene and Miocene gray loams with a compact structure and scarce permeability. In the eastern hollow of the Central Plateau (province Valenciano-Catalano-Provenzal, Sector Setabense; fig. 1d), the Oligocene gray loams alternate with gypsiferous Triassic (Keuper) outcrops. A similar stratigraphic arrangement is registered in the valley of the Mundo and Segura rivers within the biogeographic Murciano-Almeriense province, Alicantino and Murciano Sectors (fig. 1c).

The meridional sector of the latter province (Almeriense Sector) and Bética province, Nevadense, Subbético, Guadiciano-Bacense and Alpujarreño-Gadoreense Sectors (fig. 1b) are also mainly Oligo-Miocene.

These soils are included in the order Aridisols (Eswaran & Zi-Tong 1991). The principal type of soils in the studied area are the gypsid, with gypsic, petrogypsic or hypergypsic horizons (center and southern regions of the Iberian Peninsula) and gypsid with calcic or hypercalcic horizons (in southern and eastern regions of the Iberian Peninsula); both lack petrocalcic horizons. In gypsiferous soils of some areas of the Tajo Valley (Tarancón, Ontígola), there is a superposition of a hypercalcic horizon (10-20 cm) over a hypergypsic horizon. In the east and southeast of the Iberian Peninsula, the gypsiferous soils lie in termomediterranean and mesomediterranean belts with dry and arid ombroclimates (Rivas-Martínez 1984).

Floristic and phytosociological studies for central and southeastern Spain (fig. 1) have been carried out by researchers, focusing on chorological and syntaxonomic

aspects (Rivas-Goday 1956; Rivas-Goday & Esteve 1965; Rivas-Goday & Rivas-Martínez 1967; Rivas-Martínez & Costa 1970; Costa 1974; Rivas-Martínez *et al.* 1987; Peinado *et al.* 1992).

Recent phytosociological reviews (Loidi & Fernández-Gonzalez 1994; Loidi & Costa 1997) maintain the order *Gypsophyletalia* and its three alliances upon floristic affinities and biogeographic characteristics.

The three basic aims of this paper are: 1) to review the sociological groups and their characteristic taxa through the application of numerical analysis (TWINSPAN); 2) to identify the relationships between the sociological groups and their characteristic species with both edaphic and bioclimatic factors; and 3) to determine the floristic affinities between biogeographical units so as to propose epiontologic relationships according to the distribution of the most significant taxa.

MATERIALS AND METHODS

Study areas

The study areas include the basin of the central course of the Tajo river (fig. 1a); the Baza and Gádor mountain ranges, Campo de Tabernas and Sierra Filabres (fig. 1b); southeastern area of Spain from the Sierra Cabrera and both the Segura and Mundo river valleys to southern Alicante (fig. 1c). The final study area is an isolated area of gypsiferous marls in the valley of Cofrentes in the province of Valencia (fig. 1d).

Vegetation data

Vegetation relevés have been carried out according to the Braun-Blanquet methodology (Braun-Blanquet 1964).

Data sets combine our relevés (78) with those extracted from the literature (Rivas-Goday *et al.* 1956, Tab. 7, relevés 4, 5, 13; Tab. 8 relevés 15, 23; Rivas-Goday & Esteve 1965, Tab. 6, relevés 1 to 8; Tab. 7, relevés 1; Tab. 8, relevés 4, 5; Tab. 9, relevés 1, 2, 4, 9; Rivas-Martínez & Costa 1970, Tab. 1, relevés 1 to 10; Costa 1974, Tab. 4, relevés 1 to 21; Tab. 6, relevés 1 to 9; Peinado *et al.* 1992, Tab. 45, relevés 7, 8, 9; Tab. 47, relevés 1 to 14).

Only plant communities without circumstantial or short-lived ephemeral taxa (therophytes), were analysed. We believe that the study of the communities of therophytes should be the object of a specific research, not only because of the difficulty in sampling, but also because of

the variability of species and their relationships of abundance-dominance. These depend to a large extent on the annual climatic conditions. In total 146 relevés representative of the major syntaxonomic units are included. The numerical classifications were made with cover data for each species; these are transformations of the Braun-Blanquet cover values according to the following scale (Maarel 1979): r = 1; + = 2; 1 = 3; 2 = 5; 3 = 7; 4 = 8; 5 = 9. For other statistical purposes a data matrix was made.

Species present in less than 2% of relevés have not been included in the statistical process because of scarce contributing information, although later discussion is made if there is a chorological or biogeographical interest.

Climatic data

Meteorological data were obtained from the records belonging to the locations nearest the sites where the vegetation samples were taken.

The data correspond to continuous periods with a 13-year minimum (Hellín, Albacete) and a maximum of 37 years (Aranjuez, Madrid) (table 1).

The Bioclimatic Indices considered in our studies (Rivas-Martínez 1997) are (see below for the definition of parameters): Thermicity Index (It) = (T+m+M) * 10;

Compensated thermicity Index (Itc) = It ± C (C, value of compensation); Continentality Index (Ic) = Tmax - Tmin; Diurnal Index (Id) = tmx - tmn; Ombrothermic Index (Io) = Pp/Tp; Summer ombrothermic Index (Ios) = Pps/Tps; Yearly ombro-evaporation Index (Ioe) = P/PE; Aridity Index (Iar) = PE/P; Yearly positive temperature (Tp); Summer temperature (Ts); Positive precipitation (Pp); Summer precipitation (Ps).

As the basis for calculation, T = yearly average temperature; m = average temperature of the minimums of the coldest month of the year; M = average temperature of the maximums of the coldest month of the year; Tmax = average temperature of the warmest month; Tmin = average temperature of the coldest month; tmx and tmn represent the average temperature of the maximums and minimums respectively for the month of more difference among them; Pp = yearly precipitation in mm of the months with an average temperature higher than 0 °C; Ps = value in millimetres resulting from the sum of the average precipitation of the three summer months; Tp = value, expressed in tenths of degree, resulting from the sum of the average monthly temperatures higher than 0 °C; Pps = summer precipitation in mm of the three consecutive warmest months in the year; Tps = value in tenths of degree resulting from the sum of the average monthly temperatures of the three consecutive warmest months in the year; P = average yearly precipitation;

		Bioclimatic Indices (*)											
	Origin of the data	(It)	(Itc)	(Ic)	(Id)	(Io)	(Ios)	(Ioe)	(Iar)	(Tp)	(Ts)	(Pp)	(Ps)
a	Aranjuez	238	242	18,90	15,1	2,60	0,67	0,56	1,80	1636	673	425	45
	Fuentidueña	228	241	20,70	17,3	2,69	0,78	0,58	1,70	1681	705	452	55
b	Tabernas	393	393	16,20	13,3	1,03	0,19	0,24	4,20	2149	775	222	15
	Baza	313	315	18,40	14,1	1,44	0,38	0,33	3,00	1939	738	280	28
c	Hellin	298	298	17,40	16,7	1,67	0,66	0,38	2,70	1819	707	303	46
	Yecla	255	263	19,70	15,3	1,83	0,76	0,40	2,50	1756	709	322	54
	Jumilla	293	293	17,70	18,1	1,76	0,82	0,40	2,50	1783	703	314	57
	Pinoso	345	345	17,00	16,2	1,41	0,62	0,33	3,10	2047	743	289	46
	Villena	253	253	16,70	14,1	2,19	0,84	0,48	2,10	1639	649	359	54
d	Cofrentes	300	312	20,30	15,9	2,26	0,98	0,52	1,90	1977	775	447	76
	Jarafuel	303	301	10,80	18,3	3,50	1,78	0,79	1,30	1552	539	543	91
	Ayora	252	252	17,30	12,2	2,52	1,10	0,55	1,80	1609	651	406	71

(*) It, Thermicity Index; Itc, Compensated thermicity Index; Ic, Continentality Index; Id, Diurnal Index; Io, Ombrothermic Index; Ios, Summer ombrothermic Index; Ioe, Yearly ombro-evaporation Index; Iar, Aridity Index; Tp, Yearly positive temperature; Ts, Summer temperature; Pp, Positive precipitation; Ps, Summer precipitation; a, b, c, and d, biogeographic provinces as seen in fig. 1.

Table 1. Mean bioclimatic data corresponding to continuous periods with a 13-year minimum (Hellín) and 37-years maximum (Aranjuez). Sites in Manchego Sector (fig. 1a); Bético and Almeriense Sectors (fig. 1b); Murciano Almeriense and Alicantino Sectors (fig. 1c); Setabense Sector (fig. 1d).

PE= average yearly evapotranspiration (Thornthwaite); Tp= value, expressed in tenths of degree, resulting from the sum of the average temperatures of the months with averages higher than 0 °C.; Ts= value, in tenths, of the sum of the average temperatures of the summer months higher than 0 °C.

Soil data

Soil samples for each one of the relevés (78) from horizons belonging to the rhizosphere were taken using a 10 cm diameter auger to a depth of 40 cm.

Each soil sample (2355 cm³) was thoroughly mixed and dried in the open air. About 400 g of this air-dried sample was then dried in an oven at 102 °C until the dry weight became constant. A 100 g sub-sample was then used for the mechanical analysis. Soil texture was determined by mechanical sieving and classified according to the International Society of Soil Science System (Black 1968). The following grain size fractions were determined: coarse sand (2-0.2 mm), fine sand (0.2-0.02 mm), and silt and clay (< 0.02 mm).

Inorganic carbonate and lime (active calcium carbonate) were determined by a pressure calcimeter according to methods developed by Dreimanis (1962) and Drouineau (1942) respectively. Organic matter was analysed by potassium dichromate oxidation (Walkley & Black method 1934). Soluble salts in the soil were determined from measurements made on aqueous saturation extracts of soil samples, using a conductimeter (Copenhagen N.V.). From this aqueous solution, water soluble Ca²⁺, Mg²⁺, Na⁺ and K⁺ were determined using an atomic absorption spectrophotometer (Perkin-Elmer 2380). A standard method of determining gypsum in soils was applied; sulphate was dissolved from the soil samples by extracting the soil with successively greater water/soil ratios until all the sulphate was dissolved in the extract. Total sulphate was measured by gravimetry (Soil Survey Staff 1984). The field capacity was determined by aqueous saturation of 100 g of soil sample.

The edaphic values for each sample were obtained from the average values corresponding to each of the three analysis repetitions of soil samples extracted.

Numerical analysis

For the ranking of the relevés and the species, based on their floristic and ecological affinities respectively, the Two-Way Indicator Species Analysis (TWINSPAN, Hill 1994) and the Principal Components Analysis (PCA)

included in the software package for multivariate analysis (MVSP, 1998) were employed. The ecological characterisation of the principal phytosociological groups was determined through Canonical Correspondence Analysis from both species and environmental data matrix sets. Jaccard's coefficient was calculated to measure the floristic similarity between the studied areas and the cladistic ordination.

RESULTS AND DISCUSSION

Phytosociology

The gypsophilous vegetation studied presents a great chamaephytes abundance as a dominant biological form. Scrubs with, low coverage, include numerous xerophytes and gypsophilous endemics, with a high level of floristic and phytocenotic diversity.

In the ranking of the species and vegetation samples according to their sociological and ecological affinities, obtained by the application of the program TWINSPAN, a central group is constituted by taxa with no differential value and a wide ecological spectrum, including *Diploaxis harra* ssp. *lagascana*, taxon endemic of the southeast of the Peninsula, *Herniaria fruticosa*, characteristic of gypsiferous marls, *Frankenia thymifolia* and *Reseda suffruticosa*.

As seen in table 2, and from the first dichotomy resulting, two groups were established differentiated from the floristic viewpoint. In the first, the exclusive gypsophilous species prevail, those of greater differential power being *Helianthemum squamatum*, *Lepidium subulatum* and *Lauanaea fragilis*. Most of the corresponding inventories of this group belong to the central and southern zones of the Iberian Peninsula. The second group, with positive differential taxa, includes, as a rule, species from soils rich in carbonates and with the presence of sulphates; the species of greater indicative potential are *Helianthemum cinereum*, *Teucrium libanitis* and *Matthiola fruticulosa*.

As to division 2, two groups of species were formed. The first, representative of the biogeographic Castellano-Maestrazgo-Manchega province (fig. 1a) with *Thymus gypsicola* and *Centaurea hyssoipifolia* as characteristic species and the second with *Santolina viscosa*, *Coris hispanica*, as strongly gypsophilous elements (table 2). Other significant taxa are *Asphodelus ramosus* and *Helianthemum thibaudii*, basiphilous of greater ecological spectrum. These taxa, together with many narrowly dis-

Level 1	Level 2	Level 3	Level 4	Biogeographic unity and nº of relevés	
Div. 1 (*) Egv.=0.562	Div. 2. (*0) Egv.=0.583	Div. 4. (*00) Egv.=0.513	Div. 8 (*000) Egv.=0.513		
Heli squa1 (-75) Lepi subu1 (-62) Laun frag1 (-61)	Thym gyps1 (-85) Cent hisp1 (-77)	Arte herb1 (-100) Aste spin1 (-100)		Prov. Castellano- Maeztrazgo- Manchega. Sec. Manchego N=44	
		Thym gyps1 (100)	Div. 9. (*001) Egv.=0.348 Koel vall1 (-100) Stip tena1 (100)		
	Heli thib2 (78) Sant visc1 (75) Asph ramo1 (69) Cori hisp1 (69)		Div. 5. (*01) Egv.=0.329 Lepi subu1 (-86)	Div. 10. (*010) Egv.=406 Sant visc1 (-100) Onon trid1 (100) Teuc poli1 (100) Thym hiem1 (100)	Prov. Bética and Murciano-Almeriense. Sects. Almeriense (western) and Murciano (southern) N=42
			Sedu sedi1 (100)	Div. 11. (*011) Egv.=269 Anth tern1 (80) Cori hisp1 (80)	Prov. Bética Sec. Guadiciano- Bacense N=28
Heli cine1 (62) Teuc liba 1 (62) Matt frut 1 (58)	Div. 3. (*1) Egv.=0.528	Div. 6. (*10) Egv.=0.528	Div. 12 (*100) Egv.=0.331		
	Gips stru1 (-100) Rosm offi2 (-100) Thym vulg1 (-100)	Div. 7. (*11) Egv.=0.465	Div. 13. (*110) Egv.=0.494 Stip tena1 (-100) Rosm offi1 (-100) Sedu sedi1 (-100) Cist clus1 (-100) Geni spar1 (-100) Matt frut 1 (58) Fuma eric1 (100)	Prov. Val.-Cat.- Proven. Sect. Setabense Subsect. Enguerino - Cofrentino N=11	
		Brach retu 1(-100) Onon eden1 (-100)			
		Onon trid1 (100) Fuma thym1 (100)		Prov. Murciano- Almeriense Sect. Alicante N=21	

Table 2. Summary of the four dichotomy levels resulting from the application of TWINSPLAN to the gypsophilous vegetation data matrix. Indicator pseudospecies are listed together with their potentials. Each group is represented by two numbers: one in decimal; one in binary notation (*).

	Al. <i>Lepidion subulati</i>							Al. <i>Thymo-Teucrium verticillati</i>			
	Subal. <i>Lepidion subulati</i>			Subal. <i>Gypsophilo-Santolinum viscosae</i>				9	10	11	
N° order	1	2	3	4	5	6	7	8	9	10	11
N° relevés	7	27	10	17	8	17	14	14	7	11	14
Characteristics of Ord. <i>Gypsophiletalia</i>											
<i>Herniaria fruticosa</i> ssp. <i>fruticosa</i>	IV ^{1,4}	II ^{0,2}	III ^{1,0}			III ^{2,0}	I ^{1,0}		II ^{2,0}	V ^{1,0}	V ^{1,0}
<i>Ononis tridentata</i>	II ^{0,2}	V ^{2,0}	III ^{1,0}	II ^{1,0}			II ^{1,0}	IV ^{1,3}	III ^{1,0}		V ^{1,5}
<i>Gypsophila struthium</i>	II ^{0,2}	III ^{2,0}	V ^{1,3}	IV ^{1,5}	V ^{1,0}	V ^{2,0}	V ^{1,1}	IV ^{2,0}	V ^{1,1}		
Characteristics of Alliance											
<i>Lepidium subulatum</i>	III ^{1,0}	V ^{1,5}	V ^{1,0}	V ^{1,0}	V ^{1,0}	III ^{1,0}					
<i>Helianthemum squamatum</i>	III ^{1,1}	V ^{2,5}	V ^{2,3}	V ^{1,7}	V ^{1,0}	V ^{1,0}	V ^{1,2}	IV ^{1,0}	I ^{0,6}		
<i>Launaea fragilis</i>	IV ^{1,2}		V ^{1,3}					III ^{0,6}			
Characteristics of Suballiances											
<i>Thymus gypsicola</i>	IV ^{1,8}	V ^{3,5}	V ^{0,7}								
<i>Centaurea hyssopifolia</i>	III ^{0,8}	V ^{1,0}	V ^{1,3}								
<i>Koeleria valesiana</i>	IV ^{0,2}	V ^{1,0}	I ^{0,2}						III ^{0,6}		
<i>Helianthemum syriacum</i> subsp. <i>ihibaudii</i>	III ^{0,7}			V ^{1,7}	V ^{2,5}	III ^{2,0}	V ^{1,8}	IV ^{1,3}	IV ^{0,6}	III ^{1,0}	II ^{0,6}
<i>Santolina viscosa</i>				V ^{2,7}	V ^{2,5}		V ^{2,0}	IV ^{1,0}			
<i>Coris hispanica</i>				IV ^{1,0}	V ^{1,0}		IV ^{0,5}	V ^{1,0}			
<i>Asphodelus ramosus</i>				V ^{1,0}	V ^{1,0}	III ^{1,0}	V ^{1,0}	II ^{1,0}			
Characteristics of Alliance											
<i>Teucrium libanitis</i>										V ^{2,0}	V ^{1,5}
<i>Mathiola fruticulosa</i>	II ^{0,2}								IV ^{0,5}	IV ^{0,2}	III ^{1,0}
<i>Helianthemum cinereum</i> var. <i>paniculatum</i>										V ^{1,0}	V ^{1,0}
Characteristics of inferior unities (Ass, Subass.)											
<i>Sedum gypsicola</i>	III ^{0,7}	V ^{0,6}	III ^{0,2}	IV ^{1,0}				III ^{1,0}			
<i>Ononis tridentata</i> var. <i>edentula</i>						V ^{2,0}	V ^{1,3}	III ^{3,0}	V ^{2,0}		
<i>Odontites longiflora</i> var. <i>gypsicola</i>	II ^{0,2}	III ^{1,0}				III ^{0,2}					
<i>Anthyllis cytisoides</i>							II ^{0,2}		III ^{1,0}	III ^{0,2}	
<i>Helianthemum alypoides</i>							V ^{1,2}	II ^{1,0}			
<i>Teucrium pumilum</i>	IV ^{2,5}	III ^{1,0}									
<i>Teucrium turredamum</i>							V ^{1,0}	IV ^{1,7}			
<i>Diplotaxis harra</i> subsp. <i>lagascana</i>								III ^{1,0}		III ^{0,2}	
<i>Artemisia herba alba</i>	III ^{0,2}			IV ^{0,2}							
<i>Euphorbia nicaensis</i>				IV ^{1,6}	III ^{2,0}						
<i>Salvia lavandulefolia</i>		III ^{4,0}									
<i>Teucrium gnaphalodes</i>		III ^{0,2}									
<i>Jurinea pinnata</i>	II ^{0,2}	II ^{0,5}	III ^{1,0}								
<i>Launaea pumila</i>		II ^{1,0}	II ^{0,8}							II ^{1,0}	
<i>Astragalus alopecuroides</i>									II ^{2,0}		II ^{1,5}
<i>Teucrium lepicephalum</i>										III ^{3,0}	I ^{0,2}
<i>Teucrium caroli pau</i>											I ^{1,0}
<i>Teucrium balthazaris</i>								I ^{0,2}			
<i>Thymus membranaceus</i>									I ^{1,0}		

Table 3. Synthetic arrangement of the gypsophylous vegetation for the central and southern areas of the Iberian Peninsula according to the groups extracted from the TWISPAN analysis. Roman numeral= indices of presence in the table of relevés: I, present in less than 20% of the relevés; II, 21-40%; III, 41-60%; IV, 61-80%; V, present in more than 80% of the relevés. Arabic numeral = mean values of abundance. The meaning of the order number corresponds to associations and syntaxonomical units of inferior range.

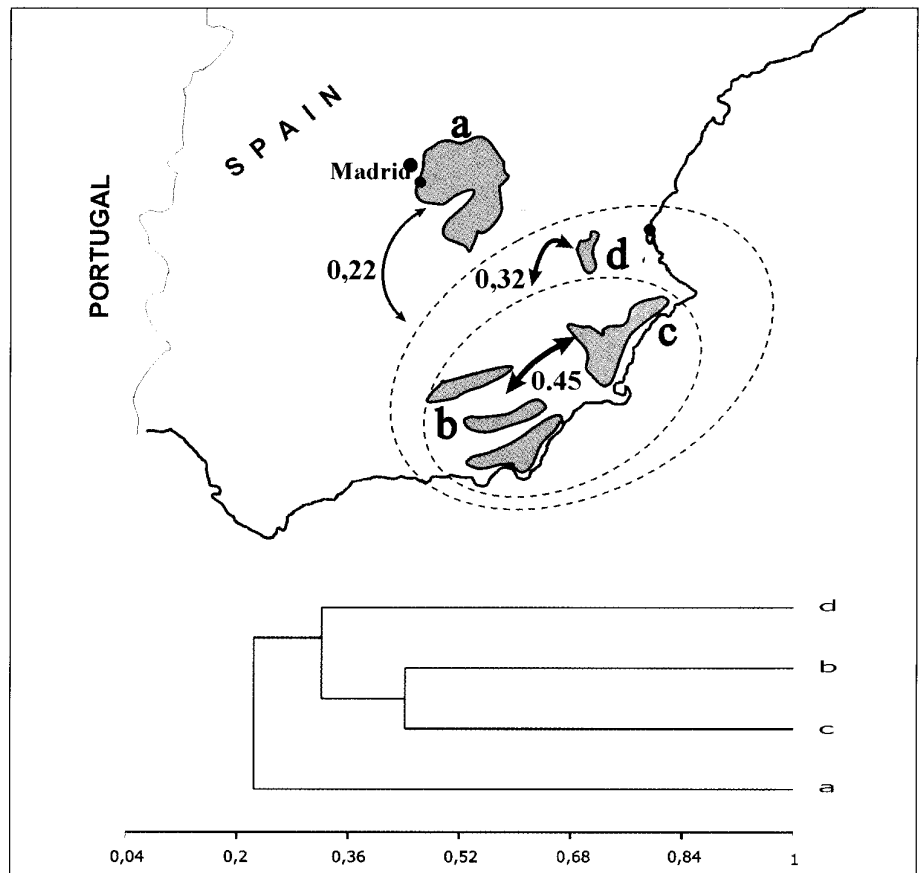
[Table 3 suite]

Characteristic of class and others

Stipa tenacissima, V^{1.7}(3); III^{0.2}(4); III^{1.0}(5); V^{1.5}(6); V^{0.8}(7); IV^{1.0}(8); II^{2.0}(9); III^{3.0}(10); III^{0.2}(11). *Plantago albicans*, II^{0.2}(1); III^{0.2}(3); III^{1.0}(4); III^{1.0}(6); III^{2.0}(7); II^{1.0}(8); IV^{0.7}(9). *Sedum sediforme*, III^{1.0}(2); III^{1.0}(6); V^{0.8}(7); V^{1.5}(8); II^{1.0}(9); III^{1.0}(10). *Anthyllis terniflora*, III^{0.2}(4); III^{1.0}(5); II^{2.0}(7); V^{0.8}(8); III^{1.0}(11). *Teucrium polium* subsp. *capitatum*, III^{1.0}(1); V^{0.6}(2); III^{0.2}(3); III^{1.0}(6); III^{0.2}(9). *Brachypodium retusum*, III^{3.0}(7); IV^{1.0}(8); III^{1.0}(9); V^{1.4}(10). *Fumana ericoides*, III^{0.2}(1); II^{1.0}(9); IV^{0.2}(10); III^{0.2}(11). *Lithodora fruticosa*, II^{0.2}(1); III^{1.0}(2); III^{0.2}(6); III^{0.6}(9). *Reseda suffruticosa*, III^{0.2}(6); III^{1.0}(8); III^{1.0}(9); III^{0.2}(10). *Rosmarinus officinalis*, IV^{0.2}(3); V^{1.5}(9); III^{0.2}(10); III^{0.2}(11). *Asparagus albus*, V^{0.7}(4); III^{0.2}(7); V^{0.8}(8). *Cistus clusii*, III^{1.0}(9); III^{1.0}(10); III^{0.2}(11). *Coris monspeliensis*, II^{0.2}(1); III^{0.2}(6); III^{1.0}(10). *Dactylis hispanica*, II^{1.0}(7); II^{2.0}(8); II^{1.0}(9). *Eryngium campestre*, II^{0.2}(7); II^{1.0}(8); II^{0.2}(9). *Frankenia thymifolia*, III^{1.0}(1); III^{1.0}(3); III^{0.2}(11). *Fumana thymifolia*, IV^{0.7}(7); III^{1.0}(9); V^{0.6}(11). *Helianthemum almeriense*, V^{1.3}(4); V^{1.5}(5); III^{1.0}(6). *Lygeum spartum*, III^{0.2}(6); III^{0.2}(9); III^{2.0}(11). *Piptatherum miliaceum*, II^{0.2}(7); II^{1.0}(9); II^{0.2}(10). *Thymus hyemalis*, V^{1.0}(6); V^{0.8}(7); V^{1.0}(8). *Allium ampeloprasum*, II^{0.2}(1); III^{0.2}(2). *Artemisia gallica*, III^{2.5}(7); II^{2.0}(8). *Asphodelus fistulosus*, II^{1.0}(7); III^{1.0}(8). *Astragalus incanus* subsp. *macrorrhizus*, III^{0.2}(8); III^{0.2}(10). *Atractylis humilis*, III^{0.2}(6); IV^{0.7}(9). *Bupleurum frutescens*, III^{0.2}(6); II^{1.0}(9). *Centaurea meliensis*, III^{3.5}(1); III^{2.0}(3). *Ctenopsis gypsophylla*, II^{0.2}(1); III^{3.0}(3). *Distichoselinum tenuifolium*, III^{0.2}(6); III^{1.0}(8). *Dorycnium pentaphyllum*, III^{0.2}(6); III^{1.0}(10). *Ephedra nebrodensis*, IV^{0.2}(3); II^{0.2}(8). *Genista spartioides* var. *retamoides*, IV^{0.7}(8); III^{1.0}(10). *Hippocrepis multisilicosa*, III^{1.0}(6); II^{0.2}(9). *Limonium virgatum*, II^{1.0}(9); II^{2.0}(10). *Pallenis spinosa*, II^{0.2}(8); II^{0.2}(9). *Poligala* sp., III^{0.2}(10); III^{0.2}(11). *Sideritis angustifolia*, II^{0.2}(9); II^{1.0}(10). *Stipa offneri*, II¹(9); II^{0.2}(10). *Tapsia villosa*, II^{1.0}(1); II^{2.1}(2). *Thymelaea hirsuta*, IV^{0.5}(7); III^{0.6}(8). *Thymus vulgaris*, III^{1.0}(3); V^{1.0}(9).

Moreover (presents in one releve). **In 1**, *Artemisia campestris* subsp. *glutinosa*, II^{1.0}; *Artemisia valentina*, II^{1.0}; *Bupleurum semicompositum*, II^{0.2}; *Catapodium rigidum*, II^{0.2}; *Fumana laevipes*, II^{0.2}; *Helianthemum croceum*, II^{0.2}; *Helianthemum salicifolium*, II^{0.2}; *Onopordon corymbosum*, II^{0.2}; *Papaver somniferum*, II^{4.0}; *Scabiosa monspeliensis*, II^{0.2}; *Thesium divaricatum* subsp. *castellanum*, II^{0.2}; *Trisetaria loeflingiana*, II^{0.2}; *Wangenhemia lima*, II^{0.2}; *Asteriscus spinosus*, III^{1.0}; *Limonium echinoides*, III^{0.2}; *Melica ciliata*, III^{1.2}; *Salsola vermiculata*, III^{4.0}. **In 2**, *Arenaria cavamillesiana*, III^{1.0}; *Helianthemum hirtum*, III^{1.0}; *Hippocrepis comosa*, III^{1.0}; *Reseda stricta*, II^{1.0}. **In 3**, *Centaureum gypsicola*, III^{1.0}; *Micropus bombicina*, III^{0.2}; *Reseda fruticulosa*, III^{0.2}; *Scabiosa stellata*, IV^{0.6}; *Reseda lutea*, V^{2.0}. **In 4**, *Linum strictum*, III^{1.0}. **In 6**, *Jurinea humilis*, III^{1.0}. **In 7**, *Andryala ragusina*, II^{0.2}; *Cuscuta epithimum*, II^{0.2}; *Rhamnus oleoides* subsp. *angustifolia*, II^{0.2}. **In 8**, *Ferula comunis*, II^{0.2}; *Helichrysum italicum*, II^{0.2}; *Helichrysum stoechas*, II^{0.2}; *Moricandia arvensis*, II^{0.2}; *Phagnalon rupestre*, II^{0.2}; *Rhynantus major*, II^{1.0}; *Satureja obovata* subsp. *canescens*, II^{0.2}; *Teucrium chamaedrys*, II^{0.2}; *Allium polianthum*, III^{1.0}; *Sideritis murgetana* (*S. pusilla*), IV^{1.0}. **In 9**, *Asperula aristata*, II^{1.0}; *Globularia alypum*, II^{1.0}; *Satureja obovata* subsp. *obovata*, II^{0.2}; *Linum fruticosum*, IV^{0.7}. **In 10**, *Centaurea seridis*, II^{0.2}; *Inula viscosa*, II^{0.2}; *Jasomia glutinosa*, II^{0.2}; *Teucrium aureum*, II^{0.2}; *Brassica fruticulosa*, III^{1.0}; *Coronilla valentina* subsp. *glauca*, III^{0.2}; *Euphorbia serrata*, III^{0.2}; *Helichrysum stoechas* var. *maritima*, III^{0.2}; *Schoenus nigricans*, III^{1.0}; *Sedum dasphyllum*, III^{0.2}; *Teucrium pseudochamaepitys*, III^{0.2}.

Fig. 2. Hypothetical relationship between the gypsophyllous vegetation areas of the Centre and Southeast of the Iberian Peninsula according to the indices of floristic similarity and clustering analysis (Jaccard's Coefficients). For biogeographic references, see fig. 1.



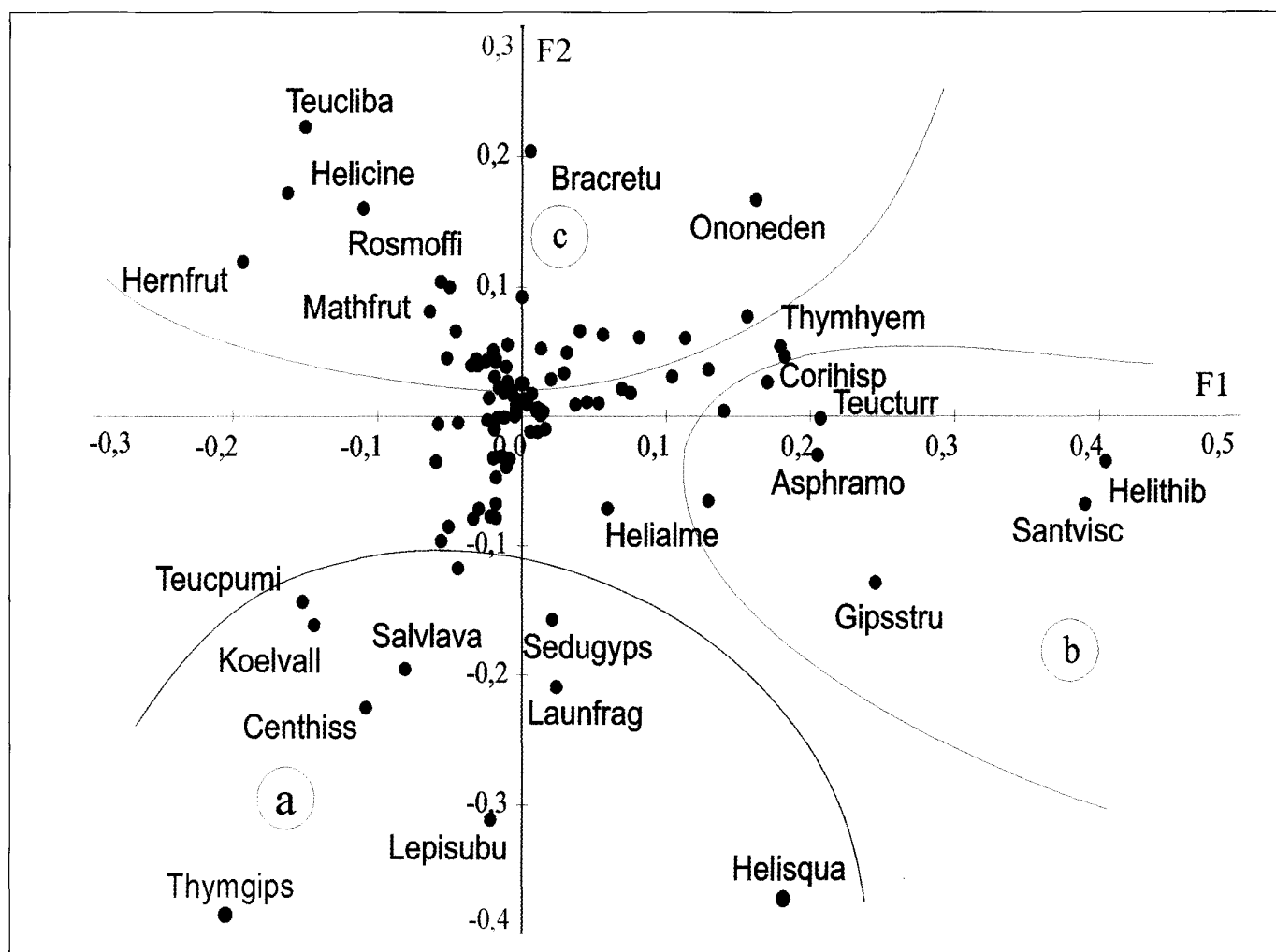


Fig. 3. Two-dimensional scatterplot of species and ecological groups related with the first two extracted factors (F1 and F2, Tab. 4). Distribution shows apparent relationship with the suballiances Lepidienion subulati (a), Gypsophilo-Santolinienion viscosae (b) and the alliance Thymo-Teucrion verticillati (c).

tributed endemisms, belong to the Murciano-Almeriense (fig. 1c) and Bética (fig. 1b) provinces in the southeast of the Iberian Peninsula.

The group derived from division 3 (table 2) possesses a more homogeneous indicative potential, with a predominance of basiphilous taxa such as *Rosmarinus officinalis* and *Thymus vulgaris*. *Gypsophila struthium* is the one gypsophilous differential species for this group.

From level 3 (divisions 4 to 13), the extracted groups include species of a broad ecological range characterising superior phytosociological ranks (Ord. *Gypsophiletalia*, Cl. *Rosmarinetea*).

The resulting groups up to level 2 (table 2) correspond to the alliances and suballiances recently carried out (Loidi & Costa 1997), but some of them differ in rank. From our results a modification, according to the groups extracted, should be made.

The alliance *Thymo-Teucrion verticillati*, previously reported in the phytosociological literature (Rivas-Goday *et al.* 1956, Rivas-Goday & Esteve 1965, Rivas-Goday & Rivas-Martínez 1967), should be maintained according to the characteristic taxa: *Teucrium libanitis*, *Matthiola fruticulosa* and *Helianthemum cinereum* var. *paniculatum* (table 3, n° order 9 to 11).

<p>Cl. <i>Rosmarinetea officinalis</i>, Br. Bl. em. Rivas-Martínez <i>et al.</i>, 1991</p> <p>Ord. <i>Gypsophiletalia</i>, Bellot & Rivas-Goday in Rivas-Goday, 1957</p> <p>*Al. <i>Lepidion subulati</i>, Bellot & Rivas Goday, 1957 <i>Helianthemum squamatum</i>, <i>Lepidium subulatum</i>, <i>Launaea fragilis</i></p> <p>**Subal. <i>Lepidenion subulati</i>, Loidi & Costa, 1997 <i>Centaurea hisspifolia</i> <i>Thymus gypsicola</i></p> <p>**Subal. <i>Gypsophilo-Santolinenion viscosae</i> (Rivas Goday & Esteve Chueca, 1965) Alcaraz, Sánchez-Gómez, de la Torre, Ríos & Álvarez Rogel, 1991 <i>Santolina viscosa</i>, <i>Helianthemum thibaudii</i>, <i>Coris hispánica</i>, <i>Asphodelus ramosus</i></p> <p>**Subal. <i>Gypsophilo hispanicae</i> (Br. Bl. & Bolós, 1958) Molina, Loidi & F. Fernández-Gonzalez, 1993 <i>Gypsophila hispánica</i></p> <p>*Al. <i>Thymo-Teucrium verticillati</i>, Rivas-Goday, 1957 <i>Teucrium libanitis</i>, <i>Helianthemum cinereum</i> var. <i>paniculatum</i>, <i>Matthiola fruticulosa</i>, <i>Gypsophila strutum</i></p>

Table 4. Syntaxonomical scheme of gypsophillous vegetation in Spain and characteristic species.

Helianthemum cinereum (Cav.) Pers. var. *eu-cinereum* Maire is present in the scrubs of *Rosmarino-Ericion*. The variety *paniculatum* shows greater preference for dry habitats and soils richer in sulphates than other communities of the same alliance (Bolós & Vigo 1984-1995). Also, *Matthiola fruticulosa* is frequent in most xerophyte communities of *Rosmarinetealia* and in mesomediterranean communities of *Gypsophiletalia* (Rigual 1972). Both taxa, found also in thyme brushwood neighbouring on calcareous or scarcely gypsiferous soils of *Thymo-Siderition*, are the differential elements as compared to the alliance *Lepidion subulati*.

The taxa *Astragalus alopecuroides* subsp. *alopecuroides* var. *grossi* and *Teucrium lepicephalum*, are included as well characteristic of the alliance *Thymo-Teucrium verticillati* for some authors (Rivas-Goday 1956, Rivas-Goday & Rivas-Martínez 1967). However, because of both the low presence index in the studied samples and their reduced dispersion area (Sierra de Gádor in Almeria, and the surrounding area of Puig Campana in Alicante respectively), we believe that they should be substituted by the above-mentioned species. The alliance *Lepidion subulati* should be maintained, according to the results (table 3 n° order 1 to 8), including two suballiances: *Lepidenion subulati* and *Gypsophilo-Santolinenion viscosae*. These are defined by the second dichotomy, division 2 (table 2).

Suballiance *Lepidenion subulati* is characterised by *Thymus gypsicola*, *Centaurea hisspifolia* and *Koeleria valesiana* (table 3, n° order 1 to 3). These species also represent the biogeographical characteristics of the suballiance.

Suballiance *Gypsophilo-Santolinenion viscosae* is characterised by *Santolina viscosa*, *Coris hispanica* and *Asphodelus ramosus*. Although *Helianthemum syriacum* subsp. *thibaudii* is a taxon of greater ecological extent, its presence as characteristic is justified according to TWINS-PAN by its high presence and abundance indices in this group. The determining ecological factors are the arid and thermal bioclimatic conditions (table 3, n° order 4 to 8).

Additionally *Teucrium turretanum*, *Teucrium balthazaris* and *Helianthemum alypoides* are included in the *Gypsophilo-Santolinenion viscosae* by other authors (Rivas-Goday & Esteve Chueca 1965; Loidi & Costa 1997) but they should be considered as territorial characteristics of the inferior syntaxa.

The suballiance *Gypsophylenion hispanicae*, not included in our study area, has long been recognised to a large extent by several authors. The suballiance is included in the syntaxonomic scheme proposed (table 4).

Biogeography

We can synthesise the distribution of the gypsophilous vegetation distributed around four centres represented in figure 1: a central focal point (a, fig. 1) on the marls of the Manchego Sector (Castellano-Maestrazgo-Manchega province) characterised by *Lepidium subulatum*, *Centaurea hisspifolia*, *Teucrium pumilum* (endemic) and *Koeleria valesiana*, which irradiates toward (2) the southern biogeographic Bética and Murciano-Almeriense (in part) provinces (b, fig. 1), where in addition to preserving its characteristic taxa, it is enriched with gypsophilous ende-

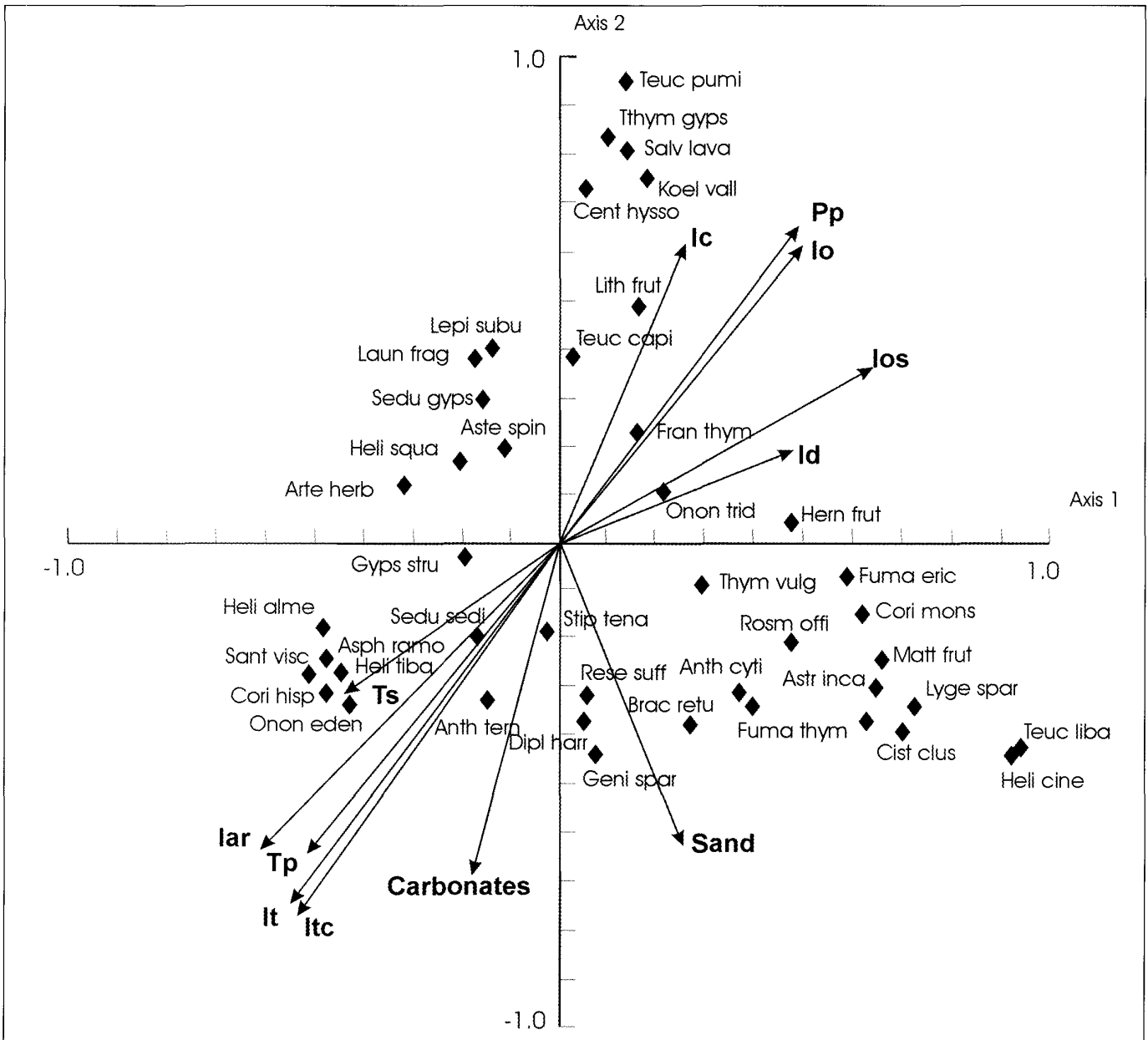


Fig. 4. Species environmental biplot from canonical correspondence analysis (CANOCO) of the significant environmental (climatic and edaphic) and data of vegetation. Associated correlations (R , Spec Env) and eigenvalues are given in Table 5. Scaling factor value for species: $x=0.5$; for environmental: $x=1$. It, Thermicity Index; Itc, Compensated thermicity Index; Ic, Continentality Index; Id, Diurnal Index; Io, Ombrothermic Index; Ios, Summer Ombrothermic Index; Iar, Aridity Index; Tp, Yearly positive temperature; Ts, Summer temperature; Pp, Positive precipitation.

misms such as *Santolina viscosa* and particularly species of the genus *Teucrium* grex *pumilum*. This influence extends from the (3) Almeriense Sector to the Alicantino Sector of the Murciano-Almeriense province (c, fig. 1), where the loss or absence of the genuine species of the

group such as *Lepidium subulatum* and *Centaurea hissiopifolia* is notable. In the (4) Setabense Sector, Cofrentino-Enguerino Subsector of the Valenciano-Catalan-Provenzal province (d, fig. 1), there is an isolated area of gypsicolous vegetation with Castellano-Manchega floristic

AXIS	EIGENVALUE	% OF TOTAL	CUMULATIVE %
1	8.296	17.28	17.28
2	7.363	15.34	32.62

SPECIES	Eigenvectors (Component Loadings)		
	Code	AXIS1	AXIS2
<i>Helianthemum squamatum</i> (*), (**)	Helisqua	-0,02	0,28
<i>Gypsophila struthium</i> (*), (**)	Gypsstru	-0,14	0,14
<i>Stipa tenacissima</i>	Stiptena	-0,14	-0,03
<i>Launaea fragilis</i> var. <i>fragilis</i>	Launfrag	0,08	0,21
<i>Lepidium subulatum</i> (**)	Lepisubu	0,16	0,27
<i>Helianthemum syriacum</i> subsp. <i>thibaudii</i>	Helithib	-0,23	-0,03
<i>Herniaria fruticosa</i> ssp. <i>fruticosa</i> (*), (**)	Hernfrut	0,11	-0,20
<i>Sedum sediforme</i>	Sedusedi	-0,21	0,03
<i>Ononis tridentata</i> (**)	Onontrid	0,03	0,05
<i>Ononis tridentata</i> var. <i>edentula</i> (*, d), (**)	Ononeden	-0,14	-0,04
<i>Santolina viscosa</i> (*b c), (**)	Santvisc	-0,22	0,16
<i>Asphodelus ramosus</i>	Asphramo	-0,19	0,15
<i>Brachypodium retusum</i>	Bracretu	-0,10	-0,18
<i>Coris hispanica</i> (*b c)	Corihisp	-0,25	0,12
<i>Sedum gypsicola</i> (*a b), (**)	Sedugyps	0,06	0,21
<i>Teucrium capitatum</i> subsp. <i>capitatum</i>	Teuccapi	0,15	0,12
<i>Thymus gypsicola</i> (*a), (**)	Thymgyps	0,22	0,18
<i>Anthyllis terniflora</i> (*)	Anthtern	-0,19	-0,02
<i>Koeleria vallesiana</i>	Koelvall	0,20	0,10
<i>Plantago albicans</i>	Planalbi	-0,10	-0,02
<i>Rosmarinus officinalis</i>	Rosmoffi	0,05	-0,18
<i>Thymus hyemalis</i> (*)	Thymhyem	-0,26	0,06
<i>Asparagus albus</i>	Aspaalbu	-0,23	0,10
<i>Centaurea hyssopifolia</i> (*a), (**)	Centhyss	0,20	0,17
<i>Fumana thymifolia</i>	Fumathym	-0,04	-0,14
<i>Fumana ericoides</i> subsp. <i>ericoides</i>	Fumaeric	0,07	-0,17
<i>Helianthemum cinereum</i> var. <i>paniculatum</i>	Helicine	0,04	-0,27
<i>Lithodora fruticosa</i>	Lithfrut	0,15	0,09
<i>Matthiola fruticulosa</i>	Mattfrut	0,06	-0,21
<i>Teucrium libanitis</i> (*c)	Teucliba	0,04	-0,27
<i>Teucrium turreadamum</i> (*b)	Teucturr	-0,27	0,06
<i>Cistus clusii</i>	Cistclus	0,03	-0,21
<i>Helianthemum almeriense</i> (*b)	Helialme	-0,07	0,14
<i>Helianthemum alypoides</i> (*)	Helialyp	-0,17	0,04
<i>Reseda suffruticosa</i> (*), (**)	Resesuff	-0,12	-0,09
<i>Teucrium pumilum</i> (*a), (**)	Teucpumi	0,17	0,09
<i>Thymelaea hirsuta</i>	Thymhirs	-0,25	0,05
<i>Anthyllis cytisoides</i>	Anthcyti	-0,01	-0,14
<i>Frankenia thymifolia</i>	Franthym	0,08	-0,01
<i>Genista spartioides</i> subsp. <i>retamoides</i> (*)	Genispar	-0,15	-0,09
<i>Lygeum spartum</i>	Lygespar	0,04	-0,15
<i>Thymus vulgaris</i>	Thimvulg	0,05	-0,11
<i>Artemisia herba alba</i>	Arteherb	0,02	0,08
<i>Asteriscus spinosus</i>	Astespin	0,05	0,00
<i>Astragalus incanus</i> (*)	Astrinca	0,02	-0,18
<i>Coris monspeliensis</i>	Corimons	0,03	-0,12
<i>Diplotaxis harra</i> subsp. <i>lagascana</i> (*c d)	Diplharr	-0,14	-0,06
<i>Salvia lavandulifolia</i>	Salvlava	0,14	0,14

(*) Endemism of area studied: a, Castellano-Maestrazgo Manchega Province ; b, Bética Province ; c, Murciano Almeriense Province ; d, Valenciano-Catalano-Provenzal. Province. (**) Gypsophyllous preferent.

Table 5. List of principal species, relative contribution of the first two components to the total variance explained (eigenvalues) and eigenvectors of each species on each component extracted from PCA.

influence. It is also lacking the two latter species but has a considerable presence of basophilic plants not exclusively gypsophilous. One of the very significant taxa, from both the biogeographical and ecological viewpoint is *Ononis tridentata* var. *edentula*.

The presence of gypsophilous vegetation patches with *Gypsophila hispanica* in the northern limit of the Setabense Sector allows us to establish the hypothesis of the irradiation southward of a third group of gypsophilous vegetation from the Monegrino Sector (Aragonesa Province; fig. 1e) continuing the emigration pathway across the valley of the Guadalaviar river occupying discontinuous patches of gypsiferous soils (regosoles and luvisoles).

The coefficients of floristic similarity (fig. 2) shows a greater likeness among the Bética and Murciano Almeriense province. A greater floristic differentiation is noted between the latter and the Setabense Sector (d, fig. 2). The former cluster is scarcely related with the Castellano-Maestrazgo-Manchega province (a, fig. 2).

Complementary studies should be conducted to define the biogeographical and ecological relationships between the studied zones and the gypsicolous vegetation north of the Ebro Valley and that of the Castellano-Duriense Sector (Castellano-Maestrazgo-Manchega Province).

	Axis 1	Axis 2
R(Spec, Env)	0,983	0,987
Eigenvalues	0,559	0,537
It	-0,530	-0,774
Itc	-0,545	-0,751
Ic	0,246	0,711
Id	0,487	0,198
Io	0,455	0,663
Ios	0,624	0,295
Iar	-0,609	-0,637
Tp	-0,507	-0,644
Ts	-0,440	-0,313
Pp	0,483	0,659
Sand	0,258	-0,620
Carbonates	-0,174	-0,683

(*) It, Thermicity Index; Itc, Compensated thermicity Index; Ic, Continentiality Index; Id, Diurnal Index; Io, Ombrothermic Index; Ios, Summer ombrothermic Index; Iar, Aridity Index; Tp, Yearly positive temperature; Ts, Summer temperature; Pp, Positive precipitation.

Table 6. Scores of environmental parameters in the CANOCO ordination, associated correlation of canonical axes and values of the significant edaphic and bioclimatic factors.

The two first factors extracted from principal component analysis explain 32,62 % of total variance. Species distribution and grouping through a two dimensional scatterplot of these factors (F1 and F2, tab. 5, fig. 3) show to *Thymus gypsicola*, *Centaurea hyssopifolia*, *Koeleria vallesiana* and *Teucrium pumilum* as gypsophilous characteristics of the Castellano-Maestrazgo-Manchega province. These species are related with negative values of both factors (fig. 3a). Species positively related with F1 factor and negatively with F2 are characteristic of both Bética and Murciano-Almeriense province. *Teucrium libanitis*, *Helianthemum cinereum* and *Herniaria fruticosa* show positive relationships with F2 and negatively with F1 factors (fig. 3c).

Ononis tridentata var. *edentula*, belonging to the sector Setabense is the best representative taxa because of its positive relationships with both factors. The established ecological groups, based on the first two factors, maintain the relationship (to the section level; tab. 2, div. 1, 2 and 3) with phytosociological groups carried out by TWINSPAN.

The presence of *Salvia lavandulifolia*, of optimum development on carbonated marls, explains the coexistence in the same site of calcareous communities over calcareous superficial horizon overlapping gypsiferous marls from the Triassic.

Environmental relationships

The relationship of both taxa and sociological groups with the edaphic and bioclimatic variables, extracted from the application of Canonical Correspondence Analysis allows us to establish the distribution of the species and emerging groups through a species-environment biplot (table 6, fig. 4). The characteristic elements of the phytosociological groups in the Manchego sector, such as *Centaurea hyssopifolia*, *Teucrium pumilum*, *Koeleria vallesiana* and *Thymus gypsicola*, are related to the positive gradient of the bioclimatic factors affecting soil moisture (Pp, Io and Ios,) and with a negative gradient of the carbonate concentration. This variable shows a high correlation with the negative values of axis 2. On the left of the biplot are grouped the species related positively with an also positive gradient of aridity and termal bioclimate indices (Iar, Tp, It and Itc). The analytical results of the soil present obviously high contents in sulphates. Organic matter, carbonates and texture (sand) result significant at a 95 % confidence level (table 7). The proportion of carbonates is greater in the eastern and southeastern areas (fig. 1b, c, and d), but with a great range in its extreme values. In the central area (fig. 1a), the variation of sulphate concentra-

		Ca ²⁺	Mg ²⁺	K ⁺	Na ⁺	Texture	OM	Carbonates	Sulphates
		meq/l				(%Sand)	%		
a (n = 22)	Average	16,17	0,44	0,33	0,44	31,37	1,14	2,03	54,28
	Std. dev.	5,10	0,32	0,13	0,33	8,79	0,80	1,92	7,37
b (n = 26)	Average	13,29	0,92	1,13	0,87	52,83	2,77	17,80	43,40
	Std. dev.	3,60	0,68	1,29	0,57	13,57	1,38	9,53	13,71
c (n = 19)	Average	17,98	1,33	0,99	1,29	61,97	1,29	16,91	37,18
	Std. dev.	6,94	0,99	0,84	1,15	7,69	0,51	2,94	20,29
d (n = 11)	Average	18,43	10,82	0,62	17,45	68,09	2,10	10,27	46,57
	Std. dev.	4,62	12,08	0,23	33,94	6,94	1,42	15,88	14,48

n= number of samples; OM= organic matter.

Analysis of Variance						
	Source	Sum of Squares	Df	Mean Square	F-Ratio	P-Value
OM	Between groups	23,14	3	7,71	4,84	0,006
	Within groups	181,74	114	1,59		
	Total (Corr.)	204,88	117			
Carbonates	Between groups	2046,44	3	682,14	11,16	0,000
	Within groups	6970,74	114	61,14		
	Total (Corr.)	9017,18	117			
Sand	Between groups	7277,10	3	2425,70	20,96	0,000
	Within groups	13193,28	114	115,73		
	Total (Corr.)	20470,38	117			
Sulphates	Between groups	984,39	3	328,131	1,73	0,1921
	Within groups	21563,84	114	189,156		
	Total (Corr.)	22548,23	117			

Table 7. Mean values, standard deviations and variance analysis of the principal edaphic factors obtained from soil analysis of the four areas studied (fig. 1), a: Manchego Sector (central); b: Bético and Almeriense Sectors; c: Murciano-Almeriense and Alicantino Sectors; d: Setabense Sector.

tions as seen in the standard deviations is smaller. Two groups of taxa appear scarcely related to the bioclimatic variables (table 1, fig. 4): at top left, *Lepidium subulatum*, *Launaea fragilis*, *Helianthemum squamatum* as strictly gypsophilous plants, and at bottom right, basophilic species in soils with carbonates and sulphates in variable proportions, in soils with a greater proportion of bulk elements.

The differential role of the taxa belonging to the genus *Helianthemum* and *Teucrium* within the studied communities is outstanding. *Helianthemum squamatum* is an exclusive gypsophilous while *Helianthemum syriacum* subsp. *thibaudii* shows a preferential affinity for basic soils with a high proportion of carbonates. *Helianthemum cinereum* var. *paniculatum* and *Helianthemum almeriense* seem to be more closely related to bioclimatic factors.

On the contrary, the presence of the *Teucrium* aggregate *pumilum* (*Teucrium pumilum*, *Teucrium turredanum*,

Teucrium libanitis, *Teucrium lepicephalum* and *Teucrium caroli-pau*) in all of the biogeographic sectors and floristic groups, permits us to consider their phytosociological and ecological differential characteristics.

The handling of many relevés and the corresponding ecological data has allowed us, by means of the statistical analysis, to establish the phytosociological similarity of the species and their relationships with certain biogeographic units.

The revision shows the close relationship among the studied syntaxa (alliance and suballiances) and the biogeography of certain characteristic species (*Thymus gypsicola*, *Centaurea hyssopifolia*, *Santolina viscosa* and *Teucrium libanitis*). Additionally, the decreased sulfate-carbonate ratio, determines a greater presence of species belonging to the order Rosmarinetalia and decreases the gypsophilous species.

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The Red Plants of Israel: a proposal of updated and revised list of plant species protected by the law

Liste rouge des végétaux d'Israël : proposition pour une liste mise à jour et révisée des végétaux protégés par la loi

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Abstract

The list of plant species protected by the law in Israel, established in 1964, includes 268 wild plant species. This list contains mainly attractive flowering plants and includes many ambiguities. The list includes plant species that are highly abundant, genera without specifying the species and plants that are not natives in Israel. Thus, the existing list of plants species protected by the law is insufficient for the current conservation needs of Israel. Since the species were not selected on the basis of any quantitative data, it is highly disadvantaged for conservation. We suggest an update and revised list of plant species to be protected. Entry criterion of the revised list is rarity, defined as less than 100 grid cells of one square km (0.5% of Israel area) in which the plant is present. The criteria for inclusion in the red list are (i) rarity, (ii) attractiveness of the plant for picking the flower or for commercial use, (iii) endemism, (iv) life form of tree or a shrub, and (v) rate of extinction or habitat destruction, combined together because of the correlation exists. The revised list includes 543 species, 0.25 of the 2167 plant species in the Israeli flora. Of the list of the "red plants", 119 species are present in 1 to 3 sites and 307 species present in less than 30 sites. The proposed list might be a better tool in nature conservation in Israel, regarding parameters affecting extinction probabilities.

Key-words

Conservation policy, endemic species, red list, habitat destruction, nature protection law, rare species.

Résumé

La liste des végétaux supérieurs d'Israël protégés par la loi, établie en 1964, comporte 268 espèces sauvages. Cette liste contient principalement de nombreuses phanérogames attractives, mais beaucoup d'ambiguïtés existent. En effet, cette liste inclut des végétaux abondants et des genres au sein desquels les végétaux non indigènes ne sont pas spécifiés et exclus. De plus, les espèces mentionnées n'ont pas été sélectionnées sur la base de données quantitatives. Ainsi, la liste actuelle des plantes protégées s'avère insuffisante par rapport aux nécessités de conservation en Israël. Nous suggérons donc une liste révisée et mise à jour des plantes protégées par la loi. Le critère d'entrée dans la liste révisée repose sur la rareté, définie comme la présence d'une plante dans moins de 100 cellules de 1 km² (0,5% de la surface d'Israël). Les critères d'inclusion dans la liste sont (i) la rareté, (ii) l'attractivité de la plante, vis-à-vis de la cueillette ou d'un usage commercial, (iii) l'endémisme, (iv) le type biologique, (v) les taux d'extinction ou de destruction des habitats, souvent combinés ensemble. La liste révisée comporte 543 espèces, soit 25% des 2167 végétaux supérieurs recensés en Israël. Dans cette liste rouge, 119 espèces ne se rencontrent que dans 1 à 3 sites, et 307 plantes sont présentes dans moins de 30 sites. Cette proposition de nouvelle liste rouge représente un outil actuellement plus adapté à la conservation de la nature en Israël, en regard des divers paramètres responsables des probabilités d'extinction des espèces végétales.

Mots-clés

Mesures de conservation, espèces endémiques, liste rouge, destruction des habitats, loi de protection de la nature, espèces rares.

INTRODUCTION

The biodiversity on Earth undergoes extinction through human activities in an increasing rate in the last decades (Pimm & Raven, 2000). Conservation efforts should rely on legal status and official policy, thus demanding special conservation laws in each country. One of the most important acts of nature conservation in Israel was the publishing the law of "Protected Natural Values" in 1964. An appendix to the law included a species list, since protected by law (Paz, 1981). Today the list includes 268 wild plant species that are protected throughout Israel. The last revision was done in 1992 and hence is no more sufficient and requires revision. Here we propose an update and revised list of plant species to be protected. The new list is a result of field, literature and herbarium surveys, and arose after re-evaluating the framework for identifying vulnerable and endangered species.

The previous list : history, advantages and deficiencies

The previous list of protected plant species was based mainly on the attractivity of plants as a major cause of destruction (e.g. flowers picking and bulb uprooting). There is no contesting the fact that this law saved some attractive plants (e.g. *Oncocylus* irises, Peony and Candid lily) from extinction or at least from drastic declining of the populations, but on the other hand, none of the 67 extinct plant species of Israel were included in the list.

The first list of plants protected by law published in 1964 consists of about 70 protected wild plant species and emphasised the need to protect plants from collecting (Paz, 1981). Paz (1981) states that "In those days, very few believed that deterioration of wild plants populations can be stopped". The list was as short as possible and included three main groups: (i) large and attractive flowers, (ii) exploitation plants, and (iii) shrubs and trees. The first group of plants contains species with attractive large flowers, mainly of the *Orchidaceae*, *Liliaceae*, *Iridaceae* and *Amaryllidaceae* families. This group includes species such as *Lilium candidum* L., *Hyacinthus orientalis* L., *Sternbergia clusiana* (Ker-Gawler) Sprengel, and all the species in genera like *Iris*, and *Tulipa*, etc. The list also included some very common geophytes such as *Anemone coronaria* L., *Ranunculus asiaticus* L. and *Cyclamen persicum* Miller, of which their populations were by then declining. All those species considered to be threatened due to massive collecting.

A second group of species was added to the list in 1977. These consisted of some commonly collected wild herbs, such as *Origanum syriacum* L., *Coridothymus capitatus* (L.) Reichenb. F. and *Salvia fruticosa* Miller. All those herbs are harvested in great quantities in the Mediterranean region for commercial use, mainly in the West Bank, and are exported to the Gulf emirates. It is interesting to note that *Gundelia tournefortii*, despite being heavily harvested, was not included in the list.

The third group of protected plants is trees and shrubs. Some of the trees are protected by the "Order of forestry", published by the British mandate at the beginning of the 20th century. Consequently, Oak, Terebinth, Olive, Poplar, Eucalyptus and Casuarina are protected. 23 tree species of the Mediterranean region of Israel are protected and all the wild trees of the Negev (Paz, 1981).

The 1983 and 1992 corrections to the law have added many new species to the original list, which now includes 286 plant species. It includes herbaceous plants and 66 tree species as well. In some cases the whole genera is listed, such as *Tamarix*, *Iris*, *Fritillaria*, *Colchicum*, *Limonium*, *Crataegus*, and *Ziziphus*.

The old list includes many ambiguities. It includes plant species that are highly abundant, whole genera without specifying the species, plants that are not natives in Israel and general groups such as "all the trees in the Negev". On top of it, picking of flowers had decreased throughout the seventies, thus the attractiveness is no longer essential for determining vulnerability. Since the species were not selected on the basis of any quantitative data, it is highly insufficient for conservation. We suggest that an updated list is needed.

Rarity as an entry threshold

We propose that rarity should be the main entry criterion, as rarest plants are the most likely to undergo extinction. We suggest attributing the highest protection priority to the rarest plants. The main question is to define what rarity is. Many studies dealing with this question of rarity have been published so far, with a wide range of definitions to rarity (e.g. Rabinowitz, 1981; Gaston, 1994; Gaston, 1997 and references therein). Cohen and Shmida (1992) assessed rarity based on summing as many as 19 quantitative parameters. Such a method is theoretically accurate, but is too complex to utilize. Therefore, we suggest to use a simple index of rarity - defined by the area of species occupancy. This can be applicable by a simple count of the number of sites where the species persist (Gaston, 1994; Gaston, 1997; Gaston *et al.* 2000).

Number of sites is an easy way to assess rarity, while also supplying information on the geographic range. It is also positively correlated to population size (Gaston *et al.*, 2000; He & Gaston, 2000).

A site is defined as one square km grid cell on the map (Gaston, 1994), hence the rarity value is the number of one square km grid cells in which the plant is present. The limits of the sites defined by the map net lines seem to be affected by the location of the start point, but this effect is not significant (Nathan & Shmida, unpublished data).

The next step is to determine how many sites are needed for a species to be considered as rare. Israel is approximately 22,000 square kilometres (22,000 potential sites). We suggest that a rare species is a species that is present in less than 0.5% of the area, which are 110 sites. Species that occur in less than 110 sites are "rare" and those occurring in less than 22 sites (0.1% of the area) are "very rare". As half a percent is an arbitrary value, we used an approximation to 100 sites for rare and 30 sites for very rare, using numbers that are easy to focus on. The quantitative parameter of rarity is a threshold readily changeable according to the area of the region in question.

Results of a survey of the rare plants (Fragman & Shmida, 1994-1997) points out that extinction occurred not to attractive plants, but rather to species that were present in very few sites (1-3 sites) previous to extinction (Fragman *et al.*, 1999a). Moreover, extinction occurred in habitats that were highly susceptible to destruction (Fragman *et al.*, 1999a).

THE NEW SUGGESTED LIST: CRITERIA FOR PROTECTION

The following criteria were used for including a plant species in the proposed list species to be protected by law. It is important to note that the criteria are not mutually exclusive and a species may be included in more than one criterion.

1. *Rarity* - Entry of a plant species into the list is primarily the rarity parameter. The list includes all the plant species present in fewer than 30 sites in Israel ("very rare") and plant species that are present in fewer than 100 sites and fulfil any of the other criteria.

2. *Attractivity* - Rare plants (fewer than 100 sites in Israel) that have big and colourful flower or inflorescence, as well as plants that are exploited for commercial or medicinal use.

3. *Endemism* - Rare plants that are endemic to Israel and neighbouring regions.

4. *Life form* - Rare plants (fewer than 100 sites in Israel) that are trees and shrubs.

5. *Rate of extinction and habitat destruction* - A plant species defined as declining if its' rate of extinction is over 30% since 1965. The rate of extinction is calculated by the number of sites from which a plant disappeared since 1965, after the establishment of the law (Fragman *et al.*, 1999a). Rare plants whose habitat is highly degradable were also included in this criterion, because the rate of extinction is correlated to habitat destruction (Fragman *et al.*, 1999a).

Following the criteria above, a new list of 543 species was prepared (see Appendix, p. 59). We examined all the plant species known from fewer than 100 sites in Israel, a total of 791 species. These comprise about a third of the Israeli flora. Species were checked in both field survey and herbarium sheets, to determine their exact distribution and relative abundance. They were also diagnosed by flower size, endemism and habitat type.

Episodic plants, vagrant species and species whose systematic is doubtful were not included (Gaston, 1994). There is no special need to preserve episodic species, such as *Gnaphalium luteo-album* L., *Plantago scabra* Moench, *Sisymbrium septulatum* DC., *Ballota nigra* L. and *Trigonella glabra* Thunb., which were found in very few sites, but do not establish a stable population. This ensures that the list consists only of native plants, which represent the ecology and biodiversity of Israel.

Of the 543 species included in the new list, 119 species are present in 1 to 3 sites only and 307 species present in 3 to 29 sites ("very rare"). The list includes 25.05% of the 2167 indigenous plant species of Israel, very similar to the suggested quartile cut-off for rarity determination (Gaston, 1994; Gaston, 1997).

Table 1 lists the distribution of plant species among the criteria suggested to be of a top priority for conser-

	Total revised list		Very rare species	
	No.	%	No.	%
Very rare (< 30 sites)	459	84.5		
Endemic	50	9.2	16	2.9
Attractive	83	15.3	39	7.2
Rate of extinction	174	32.0	36	6.6
Endangered habitat	173	31.8	30	5.5
Total	543	100	84	15.5

Table 1. Distribution of rare plant species of Israel among the criteria suggested. Criteria are not mutually exclusive

vation efforts. 84.5% of the 543 species are very rare, i.e. present in less than 30 sites. About a third are plant species, which declined over 30% since 1965, and are highly susceptible to habitat destruction. Only 15.3% of all species in the new list have attractive flowers.

84 plants (15.5%) were included not because of their rarity, but due to other major aspects of conservation: 16 species are endemic; 39 are very attractive; and about 30 species grow in declining habitats that are under immediate destruction threats. The populations of 36 species steeply declined since 1965. However, all the plants are also rare – they are present in fewer than 100 sites in Israel.

SUMMARY AND CONCLUSIONS

Based on the checklist of the Israel flora (Fragman *et al.*, 1999b) the total number of wild species in Israel (including Golan Heights and the Palestinian Authority) is 2399. The total number of wild species in the area covered by the Flora Palaestina (including also Mt. Hermon and Jordan) is 2600. The number of native plants in Israel (excluding vagrants, episodic, doubtful and species that escaped from cultivation) is 2167, and of this 25% are endangered and need to be protected. Climatic analysis of the flora of Israel revealed 1449 species in the Mediterranean region and 565 desert species. The Mediterranean Basin is a hotspot of diversity (Myers *et al.*, 2000), thus the Mediterranean flora of Israel is important on a global scale as well. 67 plant species became extinct in Israel (few are still found in the Golan Heights) since 1965 (Fragman *et al.*, 1999a).

The existing list of plants species protected by the law is insufficient for the current conservation needs of Israel. Our new proposed list is based on objective criteria to determine the plants that should be protected by the law. In addition to the attractiveness of species, we suggest the addition of very rare plants and of plants whose populations are declining rapidly. Unlike other lists, which are based mainly on rarity estimations, our list is based on quantitative unambiguous parameters. The threatened plant species in Israel comprises one quarter of the whole flora of Israel. The chances of these species to survive are highly dependent on large-scale preservation policy. Such policy is applicable with the use of an updated list of endangered plant species and identification of spatial “hot-spots” of rare plants, to point out priorities for nature conservation.

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APPENDIX: PROPOSED LIST OF "RED PLANTS" OF ISRAEL

Legend : Abu = Abundance: X - extinct; O - very rare, 1 to 3 sites; RR - very rare, 4 to 30 sites; RP - rare, 31 to 100 sites. Att = Attractivity: 1 - attractive flower; 2 - very attractive flower or colourful inflorescence; 3 - attractive for collection, e.g. Cacti or medicinal plants. End = endemism type: EI - endemic to Israel; ES - Sub endemic, present also in Sinai, Lebanon coast or in Jordan; EL - endemic to the Levant, from Syria to Egypt. Lf = life form: A - Annual; F - Biennial; C - Chamaephyte; G - Geophyte; H - Hemicryptophyte; S - Shrub; T - Tree; V - Vine; P - Parasite; Q - Aquatic plant. Dyn = rate of extinction (dynamics): D - number of sites decreased over 30% since 1966; ND - number of sites did not change since 1966. Hab V = habitat vulnerability: 1 - threatened habitat; 2 - critically endangered habitat. -1 = missing value. Species names are according the checklist of Israel plants (Fragman *et al.*, 1999b).

Species	Author	Abu	Att	End	Lf	Dyn	Hab V	Species	Author	Abu	Att	End	Lf	Dyn	Hab V
<i>Abutilon hirtum</i>	(L.) Sweet	RR			S			<i>Aristida sieberiana</i>	Trin.	RR		EI	H	D	
<i>Abutilon indicum</i>	(L.) Sweet	RR			S	ND		<i>Aristolochia billardieri</i>	Jaub. & Spach	RR		EL	V	ND	
<i>Acacia albida</i>	Delile	RP	1		T	D		<i>Arnebia hispidissima</i>	(Lehm.) DC.	RR			A	ND	
<i>Acantholepis orientalis</i>	Less	RR			A	ND		<i>Asphodelus refractus</i>	Boiss.	RR			G	ND	
<i>Acer obtusifolium</i>	Sm.	RP	1	EL	T	ND		<i>Asphodelus viscidulus</i>	Boiss.	RR			G	ND	
<i>Adonis aestivalis</i>	L.	RR			A	ND		<i>Asplenium trichomanes</i>	L.	O			H	ND	
<i>Aegialophila pumilio</i>	(L.) Boiss.	RR	1		H	ND	2	<i>Aster tripolium</i>	L.	O			H	ND	2
<i>Aegilops crassa</i>	Boiss.	O			A	ND		<i>Astragalus bombycinus</i>	Boiss.	RR			A	ND	
<i>Aegilops speltoides</i>	Tausch	RR			A	D		<i>Astragalus campylorrhynchus</i>	Fisch. & Mey.	O			A	-1	
<i>Aethionema carneum</i>	(Banks & Sol.) Fedtsch.	O			A	D		<i>Astragalus corrugatus</i>	Bertol.	RR			A	ND	
<i>Agrimonia eupatoria</i>	L.	X			H	D		<i>Astragalus deinacanthus</i>	Boiss.	RP	1		C	D	
<i>Agrostemma githago</i>	L.	O	1		A	D	2	<i>Astragalus eremophilus</i>	Boiss.	RR			A	ND	
<i>Alcea striata</i>	(DC.) Alef.	RR			H	ND		<i>Astragalus fruticosus</i>	Forssk.	RR			H	D	
<i>Alisma plantagoaquatica</i>	L.	O			H	ND	2	<i>Astragalus guttatus</i>	Banks & Sol.	RR			A	ND	
<i>Alkanna galilaea</i>	Boiss.	RR		EI	H	D	1	<i>Astragalus hauarensis</i>	Boiss.	RR			A	ND	
<i>Alliaria petiolata</i>	(M. Bieb.) Car. & Gra	O			A	ND		<i>Astragalus intercedens</i>	Sam.	RR			A	ND	
<i>Allium albotunicatum</i>	O. Schwarz	O			G	ND		<i>Astragalus ocephalus</i>	Boiss.	O	1		H	D	1
<i>Allium negevense</i>	Kollm.	RR		EI	G	ND		<i>Astragalus schimperi</i>	Boiss.	RR			A	ND	
<i>Allium papillare</i>	Boiss.	RR		ES	G	D		<i>Astragalus scorpioides</i>	Pourr.	O			A	ND	
<i>Allium sinaiticum</i>	Boiss.	RR		ES	G	D		<i>Astragalus sieberi</i>	DC.	RR			C	ND	
<i>Allium sindjarense</i>	Boiss. & Hausskn.	RR			G	ND		<i>Astragalus sparsus</i>	Delile	RR			H	ND	
<i>Allium tardiflorum</i>	Kollm. & Shmida	RR			G	ND		<i>Astragalus trimestris</i>	L.	RR			A	ND	
<i>Althaea ludwigii</i>	L.	RR			A	ND		<i>Atraphaxis spinosa</i>	L.	O			C	ND	
<i>Althaea officinalis</i>	L.	X			H	D	2	<i>Atriplex dimorphosteg</i>	Kar. & Kir.	RR			A	ND	
<i>Ammannia auriculata</i>	Willd.	RR			A	D	2	<i>Atriplex lasiantha</i>	Boiss.	O			A	ND	
<i>Amygdalus arabica</i>	Olivier	O			T	ND		<i>Bacopa monnieri</i>	(L.) Pennell	RR			H	D	2
<i>Amygdalus ramonensis</i>	Danin	RR		EI	T	ND		<i>Ballota philistaea</i>	Bornm.	RP		EI	H	D	2
<i>Anacyclus radiatus</i>	Loisel	O	2		A			<i>Bellevalia longipes</i>	Post	RP			G	D	1
<i>Anchusa negevensis</i>	Danin	O		EI	H	ND		<i>Bellevalia zoharyi</i>	Feinbrun	RR		ES	G	ND	
<i>Anchusa ovata</i>	Lehm.	RR			A	ND	1	<i>Bergia ammanioides</i>	Heyne	O			A	D	
<i>Androsace maxima</i>	L.	RR			A	ND		<i>Biarum auranticum</i>	Mout.	O			G	ND	
<i>Andzeiowskia cardamine</i>	Reichenb.	O			A	ND		<i>Biarum olivierii</i>	Blume	O		ES	G	ND	
<i>Anthemis brachycarpa</i>	Eig	-1		ES	A	-1		<i>Blumea bovei</i>	(DC.) Vatke	RR			H	ND	
<i>Anthemis chia</i>	L.	RR			A	D		<i>Boerhavia repens</i>	L.	RR			C	D	
<i>Anthehora laevis</i>	Stapf & C.E. Hubb	X			H	D		<i>Boissiera squarrosa</i>	(Banks & Sol.) Nevski	RR			A	ND	
<i>Antinoria insularis</i>	Parl.	RR			A	ND		<i>Bolanthus filicaulis</i>	(Boiss.) Bark.	O			F	ND	
<i>Antirrhinum siculum</i>	Mill.	RR	1		C			<i>Brachiaria eruciformis</i>	(Sm.) Griseb.	O			A	-1	
<i>Arabidopsis thaliana</i>	(L.) Heynh.	RR			A	ND		<i>Brachiaria mutica</i>	(Forssk.) Stapf	RR			H	-1	
<i>Arabis alpina</i>	Schlecht.	O	1		H	ND		<i>Brassica cretica</i>	Lam.	O	1		C	ND	
<i>Arabis auriculata</i>	Lam.	O			A	ND		<i>Bunium paucifolium</i>	DC.	RR			G	ND	1
<i>Arabis turruta</i>	L.	RR			H	ND									
<i>Arenaria deflexa</i>	Decne.	RR			C	ND									
<i>Arenaria tremula</i>	Boiss.	RR		EL	A	ND									
<i>Aristida adscensionis</i>	L.	RR			A	-1									

Species	Author	Abu	Att	End	Lf	Dyn	Hab	V	Species	Author	Abu	Att	End	Lf	Dyn	Hab	V
<i>Bupleurum boissieri</i>	Post	RR			A	ND			<i>Crassula vaillantii</i>	(Willd.) Roth	RR			A	ND		
<i>Bupleurum brevicaulis</i>	Schlecht.	RR			A	ND	1		<i>Crataegus azarolus</i>	L.	RR	1		T			
<i>Bupleurum gerardii</i>	All.	O			A	ND			<i>Crataegus monogyna</i>	Jacq.	RR	1		T	ND		
<i>Bupleurum orientale</i>	Snogerup	RR			A	ND	1		<i>Crepis foetida</i>	L.	RR			A	ND		
<i>Butomus umbellatus</i>	L.	RP	1		H	D	2		<i>Crepis micrantha</i>	Czerep.	RR			A	ND		
<i>Callipeltis factorovskyi</i>	(Eig) Ehrend.	RR			A	D	1		<i>Crepis pterothecoides</i>	Boiss.	RR			A	ND		
<i>Callitriche lenisulca</i>	Clav.	RR			H	D	2		<i>Crepis pulchra</i>	L.	RR			A	ND		
<i>Callitriche truncata</i>	Guss.	RR			H	ND	2		<i>Crepis zacintha</i>	(L.) Babç.	O			A	-1		
<i>Campanula damascena</i>	Labill.	RP	1	EL	C	ND			<i>Crocus cancellatus</i>	Herbert	RP	1		G	ND		
<i>Campanula peregrina</i>	L.	O			H	ND			<i>Crocus hermoneus</i>	Kotschy ex Maw	RR	1	EI	G	D		
<i>Campanula phrygia</i>	Jaub. & Spach	O	1		A	ND			<i>Crocus vitelinus</i>	Wahlenb.	O			G	ND		
<i>Campanula sidoniensis</i>	Boiss. & Blanche	RR		EL	A	ND			<i>Crucianella maritima</i>	L.	RP			C	D	2	
<i>Caralluma sinaica</i>	(Decne.) A. Berger	RP	3	ES	C	ND			<i>Crypsis acuminata</i>	Trin.	RR			A	D	2	
<i>Cardopatum corymbosum</i>	(L.) Pers.	RR	1		H	D	1		<i>Crypsis faktorovskyi</i>	Eig	RR			A	D	2	
<i>Carex acutiformis</i>	EHRH.	RR			H	D	2		<i>Crypsis minuartioides</i>	(Bornm.) Mez	O		EI	A	D	2	
<i>Carex flacca</i>	Schreb.	RP			H	ND	2		<i>Cucumis acidus</i>	Jacq.	RR			H	D	1	
<i>Carlina racemosa</i>	L.	O			A	D			<i>Cupressus sempervirens</i>	L.	O			T	ND		
<i>Catabrosa aquatica</i>	(L.) Beauv.	RR			H	D	2		<i>Cuscuta epilinum</i>	Weihb	X			P			
<i>Catapodium marinum</i>	(L.)	RR			A	ND	2		<i>Cuscuta gemmesaretana</i>	Sroelov	X		EL	P			
<i>Celtis australis</i>	L.	RP			T				<i>Cutandia maritima</i>	(L.) W. Barbey	RR			A	ND	2	
<i>Centaurea scoparia</i>	Sieb. ex Spreng.	RR			C	ND			<i>Cyclamen coum</i>	Mill.	RP	1		G	ND		
<i>Centaurea sinaica</i>	DC.	RR			A	ND			<i>Cymbopogon commutatus</i>	(Steud.) Stapf	RR			H	ND		
<i>Centaurea speciosa</i>	Boiss.	RP	1		C	ND			<i>Cymodocea nodosa</i>	(Ucria) Asch.	O			Q	-1	2	
<i>Centaureum erythraea</i>	Rafn	RP	1		F	D			<i>Cymodocea rotundata</i>	Ehrenb. & Hemprich	RR			Q	-1		
<i>Centaureum maritimum</i>	(L.) Fritsch	RR			A	D	2		<i>Cyperus corymbosus</i>	Rottb.	O			H	D	2	
<i>Cephalaria syriaca</i>	(L.) Schrad.	RP			A	D	1		<i>Cyperus dives</i>	Rottb.	RP			H	D	2	
<i>Ceratophyllum submersum</i>	L.	O			Q	D			<i>Cyperus eleusinoides</i>	Kunth	O			H	ND		
<i>Chorispora purpurascens</i>	(Banks & Sol.) Eig	O			A	ND			<i>Cyperus flavidus</i>	Retz.	RP			H	D	2	
<i>Chrozophora oblongifolia</i>	(Delile) Juss.	RR			C	ND			<i>Cyperus nitidus</i>	Lam.	O			H	D		
<i>Chrozophora plicata</i>	(Vahl) Juss.	RR			A	ND			<i>Cyperus papyrus</i>	L.	RR			H	D	2	
<i>Chrysanthemum viscosum</i>	Desf.	RP			A	D			<i>Cyperus sharonensis</i>	Danin	RR		EI	H	ND		
<i>Cirsium alatum</i>	(S. G.) Gmel.) Bobrov	O			H	ND			<i>Cytinus hypocistis</i>	(L.) L.	RP	1		P	ND		
<i>Cirsium gaillardotii</i>	Boiss.	RR		EL	H	D			<i>Cytisopsis pseudocytisus</i>	(Boiss.) Fertig	RR			C	D		
<i>Cirsium vulgare</i>	(Savi) Ten.	RR			H				<i>Dactylorhiza romana</i>	(Sebast.) Soo	O			G			
<i>Cladium mariscus</i>	(L.) Pohl	RR			H	D	2		<i>Daucus guttatus</i>	Sm.	O			A	ND		
<i>Clinopodium vulgare</i>	L.	RR			H	ND			<i>Descurainia sophia</i>	(L.) Webb	O			A	ND		
<i>Colchicum brachyphyllum</i>	Boiss. & Hausskn.	RR	1	EL	G	ND	1		<i>Dianthus sinaicus</i>	Boiss.	RP		ES	C	ND		
<i>Colchicum schimperi</i>	Janka ex Stef.	O			G	ND			<i>Dichanthium foveolatus</i>	(Delile) Stapf	RR			HN		D	
<i>Cometes abyssinica</i>	R. Br.	O			A	ND			<i>Echinops gamlensis</i>	Shmida	O	2		H	ND		
<i>Consolida scleroclada</i>	(Boiss.) Schrodgr.	O			A	ND			<i>Echinops viscosus</i>	DC.	RR	2	EL	H	ND		
<i>Convolvulus fatmensis</i>	Kunze	O			F	-1			<i>Elaeagnus angustifolia</i>	L.	RR	1		T	ND		
<i>Convolvulus lanatus</i>	Vahl	RP	1		C	ND			<i>Elatine alsinastrum</i>	L.	O			Q			
<i>Corchorus olitorius</i>	L.	RR			A	D	1		<i>Elatine macropoda</i>	Guss.	RR			A	ND	2	
<i>Corchorus trilocularis</i>	L.	RR			A	D	1		<i>Elymus elongatus</i>	(Host) Nevski	RR			H	D	1	
<i>Cordia sinensis</i>	Lam.	O			T	ND			<i>Enarthrocarpus arcuatus</i>	Labill.	RR			A	D	2	
<i>Corrigiola litoralis</i>	L.	O			F	D			<i>Emneapogon desvauxii</i>	P. Beauv.	RR			H	ND		
<i>Corrigiola palaestina</i>	Chaudh.	O			H	D			<i>Emneapogon persicus</i>	Boiss.	O			H	ND		
<i>Corydalis triternata</i>	Zucc.	RR			G	ND			<i>Ephedra alata</i>	Decne.	O			S	D		
<i>Crambe orientalis</i>	L.	O			H	ND											

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<i>Epipactis helleborine</i>	(L.) Crantz	RP			G	ND		2	<i>Halophila stipulacea</i>	(Forssk.) Asch.	RR			Q			-1
<i>Epipactis veratrifolia</i>	Boiss. & Hohen	RR	1		G	ND		2	<i>Hammada negevensis</i>	Ijlin & Zohary	RP		ES	C			ND
<i>Equisetum ramosissimum</i>	Desf.	RR			H	D		2	<i>Haplophyllum poorei</i>	Townes.	RR		ES	C			ND
<i>Eremopyrum distans</i>	(Koch) Nevski	RR			A	ND			<i>Hesperis pendula</i>	DC.	RR			H			ND
<i>Eriolobus trilobatus</i>	(Labill.) Roem.	O	1	EL	T	ND			<i>Heterantheium piliferum</i>	(Banks & Sol.) Hochst.	RR			A			
<i>Erodium subintegrifolium</i>	Eig	RP		EI	A	D		2	<i>Himantoglossum caprinum</i>	(Bieb.) Spreng.	RR			G			ND
<i>Eryngium barrelieri</i>	Boiss.	RR			H	D		2	<i>Hippocrepis constricta</i>	Kunze	RR			A			ND
<i>Eryngium maritimum</i>	L.	RP	1		H	D		2	<i>Hydrocotyle ranunculoides</i>	L. f.	RR			Q	D		2
<i>Euphorbia dendroides</i>	L.	RR			S	D			<i>Hydrocotyle sibthopoides</i>	Lam.	O			Q	ND		2
<i>Euphorbia forsskalii</i>	Gay	O			A	ND			<i>Hymenolobus procumbens</i>	(L.) Fourr.	RR			A			ND
<i>Euphorbia granulata</i>	Forssk.	RR			A	ND			<i>Hyoscyamus albus</i>	L.	RR			F			ND
<i>Euphorbia grossheimii</i>	Prokh.	RR			A	ND			<i>Hypericum amblyosepalum</i>	Hochst.	RR			C	D		1
<i>Euphorbia hirsuta</i>	L.	RR			H	D		1	<i>Hypericum hircinum</i>	L.	RR	1		S	D		2
<i>Euphorbia microsphaera</i>	Boiss.	RR			A	D		2	<i>Hypericum tetrapterum</i>	Fries	RR			C	ND		2
<i>Euphorbia pepelis</i>	L.	RR			A	D		2	<i>Hyphaene thebaica</i>	(L.) Mart.	O			T	D		
<i>Euphorbia phymatosperma</i>	Boiss. & Gaill.	O			A	D			<i>Hypochoeris glabra</i>	L.	RR			A	ND		2
<i>Fagonia tenuifolia</i>	Steud. & Hochst.	RR			C	ND			<i>Iberis odorata</i>	L.	O			A	ND		
<i>Ferula biverticillata</i>	Thieb.	RR	1		H	D		1	<i>Iphiona marismortui</i>	Feinbrun	RR		EI	C	ND		
<i>Ferula daninii</i>	Zohary	RR		EI	H	ND			<i>Ipomoea sagittata</i>	Poir.	RR			V	D		
<i>Ferula meironensis</i>	sp. nov.	O	1	EI	H	ND			<i>Iris atrofusca</i>	Baker	RP	2	EI	G	ND		
<i>Ferula oreintalis</i>	L.	RR		EI	H	ND			<i>Iris atropurpurea</i>	Baker	RP	2	EI	G	D		
<i>Ferula ovina</i>	Zohary	RP		EI	H	ND			<i>Iris bismarckiana</i>	Regel	RP	2	EI	G	ND		
<i>Ferula sinaica</i>	Boiss.	RR			H	ND			<i>Iris grant-duffii</i>	Baker	RP	2		G	ND		1
<i>Fraxinus syriaca</i>	Boiss.	RP			T	D			<i>Iris haynei</i>	Baker	RP	2	EI	G	ND		
<i>Fuirena pubescens</i>	(Poir.) Kunth	RR			H	D			<i>Iris hermona</i>	Dinsm.	RP	2		G	ND		
<i>Gagea villosa</i>	(M. Bieb.) Duby	RR			G	D		1	<i>Iris histrio</i>	Reichenb. f.	RP	1	EL	G	ND		
<i>Galium canum</i>	Req.	O			C	ND			<i>Iris lortetii</i>	W. Barbey	RP	2	EI	G	ND		
<i>Galium cassium</i>	Boiss.	RR			A	ND			<i>Iris mariae</i>	W. Barbey	RP	2	ES	G	ND		
<i>Galium chaetopodium</i>	Rech. f.	RR		EL	A	ND		1	<i>Iris petrana</i>	Dinsm.	RR			G			
<i>Galium hierochuntinum</i>	Bornm.	RR		EI	A	ND			<i>Iris pseudacorus</i>	L.	RR	2		G	D		2
<i>Galium philistaicum</i>	Boiss.	RP		EI	A	D		2	<i>Iris regis-uzziae</i>	Feinbrun	RP	1	ES	G	ND		
<i>Galium rivale</i>	(Sm.) Griseb.	RP			H	D			<i>Juncus articulatus</i>	L.	RR			H	D		2
<i>Galium spurium</i>	L.	RR			A	ND			<i>Juncus capitatus</i>	Weigel	O			A	ND		
<i>Gastroidium ventricosum</i>	(Gouan) Schinz & Thell.	RR			A	ND			<i>Juncus inflexus</i>	L.	RR			H	D		2
<i>Geranium columbinum</i>	L.	RR			A	ND			<i>Juncus punctorius</i>	L. f.	O			H	-1		
<i>Geranium libani</i>	Davis	RP	1	EL	G	ND			<i>Juncus subulatus</i>	Forssk.	RR			H	ND		2
<i>Glaucium arabicum</i>	Fresen.	RR			H	ND			<i>Juniperus oxycedrus</i>	L.	O			T	ND		
<i>Glossonema boveanum</i>	(Decne.) Decne.	RR			C	ND			<i>Jurinea staezelinae</i>	(DC.) Boiss.	RR		EL	C	ND		
<i>Glyceria plicata</i>	(Fries) Fries	O			H	D		2	<i>Kickxia judaica</i>	Danin	RP		EI	C	ND		
<i>Glycyrrhiza glabra</i>	L.	RP			H	D		2	<i>Lachnophyllum noeatum</i>	Boiss.	RR			F	ND		1
<i>Gomphocarpus sinaicus</i>	Boiss.	RR			C	ND			<i>Lactuca aculeata</i>	Boiss. & Kotschy	RP			A	ND		1
<i>Gonocytisus pterocladus</i>	(Boiss.) SP.	RR	1	EL	S	ND			<i>Lallemantia iberica</i>	(M. Bieb.) Fisch. & Mey.	O			A	D		
<i>Grewia villosa</i>	Willd.	O			S	D			<i>Lathyrus cassius</i>	Boiss.	RR			A	ND		
<i>Gypsophila pilosa</i>	Huds.	RR			A	ND			<i>Lathyrus cicera</i>	L.	O			A	-1		
<i>Gypsophila viscosa</i>	Murray	RR			A	ND			<i>Lathyrus gleospermus</i>	Warb. & Eig	RR			A	ND		1
<i>Halodula uninervis</i>	(Forssk.) Asch.	RR			Q	-1			<i>Lathyrus inconspicuus</i>	L.	RR			A	ND		
<i>Halophila ovalis</i>	(R. Br.) Hook. f.	RR			Q	-1			<i>Lathyrus lentiformis</i>	Plitm.	O		EI	A	ND		
									<i>Lathyrus nissolia</i>	L.	RR			A	ND		
									<i>Lathyrus setifolius</i>	L.	O			A	D		2

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<i>Lathyrus sphatulatus</i>	(M. Bieb.) Fiori	RP	1	EL	H	ND			<i>Monsonia heliotropioides</i>	(Cav.) Boiss.	RR			H	ND		
<i>Lathyrus sphaericus</i>	Retz.	RR			A	ND			<i>Monsonia nivea</i>	(Decne.) Decne.	RR			H	ND		
<i>Launaea spinosa</i>	(Forssk.) Sch. Bip.	RR			S	ND			<i>Morettia parviflora</i>	Boiss.	RR			C	ND		
<i>Lavandula stoechas</i>	L.	RP	1		C	ND	2		<i>Moricandia sinaica</i>	(Boiss.) Boiss.	RR			A	ND		
<i>Lavatera bryoniifolia</i>	Mill.	RR	1		S	ND			<i>Moringa peregrina</i>	(Forssk.) Fiori	RR	1		T	ND		
<i>Leersia hexandra</i>	Sw.	RR			H	D	2		<i>Mosheovia galilaea</i>	Eig	RR		EL	A	ND	1	
<i>Legousia hybrida</i>	(L.) Delarbre	O			A	ND			<i>Myagrum perfoliatum</i>	L.	RR			A	ND	1	
<i>Leopoldia deserticola</i>	(Rech. f.) Feinbrun	X			G	D			<i>Myosurus minimus</i>	L.	RR			A	ND	2	
<i>Lepidium aucheri</i>	Boiss.	O			A	-1			<i>Myriophyllum spicatum</i>	L.	RR			H	ND	2	
<i>Lepidium latifolium</i>	L.	RR			H	D	1		<i>Myrrhoides nodosa</i>	(L.) Cannon	RR			A	ND		
<i>Lilium candidum</i>	L.	RR	2		G	ND			<i>Najas minor</i>	All.	O			A	D	2	
<i>Limonium graecum</i>	(Poir.) O. Kuntze	RR			H	ND	2		<i>Narcissus serotinus</i>	L.	RR	1		G	ND	2	
<i>Linaria pelisseriana</i>	(L.) Mill.	RR			A	D	2		<i>Neotinea maculata</i>	(Desf.) Stearn	RR			G	ND		
<i>Linaria triphylla</i>	(L.) Mill.	O	1		A	D	1		<i>Nigella nigellastrum</i>	(L.) Willk.	O			A	ND		
<i>Lindenbergia sinaica</i>	(Decne.) Benth.	O			C	ND			<i>Nigella segetalis</i>	M. Bieb.	O			A	ND		
<i>Linum maritimum</i>	L.	O			H	D	2		<i>Nonea melanocarpa</i>	Boiss.	RR			A	ND		
<i>Lisaea strigosa</i>	(Banks & Sol.) Eig	O			A	ND			<i>Nuphar lutea</i>	(L.) Sm.	RR	2		H	ND	2	
<i>Lloydia rubroviridis</i>	(Boiss. & Sol.) Eig	O			G	ND			<i>Nymphaea nauchali</i>	Burm. f.	O	2		H	D	2	
<i>Lobularia libyca</i>	(Viv.) Meissn.	RR			A	ND			<i>Oenanthe fistulosa</i>	L.	RR			H	D	2	
<i>Loeflingia hispanica</i>	L.	RR			A	ND			<i>Oenanthe pimpinelloides</i>	L.	O			H	D	2	
<i>Lolium persicum</i>	Boiss. & Hohen	RR			A	ND	1		<i>Ogastemma pussillum</i>	(Coss. & Dur.) Brummitt	O			A	ND		
<i>Lotus cytisoides</i>	L.	RR			C	D	2		<i>Oldenlandia capensis</i>	L. f.	RR			A	D	2	
<i>Lotus glaber</i>	Mill.	RP			H	D	2		<i>Onopordum macrocephalum</i>	Eig	O		EL	H	D		
<i>Lotus glinoides</i>	Delile	RR			A	ND			<i>Onosma gigantea</i>	Lam.	RR	1		H	D	1	
<i>Lupinus luteus</i>	L.	RP			A	D			<i>Ophioglossum lusitanicum</i>	L.	RR			H	ND	2	
<i>Lupinus micranthus</i>	Guss.	RP			A	D	2		<i>Ophioglossum polyphyllum</i>	A. Braun	O			H	ND		
<i>Lycium depressum</i>	Stocks	O			S	ND			<i>Ophrys apifera</i>	Huds.	RP	1		G	ND		
<i>Iysimachia dubia</i>	Sol.	RR			A	D	2		<i>Ophrys iricolor</i>	Desf.	RP	1		G	ND		
<i>Iythrwm borysthenicum</i>	(Schrank) Litv.	O			A	D			<i>Orchis coriophora</i>	L.	O			G	ND		
<i>Maerua crassifolia</i>	Forssk.	O			T	ND			<i>Orchis israelitica</i>	Baumann & Dafni	RP		EI	G	ND		
<i>Malva neglecta</i>	Wallr.	RR			A	ND			<i>Orchis italica</i>	Poir.	RP	1		G	ND		
<i>Maresia nana</i>	(DC.) Batt.	RR			A	ND			<i>Orchis laxiflora</i>	Lam.	RP	1		G	D	2	
<i>Matthiola arabica</i>	Boiss.	O			H	ND			<i>Orchis punctulata</i>	Steven ex Lindl.	RR			G	ND		
<i>Medicago constricta</i>	Durleu	RR			A	ND			<i>Orchis syriaca</i>	Boiss. & Bal.	O			G			
<i>Medicago italica</i>	Fiori	RR			A	D	2		<i>Origanum ramonense</i>	(Lam.) Sweet	RR		EI	C	ND		
<i>Medicago murex</i>	Willd.	RR			A	D			<i>Ornithogalum fuscescens</i>	(L.) Sweet	RR		EL	G	D	1	
<i>Melilotus elegans</i>	Salzm.	O			A	ND			<i>Orobanchae lavandulacea</i>	Delile	RR	1		P	ND		
<i>Melilotus italicus</i>	(L.) Lam.	RR			A	ND			<i>Orobanchae palaestina</i>	Less	RR	1		P	ND		
<i>Mentha aquatica</i>	L.	RP			H	ND	2		<i>Orobanchae pubescens</i>	Sm.	RR			P	ND		
<i>Mericarpaea ciliata</i>	(Banks & Sol.) Eig	RR			A	D	1		<i>Oxystelma esculentum</i>	L.	O			V	D		
<i>Michauxia campanuloides</i>	L'Her	RP	2		H	ND			<i>Paeonia mascula</i>	(L.) Boiss.	RR	2		H	ND		
<i>Minuartia globulosa</i>	(Labill.) Schinz & Thell.	RR			A	ND			<i>Paliurus spina-christi</i>	Boiss.	RR	1		S	D		
<i>Moenchia erecta</i>	(L.) P. Gaertn.	RR			A	ND			<i>Papaver decaisnei</i>	Tausch	O			A	ND		
<i>Momordica balsamina</i>	L.	RR			V	D			<i>Parapholis filiformis</i>	(Banks & Sol.) Fedtsch.	RR			A	ND		
									<i>Paronychia echinulata</i>	L.	RR			A	D	2	
									<i>Paronychia palaestina</i>	L.	RR		ES	C	D	2	
									<i>Pentatropis nivalis</i>	(DC.) Alef.	RR			V	ND		

Species	Author	Abu	Att	End	Lf	Dyn	Hab	V	Species	Author	Abu	Att	End	Lf	Dyn	Hab	V
<i>Periploca graeca</i>	L.	O			V	ND			<i>Salsola soda</i>	L.	RR			A	D		2
<i>Petrorhagia arabica</i>	Boiss.	O		ES	A	ND			<i>Salvadora persica</i>	L.	RR			T	ND		
<i>Phlomis platystegia</i>	(M. Bieb.) Car. & Gra	RR		ES	S	ND			<i>Salvia ceratophylla</i>	Kar. & Kir.	O			H	D		
<i>Phlomis pungens</i>	O. Schwarz	RP	1		H	ND		1	<i>Salvia eigii</i>	Boiss.	RR		EI	H	ND		1
<i>Phlomis syriaca</i>	Köllm.	O			C	ND			<i>Salvia multicaulis</i>	(L.) Pennell	O			C	D		
<i>Phyllitis sagittata</i>	Boiss.	O			H	ND			<i>Salvia palaestina</i>	Bornm.	RP			H	D		
<i>Phyllitis scolopendrium</i>	Boiss.	RR			H	ND			<i>Salvia sclarea</i>	Post	RR			H	ND		1
<i>Picris cyanocarpa</i>	Boiss.	RR			A	ND			<i>Salvia syriaca</i>	Feinbrun	RP			H	ND		1
<i>Pimpinella corymbosa</i>	Köllm. & Shmida	RR			H	ND		1	<i>Sambucus nigra</i>	Heyne	RR	1		S	D		
<i>Plantago chamaepsyllium</i>	L.	O			A	ND			<i>Sarcocornia fruticosa</i>	Mout.	RR			C	D		
<i>Plantago crassifolia</i>	L.	RP			H	D		2	<i>Sarcocornia perennis</i>	Blume	RR			C	D		
<i>Platanthera chlorantha</i>	Willd.	RR			G	ND			<i>Satureja thymbriifolia</i>	(DC.) Vatke	O		ES	C	ND		
<i>Platanus orientalis</i>	Olivier	RP			T	D			<i>Saxifraga hederacea</i>	L.	RR			A	ND		
<i>Poa nemoralis</i>	Danin	RR			H	ND			<i>Saxifraga tridactylitis</i>	(Banks & Sol.) Nevski	RR			A	ND		
<i>Polygonum acuminatum</i>	Loisel	RR			H	D		2	<i>Scaligeria hermonis</i>	(Boiss.) Bark.	RR			H	ND		
<i>Polygonum lamgerum</i>	Danin	RR			H	D		2	<i>Scandix australis</i>	(Sm.) Griseb.	RR			A	ND		
<i>Polygonum maritimum</i>	Lehm.	RR			C	D		2	<i>Scandix palaestina</i>	(Forssk.) Stapf	RR			A	ND		1
<i>Polygonum senegalense</i>	L.	RP			H	-1		2	<i>Scandix stellata</i>	Lam.	O			A	ND		
<i>Populus euphratica</i>	Reichenb.	RP			T	ND			<i>Schoenus nigricans</i>	DC.	RR			H	ND		2
<i>Potamogeton berchtoldii</i>	Eig	RR			Q	-1		2	<i>Scilla cilicica</i>	Post	RP	1		G	ND		
<i>Potamogeton crispus</i>	L.	O			Q	D		2	<i>Scleranthus orientalis</i>	Schlecht.	O			A	-1		
<i>Potamogeton filiformis</i>	Stapf & C.E. Hubb	RR			Q	-1		2	<i>Scorzonera pusilla</i>	All.	RR			H	ND		
<i>Potamogeton pectinatus</i>	Parl.	RR			Q	D		2	<i>Scrophularia hierochuntina</i>	Snogerup	RP		EL	H	D		1
<i>Potamogeton perfoliatus</i>	Mill.	RR			Q	D		2	<i>Scrophularia macrophylla</i>	L.	RP			H	D		2
<i>Potamogeton trichoides</i>	(L.) Heynh.	RR			Q	D		2	<i>Scrophularia xylorrhiza</i>	(Eig) Ehrend.	RR			C	ND		
<i>Potentilla reptans</i>	Schlecht.	O			H	ND			<i>Secale montanum</i>	Clav.	RR			H	ND		
<i>Prunus ursina</i>	Lam.	RP	1		T	ND			<i>Sedum lioreum</i>	Guss.	RR			A	ND		2
<i>Psilliostachys spicata</i>	L.	RR			A	D			<i>Sedum palaestinum</i>	Labill.	RR		EL	A	ND		
<i>Pteridium aquilinum</i>	Decne.	O			H	D		2	<i>Setzenia lanata</i>	L.	RR			C	ND		
<i>Pteris vittata</i>	Boiss.	O			H	D			<i>Senna alexandrina</i>	Jaub. & Spach	X			S	D		
<i>Pteroccephalus pulverulentus</i>	L.	RR		ES	C	ND			<i>Silene grisea</i>	Boiss. & Blanche	RR		EL	C	ND		
<i>Ptilostemon chamaepeuce</i>	Trin.	O	1		C	ND			<i>Silene italica</i>	(Decne.) A. Berger	RP	1		H	ND		
<i>Puccinellia distans</i>	Jaub. & Spach	O			H	D		2	<i>Silene macrodonta</i>	(L.) Pers.	O			A	ND		
<i>Ranunculus constantinopolitanus</i>	(L.) DC.	RR	1		H	D		2	<i>Silene modesta</i>	EHRH.	RP		ES	A	D		
<i>Ranunculus lateriflorus</i>	Boiss.	RR			A	ND		2	<i>Silene oxyodonta</i>	Schreb.	RR		ES	A	ND		
<i>Ranunculus saniculifolius</i>	Boiss.	RR			Q	D		2	<i>Silene papillosa</i>	L.	O		EL	A	D		
<i>Ranunculus sceleratus</i>	L.	RR			A	D		2	<i>Silene sedoides</i>	(L.) Beauv.	RR			A	ND		
<i>Ranunculus sphaerospermus</i>	L.	RR			Q	D		2	<i>Silene swertiifolia</i>	(L.) C. E. Hubb.	RR	1		C	ND		
<i>Reichardia intermedia</i>	Boiss.	RR			A	D			<i>Silene tridentata</i>	L.	RR			A	D		
<i>Rheum palaestinum</i>	Fisch. & Mey.	RP		ES	H	ND			<i>Sison exaltatum</i>	Sieb. ex Spreng.	RR		EL	H	ND		
<i>Rhus pentaphylla</i>	Bertol.	O			T	ND		2	<i>Sisymbrium orientale</i>	DC.	RR			A	ND		
<i>Rochelia disperma</i>	Boiss.	RR			A	ND			<i>Sisymbrium runcinatum</i>	Boiss.	RR			A	D		
<i>Romulea columnae</i>	Boiss.	O			G	D			<i>Solanum incanum</i>	Rafn	RR			S	ND		
<i>Rosa phoenicia</i>	Forssk.	RP	1		S	D		2	<i>Solenostemma arghel</i>	(L.) Fritsch	O			C	ND		
<i>Rubia tinctorum</i>	Banks & Sol.	O			V	ND			<i>Sonchus suberosus</i>	(L.) Schrad.	RP		EI	C	ND		
<i>Rumex cassius</i>	Boiss.	RR		EL	H	ND			<i>Sparganium erectum</i>	L.	RR			H	D		2
<i>Rumex rothschildianum</i>	Sam.	RR		EI	A	D		2	<i>Spirodela polyrhiza</i>	(Banks & Sol.) Eig	RR			Q	D		2
<i>Rumex tuberosus</i>	Boiss.	RR			H	ND											
<i>Ruppia maritima</i>	Boiss.	RR			Q	-1		2									
<i>Salix pedicellata</i>	Pourr.	O			T	ND		2									
<i>Salsola oppositifolia</i>	DC.	O			S	ND											
<i>Salsola orientalis</i>	Delile	O			C	ND											

Species	Author	Abu	Att	End	Lf	Dyn	Hab	V	Species	Author	Abu	Att	End	Lf	Dyn	Hab	V
<i>Stachys arvensis</i>	(Delile) Juss.	RR			A	D			<i>Trigonella spicata</i>	Sroelov	RR			A	ND		
<i>Stachys longispicata</i>	(Vahl) Juss.	RR			H	ND		2	<i>Trigonella spruneriana</i>	(L.) W. Barbey	O			A	ND		
<i>Stachys spectabilis</i>	Desf.	O			H	-1		2	<i>Triplachne nitens</i>	Mill.	RR			A	ND		2
<i>Stachys zoharyana</i>	(S. G. Gmel.) Bobrov	O		EI	A	ND			<i>Tripleurospermum oreades</i>	(Steud.) Stapf	RR			H	ND		
<i>Stipagrostis drarii</i>	Boiss.	O			H	ND			<i>Tuberaria guttata</i>	(Ucria) Asch.	RR			A	D		2
<i>Suaeda monoica</i>	(Savi) Ten.	RP			S	D			<i>Tulipa biflora</i>	Ehreb. & Hemprich	RR			G	ND		
<i>Suaeda palaestina</i>	(L.) Pohl	RR		EL	C	D			<i>Turgenia latifolia</i>	Rottb.	RR			A	ND		1
<i>Suaeda splendens</i>	L.	RR			A	D		2	<i>Turritis laxa</i>	Rottb.	RR			F	ND		
<i>Suaeda vera</i>	Boiss. & Hausskn.	RR			C	D			<i>Typha elephantina</i>	Kunth	O			H	ND		
<i>Suaeda vermiculata</i>	Janka ax Stef.	RR			C	D			<i>Typha latifolia</i>	Retz.	RR			H	ND		2
<i>Syringodium isoetifolium</i>	R. Br.	O			Q	-1			<i>Ulmus minor</i>	Lam.	RR			T	D		
<i>Tanacetum negevensis</i>	(Boiss.) Schrodgr.	RR		EI	C	ND			<i>Urtica kioviensis</i>	L.	O			H	ND		
<i>Tephrosia nubica</i>	Kunze	O			C	D			<i>Utricularia exoleta</i>	Danin	O			Q	-1		
<i>Tetragonolobus requienii</i>	Vahl	RP			A	ND		1	<i>Valantia muralis</i>	(L.) L.	RR			A	ND		2
<i>Teucrium montbretii</i>	L.	RR			C	ND			<i>Valerianella carinata</i>	(Boiss.) Fertig	O			A	ND		
<i>Teucrium parviflorum</i>	L.	RR			H	D		1	<i>Valerianella echinata</i>	(Sebast.) Soo	RR			A	ND		
<i>Teucrium procerum</i>	Lam.	RR	1		H	D		2	<i>Valerianella oxycrhynga</i>	Sm.	RR			A	ND		
<i>Teucrium scordium</i>	L.	RR			H	D		2	<i>Valerianella sclerocarpa</i>	(L.) Webb	RR			A	ND		
<i>Teucrium spinosum</i>	Chaudh.	RR			A	D		1	<i>Velesia fasciculata</i>	Boiss.	O			A	ND		2
<i>Thalictrum isopyroides</i>	Zucc.	O			H	ND			<i>Verbascum berytheum</i>	(Delile) Stapf	O		ES	H	D		2
<i>Thelypteris palustris</i>	L.	O			H	D		2	<i>Verbascum caesareum</i>	Shmida	RR	1	EL	H	ND		
<i>Thymelaea gussonei</i>	(Willd.) Roth	O			A	ND			<i>Verbascum galilaeum</i>	DC.	RP	1	EL	H	ND		1
<i>Thymus bovei</i>	L.	RR			C	ND			<i>Verbascum qualebicum</i>	L.	RR	1	EL	H	ND		
<i>Tolpis barbata</i>	Jacq.	RR			A	ND		2	<i>Veronica anagalloides</i>	L.	RR			Q	ND		
<i>Tordylium syriacum</i>	L.	X			A	D			<i>Veronica persica</i>	Guss.	RR			A	ND		
<i>Trachomitum venetum</i>	Czerep.	RR	1		H	D		2	<i>Viburnum tinus</i>	(Host) Nevski	RP			T	ND		
<i>Tragopogon collinum</i>	Boiss.	RR			H	ND			<i>Vicia basaltica</i>	Labill.	O			A	ND		1
<i>Tribulus bimucronataus</i>	L.	RR			A	ND			<i>Vicia cyprica</i>	P.Beauv.	O		EL	A	D		
<i>Tribulus pentandrus</i>	(L.) Babc.	RR			A	ND			<i>Vicia esdraelonensis</i>	Boiss.	O		EI	A	D		1
<i>Trifolium angustifolium</i>	Herbert	O			A	D			<i>Vicia hulensis</i>	Decne.	RR		EI	A	ND		1
<i>Trifolium billardieri</i>	Kotschy ex Maw	O		ES	A	D			<i>Vicia lathyroides</i>	(L.) Crantz	RR			A	ND		
<i>Trifolium grandiflorum</i>	Wahlenb.	RP	1		A	ND			<i>Viola modesta</i>	Boiss. & Hohen	RR			A	ND		
<i>Trifolium hirtum</i>	L.	O			A	ND			<i>Wolffia arrhiza</i>	Desf.	RR			Q	D		2
<i>Trifolium salmoneum</i>	Trin.	RR		EL	A	D			<i>Xeranthemum cylindraceum</i>	(Koch) Nevski	RR			A	ND		
<i>Trifolium suffocatum</i>	Eig	RR			A	D			<i>Ziziphora tenuior</i>	(Labill.) Roem.	O			A	ND		
<i>Trigonella astroites</i>	(Bornm.) Mez	RR			A	ND			<i>Ziziphus nummularia</i>	Eig	O			T	ND		
<i>Trigonella hamosa</i>	L.	O			A	-1			<i>Zoega purpurea</i>	Boiss.	O			A	ND		
<i>Trigonella noeana</i>	Weihb	O			A	ND											

Les lichens de l'Etna et d'Augusta (Sicile) : indicateurs de la pollution atmosphérique liée aux activités volcaniques et anthropiques

Volcanic and anthropic metal pollution monitored by lichens - two case studies : Mt.Etna and Augusta (Sicily)

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Résumé

Une quinzaine d'éléments ont été dosés par ICP-MS (Inductively Coupled Plasma-Mass Spectrometer) dans plusieurs espèces de lichens recueillis sur l'Etna et à proximité d'une raffinerie de pétrole à Augusta. Les lichens proches de la raffinerie sont enrichis, par rapport à leur substrat calcaire, en Pb, Zn, Sn, Co, Mo, Ag, Cs, As, Bi, Cu tandis que les lichens de l'Etna sont enrichis, par rapport à leur substrat lavique, en Sb, Se, Pb, Zn et Bi. La quantité d'éléments piégés par les lichens d'Augusta est cinq fois supérieure à celle des lichens de l'Etna. Les coefficients d'enrichissement en métaux lourds au sol à Augusta sont supérieurs de 10 à 100 fois à ceux mesurés à l'Etna. À l'échelle des retombées locales, le volcan est moins polluant que les industries humaines.

Abstract

We have determined fifteen trace elements with ICP-MS (Inductively Coupled Plasma-Mass Spectrometer) in lichens from Etna volcano and in the vicinity of the Augusta (Sicily) oil refinery. The latter are enriched in Pb, Zn, Sn, Co, Mo, Ag, Cs, As, Bi, and Cu relative to their limestone substrate whereas Etna lichens are enriched in Sb, Se, Pb, Zn, and Bi relative to lavas. The Augusta specimens have overall trace concentrations that are five-fold higher than the etnean samples. Enrichment factors relative to the substratum are 10 to 100 fold higher in lichens next the refinery than in those of the volcanic area. Locally over Sicily, the volcano is much less of a nuisance than human industry.

English Abridged Version

Several samples of five lichens species [Parmelia tinctoria Mab. et Gill., Pseudevernia furfuracea (L.) Zopf, Ramalina fraxinea (L.) Ach., Xanthoria calcicola Oxner, Xanthoria parietina (L.) Th. Fr.] have been collected on blocks of lava flows and on oak-tree barks on Etna volcano from about ten km of the source of the panache and close to the petro-chemical complex of Augusta on limestone and almond-tree barks far from more than 3 km from chimneys of the refinery (Fig. 1). The thallus of lichens, of which a standard lichen

(336-AEIA), three samples of present lavas of Etna and three aquitaniens limestone, have been dissolved and analysed by ICP-MS. About fifteen elements (V, Cr, Co, Ni, Cu, Zn, As, Se, Mo, Cd, Sn, Sb, Pb, Bi, U) have been analyzed from each sample. The whole elements content in the thallus of lichens of Augusta area is five times higher than the one from Etna. At Etna zone, the elements of arsenic group (As, Sb, Bi) fit with each other and with the other metals except for Bi, which fits with Zn. and for Cd which doesn't fit at all (Fig. 2). In comparison with lavas, the thallus of lichens are enriched in Sb ($F_{x,mean} = 90$), Se ($F_{x,mean} = 10$), Pb ($F_{x,mean} = 8$) and Zn and Bi ($F_{x,mean} = 5$). At Augusta, vanadium element, which is considered characteristic of refineries emissions, fits Ni, Cu, Zn, Mo, Sn and Pb. The comparison between the thallus of lichens and the aquitaniens limestone of the bedrock exhibits that the lichens are strongly enriched in Pb ($F_{x,mean} = 110$), in Zn ($F_{x,mean} = 43$), in Sn ($F_{x,mean} = 36$) and a little bit less in Co, Mo, Cs, Ag, V. with values of $F_{x,mean}$ between 22 and 15 (Fig. 3). The enrichment factors in metals for thallus of lichens of Augusta are 10 to 100 fold higher than those for thallus of lichens of Etna (Tab. I). Figure 5 shows that the proportions of the three main metals Zn, Pb, Cu, characteristic of volcanic panache, are very similar in the panache and in the lichens of Etna, on the opposite they are different from those of lavas. The difference between the proportions of metals in lichens of Augusta and those of Etna is less clear despite a shift of the composition of Augusta's lichens towards Zn pole. The impact of the anthropogenic source on environment close to the refinery is far more important than the one close to the volcano. This is because the panache of volcano at altitude of 4 or 5 km can cover many tens or so, even hundreds of km before it disappeared. While the emission products of the refinery cover, at altitude of a few tens of meters, just hundreds or so of meters before they fall down. The chemical composition of lichens and especially the enrichment level allow to characterize easily the two sources of heavy metals.

Mots-clés / Key-words

Activité volcanique, lichens, bio-enregistreurs, Sicile.
Volcanic activity, lichens, bio-indicators, Sicily.

INTRODUCTION

Les lichens sont des organismes vivant en symbiose avec une algue ou une cyanobactérie. En raison de leurs caractéristiques physiologiques ils sont capables d'accumuler des éléments chimiques présents dans l'atmosphère pendant de longues périodes à des teneurs élevées, bien supérieures à celle de leur environnement et sans rapport avec de leurs besoins propres. De nombreux auteurs s'accordent à considérer les lichens comme de fidèles indicateurs de la pollution atmosphérique, notamment en métaux lourds (Garty 1985, Bargagli 1998, Bargagli & Barchigiani 1991, Bargagli *et al.* 1991, Nimis *et al.* 1993).

L'idée initiale à l'origine de ce travail a été de comparer les teneurs en métaux de lichens récoltés sur le pourtour de l'Etna à celles de lichens situés à proximité d'une raffinerie de pétrole voisine, afin d'estimer l'importance de la contribution respective de ces deux sources de pollution sur leur proche environnement.

Le choix de la région de l'Etna a été dicté par les arguments suivants :

– les lichens y sont abondants et omniprésents. Ils colonisent les laves en une quinzaine d'années ; à titre d'exemple, les laves de 1983 ont commencé à être envahies par *Stereocaulon vesuvianum* Pers. en 1998 (Poli Marchese & Grillo 2000). Au dessus de 2000 m ils deviennent rares et disparaissent totalement à partir de 2500 m dans une zone abiotique continuellement envahie par les produits des éruptions récentes et balayée par de très forts vents.

– l'Etna est un volcan qui fonctionne en système ouvert. Il émet un panache qui transporte une quantité d'éléments non négligeable même en dehors des périodes éruptives. Son activité et la nature des matériaux émis sont bien connus (Tanguy & Clocchiatti 1984). Depuis le dix-septième siècle ses laves sont des hawaïtes de composition peu variable, comme le montre leur teneur en U comprise entre 2,1 et 2,5 ppm (Joron & Treuil 1984, Clocchiatti *et al.* 1988).

– enfin à une trentaine de km au sud du volcan, entre les villes de Catane et Syracuse, se trouve l'un des plus grands centres industriels de la péninsule italienne, les raffineries de pétrole d'Augusta.

En pays volcanique actif, des travaux récents (Grasso 1996, Grasso *et al.* 1999) indiquent que la composition chimique des lichens résulte essentiellement de l'incorporation de particules solides provenant de poussières volcaniques (retombées directes et remobilisation de cendres) caractérisées par les éléments lithophiles (Al, Ti, Sc, Th, U, etc.) et par des particules provenant du panache enri-

chies en éléments volatils (S, Sb, As, Se) et en certains métaux (Zn, Cu, Cd, Ni, Co, etc.). Ceux-ci peuvent avoir deux sources possibles : le panache de l'Etna et/ou les industries humaines.

Le stéréomicroscope permet d'observer des particules de taille comprise entre quelques micromètres et quelques dizaines de micromètres, piégées dans les anfractuosités des thalles lichéniques. Il s'agit d'esquilles vitreuses plus ou moins bien conservées et de débris de cristaux caractéristiques des laves de l'Etna (Tanguy & Clocchiatti 1984).

Les métaux, qui se séparent du magma lors du dégazage, sont transportés dans le panache sous formes de chlorures, de composés soufrés ou encore d'éléments natifs (Buat-Menard & Arnold 1978, Le Guern 1988, Lefèvre *et al.* 1986, Pennisi *et al.* 1988, Gauthier & Cloarech 1998) auxquels peuvent s'associer des particules silicatées.

Il est notoire que les industries humaines : circulation automobile, chauffage urbain, industries chimiques et notamment les raffineries d'hydrocarbures, figurent parmi les plus grandes sources de pollution en métaux. Les cendres issues de la combustion de fuel sont enrichies en métaux V, Ni, Pb, Zn et en soufre, avec des teneurs supérieures à un % et pouvant atteindre plusieurs dizaines de % (Fitzer & Schwab 1956, Moliere & Sire 1993, Martinez-Villemame *et al.* 1998). La circulation automobile est encore en Sicile, où l'utilisation des essences sans plomb est peu développée en raison de la vétusté du parc automobile, caractérisée par l'émission de Pb.

Les lichens sont depuis longtemps utilisés pour suivre ce type de pollution (Deruelle 1983, Sarret *et al.* 1998).

MATÉRIEL ET MÉTHODES

Quatre espèces de lichens ont été récoltés sur l'Etna : deux saxicoles, *Parmelia tinctoria* et *Xanthoria calcicola*, sur des roches basaltiques, généralement dans des biotopes sans ou à faible couvert végétal, et deux corticoles, *Ramalina fraxinea* et *Pseudevernia furfuracea*, sur des écorces de chêne et de pin dans des biotopes à couvert végétal plus dense. Les prélèvements (fig. 1) sont répartis de manière régulière autour du volcan, à des altitudes comprises entre 300 et 1 200 m et à une distance de 10 à 15 km de la zone d'émission du panache. Tous les prélèvements ont été faits à une grande distance des axes routiers afin d'éliminer la contamination par le plomb. Le substratum de cette zone est constitué par les laves de l'Etna.

A Augusta les lichens *Xanthoria calcicola* et *Xanthoria parietina* ont été prélevés à proximité de la raffinerie, respectivement sur des calcaires et des écorces d'amandier, à 5 km au maximum du point d'émission. Leur substrat est constitué par les calcaires de l'Aquitaniens qui constituent le fond géochimique régional. Les troncs d'amandiers sont situés dans des biotopes sans ou à très faible couvert végétal. Dans la mesure du possible les prélèvements ont été faits à plusieurs dizaines de mètres de distance des axes routiers en raison de la forte urbanisation.

Vingt-cinq grammes d'échantillon sont broyés et séchés dans un mortier en agate. On prélève environ 25 mg, pesés exactement, puis introduits dans un matras en téflon pour être minéralisés par des microondes focalisées.

Le facteur de dilution est de 1000 (25 mg dilués dans 25 ml).

Le protocole de la minéralisation est le suivant :

5 ml de HNO₃ (Normatom). Puissance maximale du microonde 50. Temps 5 minutes.

5 ml de H₂O₂ (Merk). Puissance maximale du microonde 50. Temps 5 minutes.

5 ml de HF. Puissance 50. Temps 5 minutes avec mise à sec.

3 ml de HNO₃ (Normatom). Temps 4 minutes avec mise à sec.

10 ml de H₂O (aQ millipore) Puissance 50. Temps 3 minutes.

Amener le volume total à 25 ml.

Pour chaque échantillon, 15 éléments sont analysés en ICP-MS (Plasma Quad. PQ 2+ Fisons) : V, Cr, Co, Ni, Cu, Zn, As, Se, Mo, Cd, Sn, Sb, Pb, Bi, U.

Des blancs de réactif et une référence certifiée de lichen (336-AIEA) sont traités de la même façon (Grasso *et al.* 1999).

On utilise une gamme étalon pour tous les éléments de 0,5 ppb à 20 ppm, et des étalons internes (Be, In, Re) sont ajoutés afin de corriger des dérives éventuelles de l'appareil. Le logiciel PQ Vision permet ensuite de traiter les spectres obtenus et de donner les résultats.

RÉSULTATS

Parmi les métaux analysés dans les lichens de l'Etna et d'Augusta, certains couples montrent des corrélations linéaires passant par l'origine.

Pour chaque échantillon, indépendamment de l'espèce du lichen et de la nature du support, arbre ou roche, le rapport entre deux éléments reste constant conformément aux résultats obtenus par Grasso *et al.* (1999) à partir d'une étude par activation neutronique des lichens de l'Etna et du Vulcano. Dans le cas d'Augusta, le vanadium, élément considéré comme marqueur des rejets de l'industrie pétrolière (Fitzer & Schwab 1956, Molier & Sire 1993, Martinez-Villefrance *et al.* 1998), présente des corrélations linéaires avec Ni, Cu, Zn, Mo, Sn et Pb. Les éléments comme As et Sb, qui ont une grande affinité avec du soufre, montrent de bonnes corrélations avec le Co, le Cr, le Cu et le Mo (fig. 2). Sn est corrélé uniquement avec Bi.

À l'Etna, les métaux de la famille de l'arsenic (As, Sb, Se) sont corrélés entre eux et avec quasiment tous les

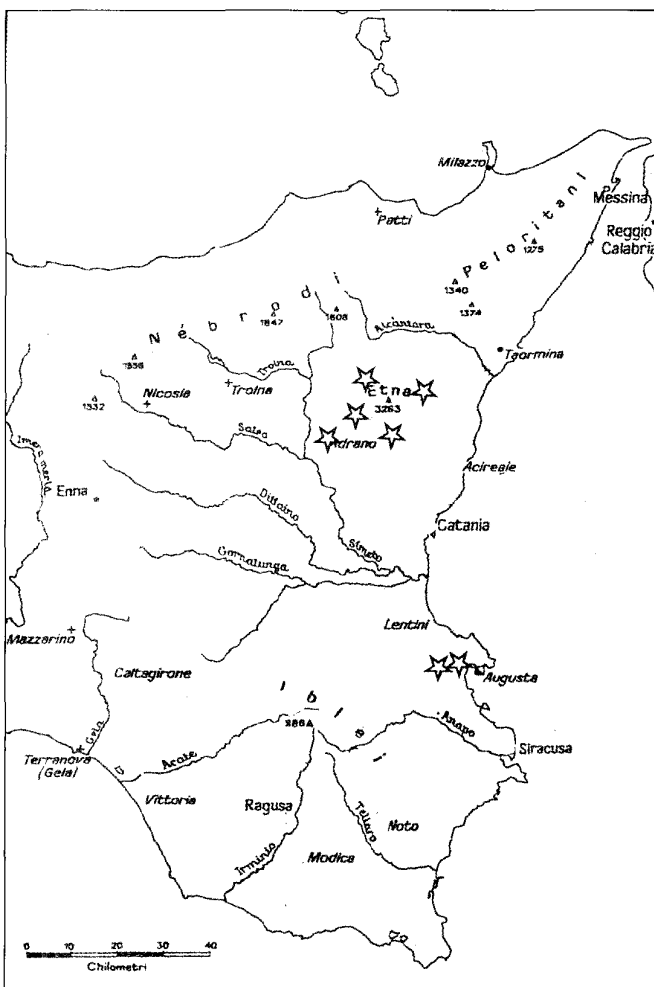


Fig. 1 Situation géographique des deux zones étudiées et localisation des prélèvements (étoiles).

Fig. 1 Location of the two investigated areas and sampling stations (stars).

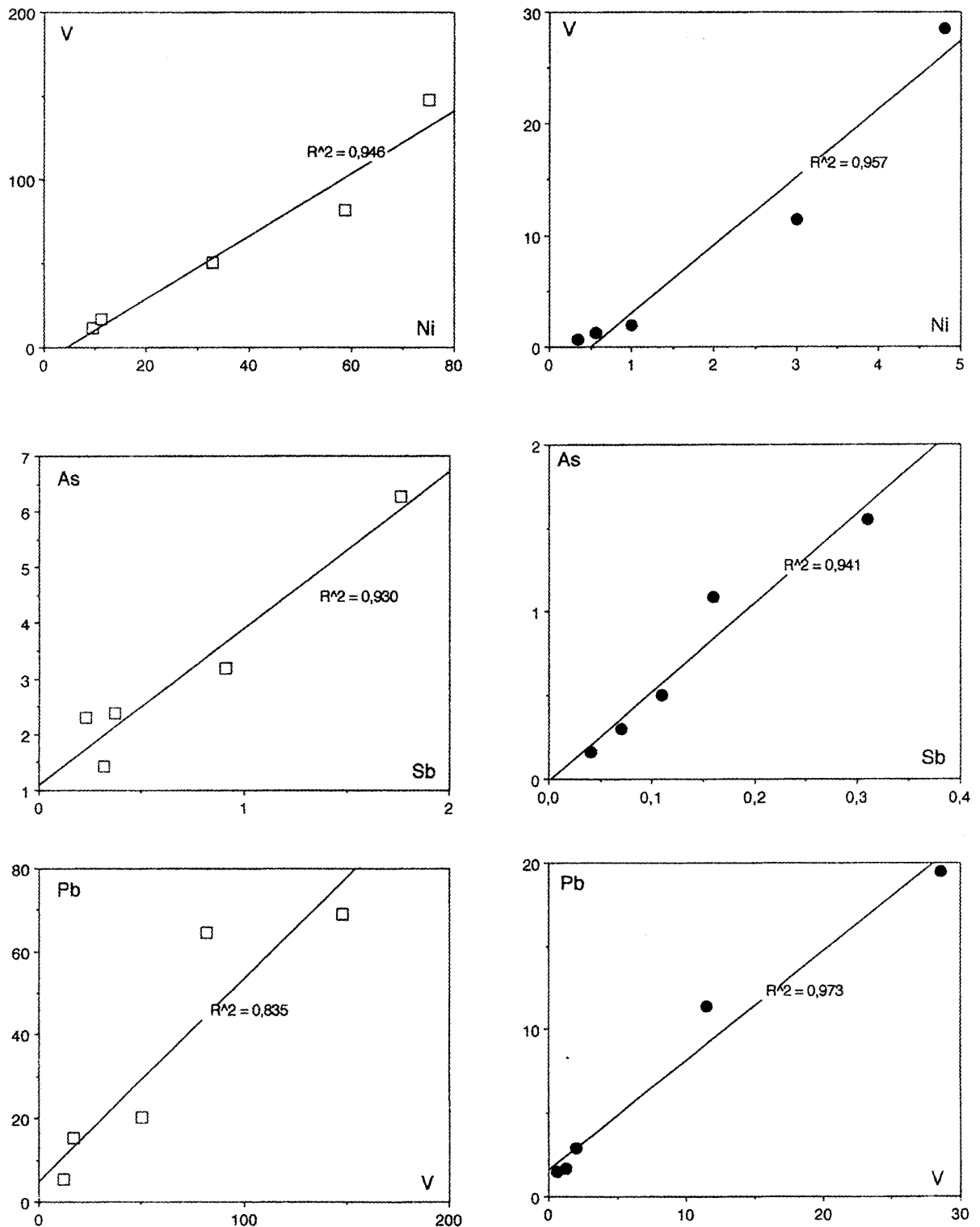


Fig. 2 Corrélations linéaires entre cinq éléments analysés dans les thalles des lichens de la raffinerie d'Augusta (carrés évidés) et dans ceux de l'Etna (cercles pleins).
 Fig. 2 Linear correlations between five trace elements analyzed in lichen thalli from Augusta refinery (squares) and from Etna volcano (circles).

autres métaux, à l'exclusion de Bi qui est corrélé uniquement avec Zn et Cd qui ne présente aucune corrélation.

Pour s'affranchir de l'influence du fond géochimique local, les données ont été normalisées, d'une part par rapport à la composition des laves de l'Etna, d'autre part par rapport à celle des calcaires de l'Aquitainien (tab. 1, p. 71). On a choisi comme élément de normalisation l'uranium après avoir comparé des dosages de cet élément par ICP-MS et INAA dans les échantillons de laves de l'Etna.

On définit ainsi le facteur d'enrichissement F_x :

$$F_x = X/U_{lic} : X/U_{sub}$$

où X est la concentration de l'élément pris en considération exprimée en ppm.

Le tableau I, montre que les valeurs élevées des écarts types traduisent une assez grande hétérogénéité, ce qui nous a conduits, pour avoir une vue d'ensemble, à utiliser des valeurs d'enrichissement moyen F_m .

Dans le cas d'Augusta, Pb présente le plus fort enrichissement ($F_m = 110$), suivi par Zn ($F_m = 43$), Sn ($F_m = 36$) ; suivent Co, Mo, Cs, Ag, V, avec des F_m compris entre 22 et 15 (fig. 3). As et Bi ont des F_m proches de 10 ; Cu un F_m proche de 6.

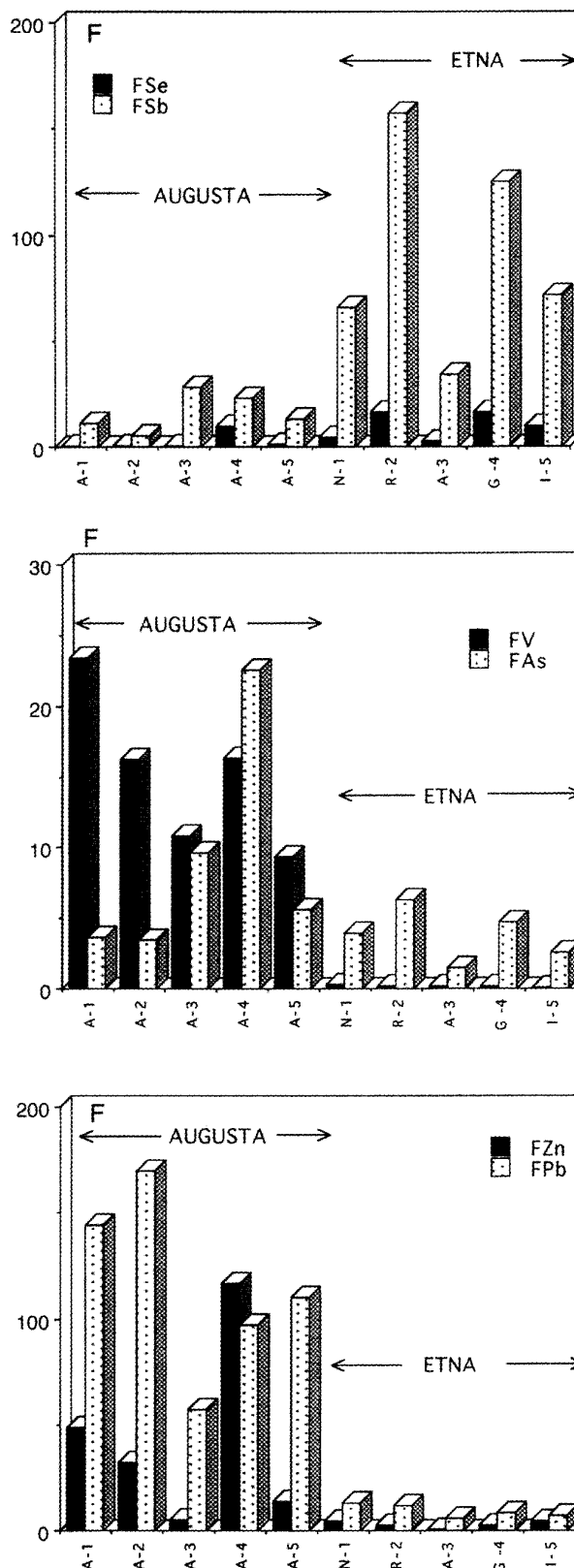
À l'Etna, l'élément le plus enrichi est de loin Sb avec un $F_m = 90$, en accord avec les données de Grasso *et al.* (1999), obtenues par INAA ; viennent ensuite Se ($F_m = 10$), puis Pb ($F_m = 8$), et Zn et Bi avec des F_m proches de 5 (fig. 3).

La charge élémentaire totale (quantité d'éléments dosés) d'un échantillon à l'autre, varie d'un facteur 10, aussi bien dans le cas de l'Etna que dans celui d'Augusta. La charge élémentaire moyenne des lichens d'Augusta est cinq fois supérieure à celle des lichens de l'Etna.

DISCUSSION

La nature des métaux et leur degré d'enrichissement dans les lichens permettent de distinguer clairement les deux sources d'émission. Les lichens d'Augusta sont caractérisés par de forts enrichissements en métaux lourds

Fig. 3 Facteurs d'enrichissement (F_x) de quelques éléments caractéristiques de la composition des thalles des lichens de l'Etna (E-1 à I-5) et de la raffinerie d'Augusta (A-1 à A-5).
Fig. 3 Enrichment factors for some characterized elements in lichens samples from Etna (E-1 to I-5) volcano and from Augusta area (A-1 to A-5).



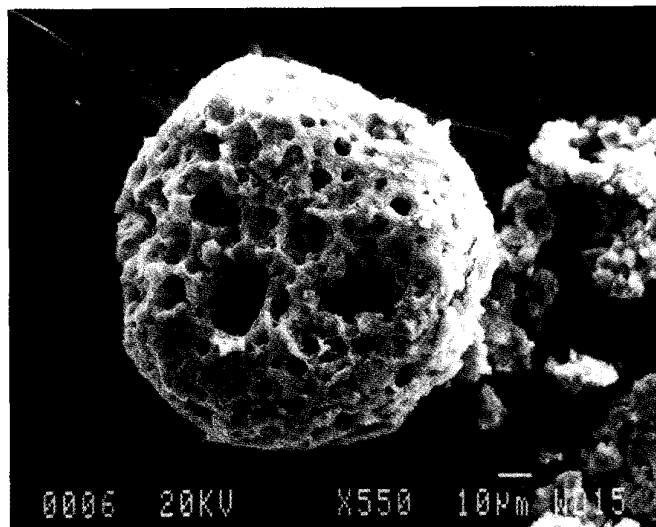


Fig. 4 Particule sulfuro-carbonée piégée par les lichens d'Augusta (diamètre 20 micromètres).

Aspect vacuolaire indique qu'il s'est formé dans un milieu riche en gaz.
Cliché de microscopie à balayage.
I. Lefèvre, CFR Gif Sur Yvette.

Fig. 4 Sulfur and carbone rich globule (20 micrometers in diameter) trapped in lichen thalli from Augusta area.

The vacuolar structure indicates that it formed in a gaz rich medium (twenty micrometers in diameter). SEM picture by I. Lefèvre LSCE, Gif Sur Yvette.

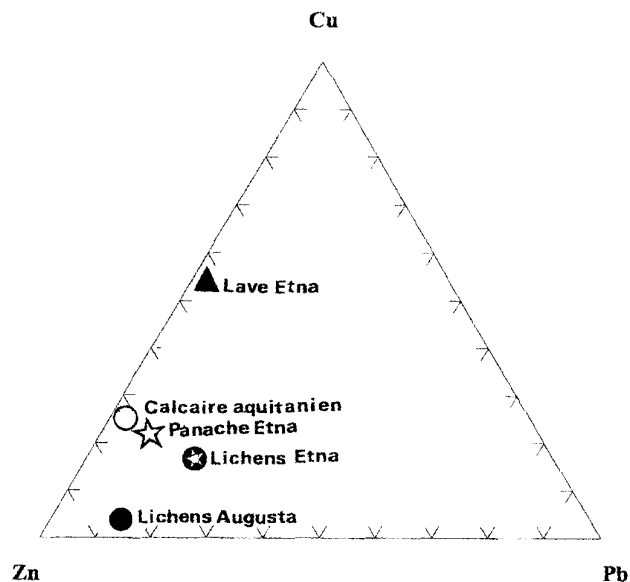


Fig. 5 Diagramme ternaire Cu, Zn, Pb.

Comparison des proportions des trois principaux métaux contenus dans le panache de l'Etna d'après Hinkley et al., (1999) et teneurs moyennes mesurées dans les lichens et dans les laves de l'Etna et dans les lichens et le calcaire aquitanien du complexe pétrolier d'Augusta.

Fig. 5 Plot of variation in proportions of Cu, Zn and Pb. Comparison between mean content of this metals in Etna plume (data from Hinkley et al., 1999), lichens and lavas of etnea area, and lichens and aquitanian limestone from Augusta area.

AUGUSTA		V	Cr	Co	Ni	Cu	Zn	As	Se	Zr	Mo	Ag	Cd	Sn	Sb
A-1	Xanthoria calcicola	148	27	6,35	75,13	13,79	590	3,18	1,5	28,3	1,47	0,19	0,29	1,89	0,91
A-2	Xanthoria calcicola	82	14,3	4	58,8	10,15	305	2,39	1,29	22,64	0,82	0,99	0,37	1,97	0,37
A-3	Xanthoria calcicola	50,6	27	20,1	33	12,3	48,8	6,27	1,58	18,4	0,86	0,37	0,24	0,55	1,76
A-4	Xanthoria parietina	12,02	3,56	1,28	9,62	7,78	168	2,31	2,78	6,21	0,39	0,21	0,06	0,37	0,23
A-5	Xanthoria parietina	17,2	6,9	3,9	11,2	7,4	50	1,43	0,94	9,1	0,44	0,27	0,22	0,21	0,32
Moyenne		62	16	7	38	10	232	3	2	17	1	0	0	1	1
Ecart type		56	11	7	29	3	226	2	1	9	0	0	0	1	1
Calcaire		5,16	11,91	0,5	13,91	3,5	10	0,72	1,99	4,93	0,07	0,04	0,14	0,03	0,07
ETNA		V	Cr	Co	Ni	Cu	Zn	As	Se	Zr	Mo	Ag	Cd	Sn	Sb
E-1	Parmelia tinctoria	11,45	5,4	1,88	3	10,8	58,3	1,09	0,32	14	0,32	0,1	0,42	0,43	0,16
E-2	Ramalina fraxinea	1,98	1,28	0,32	1	3,7	9,9	0,5	0,32	2,8	0,11	0	0	0,13	0,11
E-3	Xanthoria calcicola	28,55	7,8	9	4,8	11,5	36,8	1,55	0,67	46	0,93	0,41	0,12	0,8	0,31
E-4	Pseudevernia furfuracea	1,3	0,76	0,21	0,56	3,1	7,7	0,3	0,26	1,75	0,07	0	0,42	0,09	0,07
E-5	Ramalina fraxinea	0,65	0,48	0,14	0,35	3	12,1	0,16	0,15	0,98	0,1	0	0,03	0,05	0,04
Moyenne		8,79	3,14	2,31	1,94	6,42	24,96	0,72	0,34	13,11	0,31	0,10	0,20	0,30	0,14
Ecart type		11,90	3,28	3,81	1,91	4,33	22,03	0,58	0,20	19,14	0,36	0,18	0,21	0,32	0,11
S.E.Hawaïte		244	12,97	32,05	15,35	103,9	83,87	1,94	0,48	170,1	2,48	0,53	0,26	1,49	0,016

Tableau 1 (voir légende page 71).

AUGUSTA		Te	Cs	W	Pb	Bi	U	CHARGE _{mg}	DISTANCE	F V	F Cr	F Co	F Ni	F Cu
A-1	Xanthoria calcicola	0,6	2,75	0,35	69	0,13	1,2	972,03	700m	23,42	1,85	10,4	4,4	3
A-2	Xanthoria calcicola	0,31	2,61	0,31	64,73	0,16	50	623,21	700m	16,22	1,23	8,2	4,3	3
A-3	Xanthoria calcicola	0,05	0,61	0,19	20,26	0,05	0,89	243,88	0	10,8	2,5	44,3	2,6	3,9
A-4	Xanthoria parietina	0	0,28	0,18	5,46	0,07	0,14	220,95	1000m	16,3	2,1	18	4,8	16
A-5	Xanthoria parietina	0,07	0,45	0,06	15,4	0,05	0,35	125,91	2500m	9,33	1,6	22	2,25	5,9
Moyenne		0	1	0	35	0	11	437		15	2	21	4	6
Ecart type		0	1	0	30	0	22	199		6	0	14	1	6
Calcaire		0,11	0,08	0,05	0,39	0,02	0,98							
ETNA		Te	Cs	W	Pb	Bi	U	CHARGE _{mg}	DISTANCE	F V	F Cr	F Co	F Ni	F Cu
E-1	Parmelia tinctoria	0,03	0,64	0,08	11,4	0,16	0,35	166,48	15000m	0,33	2,93	0,41	1,37	0,73
E-2	Ramalina fraxinea	0	0,15	0,04	2,9	0,02	0,1	38,76	14000m	0,20	2,43	0,25	1,60	0,88
E-3	Xanthoria calcicola	0	0,7	0,36	19,5	0,06	1,3	194,25	17000m	0,22	1,14	0,53	0,59	0,21
E-4	Pseudevernia furfuracea	0	0,07	0	1,7	0,02	0,08	24,23	10000m	0,16	1,80	0,20	1,12	0,92
E-5	Ramalina fraxinea	0,01	0,06	0	1,5	0,014	0,08	23,494	8000m	0,08	1,14	0,13	0,70	0,89
Moyenne		0,01	0,32	0,10	7,40	0,05	0,38	89,44		0	2	0	1	1
Ecart type		0,01	0,32	0,15	7,91	0,06	0,53	75		0	1	0	0	0
S.E.Hawaïte		0,12	0,88	0,74	6,14	0,11	2,46							

AUGUSTA		F Zn	F As	F Se	F Zr	F Mo	F Ag	F Cd	F Sn	F Sb	F Te	F Cs	F W	F Pb	F Bi
A-1	Xanthoria calcicola	48,2	3,6	0,6	4,8	17,2	3,9	1,7	51	11	4,5	28	6	144	5,4
A-2	Xanthoria calcicola	32	3,4	0,7	4,8	12	25	2,7	66	5	3	33	6	170	8,3
A-3	Xanthoria calcicola	5,4	9,6	0,8	4,2	13,6	10	2	28	28	0,5	8	4	57	2,8
A-4	Xanthoria parietina	117	22,5	9,8	8,8	39	37	3	23	23	0	24	25	97	25
A-5	Xanthoria parietina	14	5,6	1,3	5,2	17,7	19	4,4	13	13	1,8	16	3,4	110	7
Moyenne		43	9	3	6	20	19	3	36	16	2	22	9	116	10
Ecart type		44	8	4	2	11	13	1	22	9	2	10	9	44	9
Calcaire															
ETNA		F Zn	F As	F Se	F Zr	F Mo	F Ag	F Cd	F Sn	F Sb	F Te	F Cs	F W	F Pb	F Bi
E-1	Parmelia tinctoria	4,89	3,95	4,69	0,58	0,91	1,33	11,32	2,03	65,31	1,75	5,11	0,76	13,05	10,16
E-2	Ramalina fraxinea	2,90	6,34	16,41	0,41	1,09	0,00	0,00	2,15	157,14	0,00	4,19	1,33	11,62	4,44
E-3	Xanthoria calcicola	0,83	1,51	2,64	0,51	0,71	1,47	0,87	1,02	34,07	0,00	1,50	0,92	6,01	1,03
E-4	Pseudevernia furfuracea	2,82	4,75	16,67	0,32	0,87	0,00	49,53	1,86	125,00	0,00	2,44	0,00	8,51	3,56
E-5	Ramalina fraxinea	4,44	2,54	9,62	0,18	1,24	0,00	3,54	1,03	71,43	2,55	2,10	0,00	7,51	3,89
Moyenne		3	4	10	0	1	1	13	2	91	1	3	1	9	5
Ecart type		2	2	6	0	0	1	21	1	50	1	2	1	3	3
S.E.Hawaïte															

Tableau 1. Genres et espèces des lichens prélevés. Analyses élémentaires exprimées en ppm des lichens prélevés et des roches de référence (lavas actuelles de l'Etna et calcaires aquitaniens) : compositions moyennes et écarts types ; charge élémentaire totale ; distance entre le lieu de prélèvement et la source d'émission. Facteurs d'enrichissement (F) ; facteurs d'enrichissement moyen (F_m) et écart type.

Table 1. Metal content in studied lichens thalli and substratum reference rocks (etna lavas and aquitanian limestone): mean composition and standard deviation. Amount of analyzed elements ; distance between lichen location and elements source ; enrichment factor (F) ; mean enrichment factor (F_m) and standard deviation.

tels que Pb, Zn, V, Cu, As, conformément à ce que l'on connaît sur les cendres issues de la combustion de fuel (Fitzer & Schwab 1956, Moliere & Sire 1993, Martinez-Villeframe *et al.* 1998).

Une étude préliminaire des particules piégées dans les lichens, aux microscopes photonique et électronique à balayage équipé d'un détecteur solide, a montré la présence, dans les lichens d'Augusta, de nombreux débris carbonés associés à des sphérules brunes spongieuses de quelques dizaines de micromètres (fig. 4) constituées de soufre et de carbone riches en vanadium, ainsi que d'autres sphérules de couleur claire de mullite. Ces particules n'ont pas été observées dans les lichens de l'Etna.

Les lichens de l'Etna sont chargés en Sb, Se, As, éléments traditionnellement associés à la phase volatile des magmas constituée majoritairement par de l'eau, de l'anhydride carbonique, du soufre et du chlore. Il est à remarquer que ces trois derniers constituants sont fortement enrichis dans les lichens corticoles (*Ramalina fraxinea* et *Pseudevernia furfuracea*) de l'Etna qui, par ailleurs, présentent les plus faibles charges élémentaires par rapport aux lichens saxicoles (*Parmelia tinctoria*, *Xanthoria calcicola*) de la même région.

Les autres métaux qui montrent un enrichissement sensible sont par ordre décroissant : Pb, Bi, Cd et Zn ; leur F_m ne dépasse pas 10.

On constate que les F_m des métaux contenus dans les lichens d'Augusta sont supérieurs de 10 à 100 fois à ceux des lichens de l'Etna.

La figure 5 montre que les proportions des trois principaux métaux Zn, Pb et Cu, caractéristiques des panaches volcaniques (Hunkley *et al.* 1999), sont très proches dans le panache et dans les lichens de l'Etna ; par contre elles sont nettement différentes de celles des laves.

La distinction entre la proportion de ces trois métaux contenus dans les lichens d'Augusta et ceux de l'Etna est moins nette malgré un déplacement de la composition des lichens d'Augusta vers le pôle Zn.

CONCLUSION

L'impact de la raffinerie sur l'environnement proche est beaucoup plus important que celui du volcan. En effet, le panache du volcan qui s'élève à 4-5 km d'altitude, peut parcourir horizontalement plusieurs dizaines, voire une centaine de kilomètres (Bergametti *et al.* 1984) avant de se dissiper, tandis que les produits émis par la raffinerie se déplacent à quelques dizaines de mètres d'altitude pour

retomber, le plus souvent, à quelques centaines de mètres, voire quelques kilomètres du point d'émission.

La composition chimique des lichens et notamment leur degré d'enrichissement en métaux permet de distinguer aisément les deux sources de métaux lourds.

La présente étude est loin d'être exhaustive et de nombreuses interrogations subsistent quant à la signification de la composition chimique des lichens en tant qu'indicateurs et bioaccumulateurs de la pollution atmosphérique. Ces problèmes sont de deux types :

– les uns, intrinsèques, sont liés à la physiologie du lichen, comme la capacité à retenir des particules, la localisation et la spéciation (environnement chimique de l'élément considéré) des éléments, leur vitesse de croissance, etc. ;

– les autres, extrinsèques, sont liés à des facteurs indépendants du lichen, comme les variations climatiques, la direction des vents dominants.

Pour progresser dans ce domaine, il serait nécessaire d'entreprendre des études pluridisciplinaires regroupant des géochimistes, des biologistes, des climatologues et des industriels.

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Are animal trophic systems as reliable expression of climate as are plant communities?

Preliminary evidence from the tyrrhenian belt in Italy

Est-ce que les systèmes trophiques animaux peuvent fournir une expression du climat aussi valable que les communautés végétales ? Premiers éléments en région tyrrhénienne (Italie)

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Abstract

A comparative study of eleven plant and animal communities was carried out in the subcoastal sectors of a geographic belt running from North to South Italy on the Tyrrhenian side of the peninsula. The bioclimatic and climatic characteristics were determined on the basis of temperature and rainfall data recorded by meteorological stations near the study areas.

The Tyto alba-mammals trophic systems were studied collecting data already published in the literature. The vegetation was studied in plant associations in a Mediterranean macro-bioclimatic context. The results show, even at a meso-scale level, that the correlations between climatic and Tyto alba-trophic system indices are no less significant than those regarding vegetation indices. Very likely, the effects of geological and edaphic as well as historical and evolutive factors overlap more extensively with those of climate in plant than in mammal communities, at least at mesoclimate level; moreover, the differences among the relevant sampling scales probably play an important role in emphasizing the linkage with local factors, strongly influencing plant communities composed of sessile and long-living individuals.

Key-words

Climate, flora, vegetation, mammals, trophic systems.

Résumé

Une étude comparative a été conduite sur onze communautés animales et végétales depuis le nord jusqu'au sud de l'Italie, le long des côtes tyrrhéniennes de la péninsule. Les caractéristiques du bioclimat et du climat ont été déterminées par les données de température et de précipitations enregistrées dans les stations météorologiques proches des aires d'étude. Les systèmes trophiques Tyto alba-mammifères ont été étudiés sur la base des données déjà publiées dans la littérature. La végétation a été étudiée par associations dans le contexte macro-bioclimatique méditerranéen. Les résultats confirment qu'il existe, même à un niveau régional, une relation entre les données climatiques et les communautés animales et que, en outre, les relations mises en évidence ne sont pas moins significatives que celles qui prennent en compte les données végétales. Il est probable que les effets des facteurs géologiques et édaphiques, ainsi que les facteurs historiques et évolutifs, pèsent plus fortement que ceux du climat régional dans le cas des plantes comparativement aux communautés animales. En outre, les différences d'échelle entre les échantillons considérés accentuent certainement le lien avec les facteurs locaux qui influencent fortement les communautés végétales composées d'individus sessiles et à longue durée de vie.

Mots-clés

Climat, flore, végétation, mammifères, systèmes trophiques.

INTRODUCTION

In bioclimatology, studies comparing plant and animal communities are relatively few (Contoli, 1988; Stohlgren *et al.* 1995) and bioclimate has been studied mainly by focusing on vegetation (Tomaselli *et al.*, 1973; Rivas-Martinez, 1990; Blasi, 1994). At the macro-scale level, a good agreement among many features of climate and plant indicators has been observed (Gandullo, 1972; Box, 1982; Miller, 1982; Woodward & Williams, 1987; Pignatti, 1984; Mitrakos, 1982; Mazzoleni *et al.*, 1992).

As concerns the animals-climate relation (available quantitative data concern mainly homeotherm vertebrates), small mammals should be a good tool for the above mentioned kind of study in relation to their ecological characteristics: abundant, ubiquitous, not too "vagrant", euryoecious, euryphagous and so on (Cagnin *et al.*, 1998).

Data on small mammals collected from *Tyto alba* (Scopoli, 1769)-mammal trophic systems (i.e., linking organisms through food relations) show the advantage of reducing the degree of freedom number of the studied ecological context. In fact, these systems are based on a single predatory taxon. Thus, quali-quantitative parameters of the habitat are fixed, the differences in trap effi-

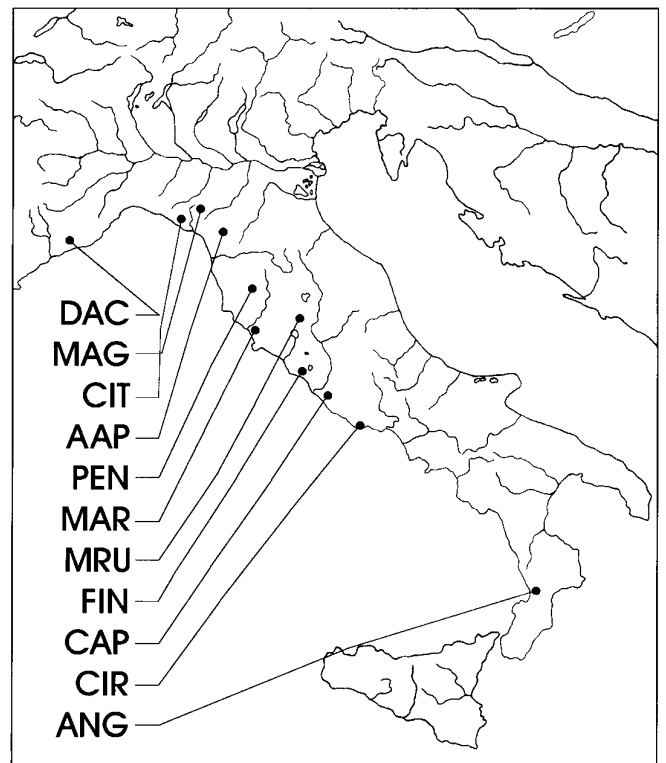
ciency avoided and the number of prey is linked to predator food requirements rather than to different sampling efforts by different researchers and contexts (Contoli, 1981; Contoli, 1982). Moreover, several studies have shown a significant correlation between the frequencies of the preyed taxa found in the diet and their frequencies in the communities. This suggests that the individual food preferences of *Tyto alba* are negligible compared with environmental availability (Aloise *et al.*, 1993).

Spitz (1981) made a careful correlation between abiotic climatic factors and small mammal species in France, especially through owl pellet analysis. In Italy, one of the authors proposed some "Thermoxerophily" indices based on semi-qualitative relationships between *Tyto alba*-mammal trophic systems and climatic parameters such as temperature and rainfall (Contoli, 1976; Contoli *et al.*, 1978). These indices were proved to be well correlated to macroclimate and macro-bioclimate patterns in Italy (Contoli, 1984; Contoli *et al.*, 1985; Amori *et al.*, 1987).

The usefulness of such indices has been confirmed by Boldreghini *et al.* (1988), Mazzotti *et al.* (1995), Salvati *et al.* (1997).

Concerning plants, data coming from phytosociological studies, give structural and dynamic information describing the phytocoenoses (Pignatti *et al.*, 2000).

Figure 1. Location of the study areas.
 DAC = Dolceacqua (West Liguria),
 MAG = Magra river (East Liguria),
 CIT = Cinque Terre (East Liguria),
 AAP = Alpi Apuane (Tuscany),
 PEN = Pentolina (Tuscany),
 MAR = Maremma natural park (Tuscany),
 FIN = F. Infernaccio (Latium),
 MRU = M. Rufeno (Latium),
 CAP = Castelporziano (Latium),
 CIR = Circeo (Latium),
 ANG = Angitola (Calabria)



The aim of this work was to make a contribution to the study of the relations among climate, animals and plants in the Tyrrhenian belt of Italy, using some bioclimatic and climatic indices.

STUDY AREAS AND METHODS

Eleven areas sharing available plant and animal data were selected for this study (figure 1, table 1). They are located in the subcoastal sectors of the Tyrrhenian side

of the peninsula, on the SW Apennines slopes, up to 81 km from the sea (M. Rufeno) and at an altitude ranging from 5 m (Castelporziano) to 460 m (M. Rufeno) above sea level; the areas are characterized by a Mediterranean climate ranging from thermoxerophilic to subhumid features.

The climatic and bioclimatic characteristics were determined on the basis of temperature and rainfall data (Ufficio Centrale di Meteorologia) recorded by the meteorological stations nearest the study areas (up to 20 km) during the period 1951-1987; some related indices were calculated (table 2):

Abbreviated names	Areas	Geographical coordinates	Altitude m. a.s.l.	Phytosociological status	Landscape features
DAC	Dolceacqua	43°51'N; 7°38'E	57	<i>Quercetum ilicis</i> Br.BI.1915	Extensive <i>Quercus ilex</i> woods on the internal hills
CIT	Cinqueterre	44° 7'N; 9°44'E	95-320	<i>Quercetum ilicis galloprovinciale pistacietosum</i> Br.BI. 1952	High habitat and species diversity; presence of natural communities and farmed fields
MAG	Magra	44°4'N; 9°58'E	69-200	<i>Alno-Fraxinetum oxycarpae</i> Tchou 1946	Meso-hygrophile vegetation at the mouth of the Magra river
AAP	Alpi Apuane	43°58'N ; 10°15'E	440	<i>Quercetum ilicis</i> Br.BI.1915	Numerous endemic species and different vegetation belts: from maqui to grasslands of high altitude (over 1000 m)
PEN	Pentolina	43°11'; 11°12'E	270-440	<i>Quercion pubescenti-petraeae</i> Br.BI.1931 (original relevés)	Presence of Mediterranean evergreen and deciduous woods
MAR	Parco della Maremma	42°37'N; 11°5'E	45-380	<i>Orno-Quercetum ilicis</i> Horvatic (1956) 1958	Uccellina hills covered by Mediterranean vegetation and the Ombrone coastal plain, covered partly by dunes and partly by marshes of both fresh and salt water
FIN	Fosso Infernaccio	42°5'N; 11°50'E	90	<i>Oleo-Ceratonion</i> Br.BI. 1936 (original relevés)	Presence of thermophilic shrublands belonging to the more xerophile Mediterranean belt
MRU	M. Rufeno	42°47'N; 11°55'E	460	<i>Quercion pubescenti-petraeae</i> Br.BI.1931 (original relevés)	<i>Quercus cerris</i> , <i>Quercus pubescens</i> and <i>Quercus ilex</i> woods constitute a mixed communities
CAP	Castelporziano	41°44'N; 12°26'E	50	<i>Asplenio-Quercetum ilicis</i> Rivas-Martinez 1974	Presence of one of the most important alluvial coastal plains in Italy: vegetation series from dunes to the deciduous woods
CIR	Parco del Circeo	41°20'N; 13°00'E	13	<i>Asplenio-Quercetum ilicis</i> Rivas-Martinez 1974	High environmental eterogeneity: Mediterranean maquis on the calcareous promontory, hygrophile alluvial-plain forest, <i>Quercus ilex</i> woods on the rocky steep slopes
ANG	Angitola	38°46'S; 16°13'E	75	<i>Helleboro-Quercetum suberis</i> Signorello 1984	A mesophile <i>Quercus suber</i> wood in a strongly thermophile context represents a peculiarity

Table 1. Data relative to the sampling areas.

	T° mean annual	Rainfall mm/year	Rainfall summer	N° drought days	De Martonne Index	I _(t)	I _(ov)
DAC	13.90	894.90	93.70	70	35.50	245	1.45
CIT	14.50	769.10	165.03	69	31.40	298.30	2.57
MAG	14.10	1229.80	135.09	40	51.02	271	2.09
AAP	14.05	1960.80	239.40	0	81.50	271.60	3.84
PEN	13.50	794.10	133.60	49	33.80	237.40	2.07
MAR	14.50	616.60	55.70	100	25.20	280	0.85
FIN	16.30	684.70	56.14	102	26.30	349	0.88
MRU	12.60	1004.60	136.01	36	44.50	219.10	2.21
CAP	15.50	725.70	53.18	105	28.50	324.20	0.78
CIR	15.70	845.20	66.80	104	32.90	343	0.96
ANG	17.50	857	58	110	31.20	381	0.84
MEAN	14.74	943.86	108.42	71.36	38.34	292.69	1.69
SD*	1.39	376.05	59.60	36.44	16.23	51.33	0.97
VC**	31.32	32.84	59.39	51.03	40.57	17.53	56.91

* Standard deviation; ** Variation coefficient.

Table 2. Climatic indices of the sampling areas.

1. Summer rainfall
2. N° of drought days,
3. De Martonne index* (1926) ($*P / T+10$ with $P=$ mean annual rainfall, $T=$ mean annual temperature),
4. Thermic index (I_(t))** (Rivas-Martinez 1990) (** $(T+M+m) \times 10$ $M=$ mean of the maxima temperatures of the coldest month, $m=$ mean of the minima temperatures of the coldest month),
5. Ombrothermic index (I_(ov))*** (Rivas-Martinez 1990) (***) \sum summer rainfall / \sum mean temperatures of summer months),
6. The \sum of the ranks of the “C” indices (used only in the non-parametric tests).

Annual mean temperatures and annual mean rainfall (T and P in table 2) were not used in the statistical analyses because they are redundant with other climatic parameters.

Tyto alba-mammals trophic systems were studied collecting data from literature (Santini & Farina, 1978; Sigillo, 1983; Contoli and A.s.t.e.r.o., 1985; Aloise *et al.*, 1990; Lovari *et al.*, 1976; Martelli, 1980; Sforzi, 1991), according to a consolidated methodology now based at a high

level of standardization, e.g. sampling sorting of bones, specimen number estimation, and taxa classification (Saint-Girons, 1973; Chaline *et al.*, 1974; Bunn *et al.*, 1982; Mikkola, 1983; Contoli, 1980, 1984; Contoli *et al.*, 1981, 1983, 1993) (table 3). As stated by Geroudet (1965) and experimentally confirmed by Taberlet (1983), a *Tyto alba* site corresponds to a circle ranging from 2 to 4 km in diameter.

Faunistic data were obviously based on a much smaller number of species than plants (17 mammals species *vs.* 329 plants). Moreover some mammalian species were excluded from analysis because they are locally absent for biogeographical reasons from a part of the range studied. Thus, we decided that instead of raw data, a set of indices already tested as good estimators of bioclimatic features for plants and mammals should be used.

The “thermoxerophily” indices (“M”) were calculated from the number of individuals of each taxon considered, preyed in each study area (table 3A): 7. ITX = *Crocidurinae/Soricidae*; 8. ITX1 = (*Suncus-Sorex*)/*Soricidae*; 9. ITX2 = $\{(Suncus / Soricidae) + (Mus + Rattus rattus) / Rodentia\} / 2$; 10. ITX3 = $(Mus + R.rattus) / Rodentia$;

11. Σ of the ranks of the "M" indices (used only in the non-parametric tests).

It should be underlined that the ITX2 index is well suited to more isolated conditions such as insular areas in Italy, where in fact *Soricidae* not belonging to *Crocidurinae* are absent for biogeographic rather than ecological reasons, excluding the use of ITX and ITX1.

The vegetation (tables 1 and 4) was studied by phytosociological relevés using the Braun-Blanquet method (1952), mainly plant associations of *Quercion ilicis* (Gentile *et al.*, 1984, 1985; Mariotti, 1984; Ansaldi & Tomei, 1988; Arrigoni, 1985; Lucchese & Pignatti, 1990; Brullo, Di

Martino & Marcenò, 1977; Signorello, 1984), *Quercion pubescenti-petraeae* (Mariotti, 1988-1989; Montanari & Gentile, 1979) and *Oleo-Ceratonion*.

As plant indices (table 4A), we adopted life forms spectra (Box, 1982) (expressed as percentages of occurrence) and the importance values of thermophilous species (Tomaselli, 1977; Bullini *et al.*, 1998). Their distributional values were calculated for each plant association, as the proportion of species number, species coverage and total species coverage for the eleven samples (Arroyo and Marañón, 1990). The proportion of thermophilous species was successfully applied to examine the vegetation in relation to

INSECTIVORA	DAC	CIT	MAG	AAP	PEN	MAR	FIN	MRU	CAP	CIR	ANG
<i>Crocidura leucodon</i> (Hermann, 1780)	25	5	25	14	46	55	11	22.1	12	10	32
<i>Suncus etruscus</i> (Savi, 1822)	5		19	4	31	90	10	6.8	16	8	69
<i>Crocidura sp.</i>											4
<i>Crocidura suaveolens</i> (Pallas, 1811)		1	44	5	21	82	9	19.6	15	7	96
<i>Sorex araneus</i> (Linné, 1758)			27	21			1	49			25
<i>Sorex minutus</i> (Linné, 1766)					6	131		18			
<i>Neomys cfr. anomalus</i> (Cabrerá, 1907)								0.47			
* <i>Talpa romana</i> (Thomas, 1902)										1	3
RODENTIA											
<i>Apodemus sylvaticus</i> (Linné, 1758)	113	30	135	35	255	588	44	193	41	38	182
<i>Mus domesticus</i> (Rutty, 1772)	2		38	3	9	303	34	4.4	24	7	69
<i>Rattus sp.</i>											3
<i>Rattus rattus</i> (Linné, 1758)	11	15	12			7		0.2	5	16	4
* <i>Microtus savii</i> (de Sélýs Longchamps, 1838)					130		18	97.4	174	16	322
* <i>Microtus multiplex</i> (Fatio, 1905)		7	36	20							
<i>Muscardinus avellanarius</i> (Linné, 1758)			18	4	16	12		17.2	3	2	17
<i>Myoxus glis</i> (Linné, 1766)				1							
<i>Clethrionomys glareolus</i> (Schreber, 1780)				10	129			19.3			
<i>Eliomys quercinus</i> (Linné, 1766)								0.06			13
<i>Arvicola terrestris</i> (Linné, 1758)										2	2
<i>Microtinae</i> indet.											1
<i>Apodemus</i> vel <i>Mus</i>											5
Total small-mammals	156	58	354	123	768	1137	127	447.5	290	107	847
Species number	5	5	9	11	9	7	7	13	8	9	12
* Species not ever present for biogeographical reasons.											

Table 3. Number of prey hunted by *Tyto alba* in the study areas. In the *M. Rufeno* area, the values are the average of seven *Tyto alba* sites.

soil factors (Dow Giallo *et al.*, 1997). We have also tested the values of thermophily for the character species of alliance and association in each community, to explore the relationship between climatic species and climate.

Plant Indices (“P”) (table 4A): 12. Σ of the ranks of the thermophilous species coverage and number (Thermophilous species are Mediterranean species of *Quercetalia-ilicis*); 13. Σ of the ranks of the thermophilous species coverage belonging to the lowest phytosociological ranks: alliance and association; 14. Σ of the ranks of thermophilous species shared by all areas; 15. (therophytes % frequency - hemicryptophytes % frequency) x phanerophytes % frequency (the difference between therophytes and hemicryptophytes, respectively indicators of thermoxerophily and mesophily, was multiplied by phanerophytes to normalize the differences); 16. Σ of the ranks of the “P” indices (used only in the non-parametric tests).

P 12 expresses a more general approach, P13 expresses particularly the phytocoenotic component belonging to the climatic stages, P14 excludes the biogeographic

absences, P15 expresses the importance of the adaptive strategies of the life forms to climate (Box, 1982; Mitrakos, 1980). In the M. Rufeno area, more detailed data for both mammals and vegetation relating to the same sites were available for the whole area, thus making a more “fine-grained” analysis. A thermoxerophily index for the vegetation (ITXV) was calculated with the same algorithm suggested by Dugrand (*in Lausi et al.*, 1978) for the evaluation of anthropization degree: $ITXV = \sum p_i TX_i / 400$. (P_i = % frequency of the vegetation types, whose areas were calculated from the “Forestry map”; TX_i = the degree of thermoxerophily assigned to each vegetation type). TX_i , ITXV and ITX’s values are reported in table 7. It is important to point out that the *Tyto alba* sites and the vegetation relevés share the same biotope, bioclimate and ecosystem, but do not correspond exactly in their location. It was impossible to find an exact correspondence between plant and mammal data in the literature, given that raptor sites are linked to objective environmental availability, unlike vegetation survey sites that can be chosen by researchers.

TYTO ALBA-MAMMALS TROPHIC SYSTEMS

	ITX	ITX1***	ITX2	ITX3
DAC	1	0.17	0.135	0.103
CIT	1	0	0.144	0.288
MAG	0.77	-0.07	0.218	0.27
AAP	0.46	-0.46	0.061	0.041
PEN	0.43	-0.44	0.076	0.017
MAR	1	0,4	0.369	0.341
FIN	0.97	0,29	0.338	0.354
MRU	0.42	-0.52	0.036	0.014
CAP	1	0.37	0.245	0.117
CIR	1	0.32	0.302	0.284
ANG	0.89	0.19	0.216	0.126
MEAN	0.81	1.02	0.194	0.178
SD*	0.25	0.349	0.114	0.131
VC**	30.71	34.29	58.13	72.67

* Standard deviation; ** Variation coefficient; *** $-(ITX1 - 1)$.

Table 3A. “Tyto alba-mammals trophic systems” indices.

	DAC	CIT	MAG	AAP	PEN	MAR	FIN	MRU	CAP	CIR	ANG
	(Average coverages for each species %)										
<i>Quercus ilex</i>	100	95		41.6	83	65	1.5	45	28	80	18
<i>Asplenium onopteris</i>	2.5	7.5								0.25	18
<i>Rosa arvensis</i>	0.1										
<i>Viola alba</i>	0.1	0.1			0.1						
<i>Laurus nobilis</i>	2.5	2.6					0.1				
<i>Lonicera implexa</i>	0.2		0.25				6.5		0.1	0.25	
<i>Smilax aspera</i>	2.5	15	2.5	0.5	0.1	0.1	0.5	5	10	10	6
<i>Asparagus acutifolius</i>	0.2	0.3	6	0.5	0.3	0.3	0.5		7.5	0.5	6
<i>Arisarum vulgare</i>	0.1	0.1									
<i>Rubia peregrina</i>	8	7.6	0.4	0.5	0.5	0.5	0.5	0.5	0.5	5	30
<i>Arbutus unedo</i>	0.2	2.6		23	5	5	5	5	5	10	22
<i>Phyllirea angustifolia</i>	0.2				0.2	18					
<i>Phyllirea latifolia</i>			18	13	20	0.1	8	40	20		
<i>Pistacia lentiscus</i>	0.1	2.7	33.5		6	60		7.5	0.25	18	
<i>Myrtus communis</i>	0.2	2.6	33.5			9		2.5	0.5	22	
<i>Clematis flammula</i>	0.1	0.1	0.3			1		0.1	0.5		
<i>Quercus pubescens</i>	30				40	0.1	15				
<i>Coronilla emerus</i>	0.1	5	0.1	0.4		0.1					
<i>Sesleria autumnalis</i>	5										
<i>Daphne laureola</i>	0.1			0.02							
<i>Castanea sativa</i>	8										
<i>Cornus sanguinea</i>	2.5										
<i>Cotinus coggygria</i>	2.5		19								
<i>Cephalanthera rubra</i>	0.1										
<i>Fraxinus ornus</i>	8	0.1	3	5	20	0.1	9				6
<i>Tamus communis</i>	0.3	2.7	4	0.01		0.1					22
<i>Hedera helix</i>	12	0.25	12	7.3		0.1		0.1	20		
<i>Erica arborea</i>	2.6	2.6	17	0.1	10		0.5	30	30		6
<i>Stachys officinalis</i>	0.25					0.1	0.5				
<i>Rubus ulmifolius</i>	0.25	0.5	12.3								
<i>Viola riviniana</i>	2.5										
<i>Brachypodium pinnatum</i>	0.1	2.6			0.2						
<i>Melica minuta</i>	0.2										
<i>Rosa sempervirens</i>		0.25		6	0.5			0.1	0.5	6	
<i>Viburnum tinus</i>		2.6									
<i>Carex distachya</i>		2.5		0.1	0.5			0.25			
<i>Ruscus aculeatus</i>		12.5	0.5	20	0.2	0.1	10	0.5			
<i>Clematis vitalba</i>		0.3	13								
<i>Neottia nidus-avis</i>		0.1									
<i>Lonicera etrusca</i>		0.25		0.1							
<i>Galium scabrum</i>		0.1									
<i>Lathyrus latifolius</i>		0.1									
<i>Pinus halepensis</i>		2.5									
<i>Ptilicaria odora</i>		0.2							0.25	2.2	
<i>Euphorbia characias</i>		0.2									
<i>Ampelodesmos mauritanicus</i>		0.1									18
<i>Olea europaea</i>				16		9					
<i>Dorycnium hirsutum</i>				0.5		1	0.1				
<i>Pistacia terebinthus</i>				1.7							4
<i>Crataegus monogyna</i>			13	0.1	0.1	1		2.6			10
<i>Spartium junceum</i>				8.3							
<i>Cistus salvifolius</i>				5.5							
<i>Helichrysum italicum</i>				2.1							
<i>Psoralea bituminosa</i>				0.4							
<i>Satureja montana</i>				0.25							
<i>Odontites lutea</i>				0.2							
<i>Cleistogenes serotina</i>				0.1							
<i>Centaurea deusta</i>				0.2							
<i>Fumana procumbens</i>				0.2							
<i>Globularia punctata</i>				0.2							
<i>Potentilla hirta</i>				0.1							
<i>Cymbopogon hirtus</i>				8.5							
<i>Ruta chalepensis</i>				2							
<i>Galium parisiense</i>				0.1							
<i>Bellis sylvestris</i>				0.1							
<i>Cyclamen repandum</i>					0.5	0.3			0.25	5	0.3
<i>Carex otrubae</i>						0.2					
<i>Cyclamen hederifolium</i>						0.2	0.1				
<i>Melica uniflora</i>			5			0.2					
<i>Daphne sericea</i>						0.2					
<i>Paliurus spina-christi</i>						0.2					
<i>Rhamnus alaternus</i>		0.2		3		1					4
<i>Contaurium erythraea</i>							0.1				
<i>Osyris alba</i>					3.5			0.5			
<i>Aristolochia rotunda</i>					0.1		0.1				
<i>Cornus mas</i>					0.1						
<i>Teucrium chamaedrys</i>					0.1						
<i>Quercus cerris</i>					1			35			

	DAC	CIT	MAG	AAP	PEN	MAR	FIN	MRU	CAP	CIR	ANG
	(Average coverages for each species %)										
<i>Helleborus foetidus</i>			0.1		0,1						
<i>Juniperus communis</i>					1			3.5			
<i>Acer monspessulanum</i>								15			
<i>Rubus sp.</i>					0.1		0.5				
<i>Pyrus pyraster</i>					0.5						
<i>Prunus sp.</i>					0.1						
<i>Viburnum tinus</i>								3			
<i>Ligustrum vulgare</i>		0.1	5					0.5			
<i>Sorbus torminalis</i>								0.1			
<i>Malus florentina</i>								0.1			
<i>Asparagus tenuifolius</i>								0.5			
<i>Melica nutans</i>								0.1			
<i>Rosa sp.</i>							1				
<i>Trifolium pallidum</i>							0.1				
<i>Daphne gnidium</i>							0.1		0.25	0.25	
<i>Lolium multiflorum</i>							0.3				
<i>Dactylis glomerata</i>			0.1				0.1				22
<i>Cymara cardunculus</i>							0.1				
<i>Linum trigynum</i>							0.3				
<i>Galium lucidum</i>							0.1				
<i>Trifolium campestre</i>							0.1				
<i>Phalaris bulbosa</i>							0.1				
<i>Brachypodium distachyum</i>							0.3				
<i>Dianthus carthusianorum</i>							0.1				
<i>Hedysarum coronarium</i>							0.1				
<i>Blackstonia perfoliata</i>							0.1				
<i>Koeleria splendens</i>							0.1				
<i>Primula sp.</i>							0.1				
<i>Crepis sp.</i>							0.1				
<i>Onobrychis caput-galli</i>							0.1				
<i>Anthyllis vulneraria</i>							0.1				
<i>Medicago hispida</i>							0.1				
<i>Lotus ornihopodioides</i>							0.1				
<i>Parentucellia viscosa</i>							0.1				
<i>Vicia tenuissima</i>							0.1				
<i>Gastridium ventricosum</i>							0.1				
<i>Hypochoeris achyrophorus</i>							0.1				
<i>Mentha sp.</i>							0.1				
<i>Euphorbia dendroides</i>							0.1				
<i>Allium subhirsutum</i>							0.1				
<i>Pulicaria odora</i>							0.1				
<i>Scorpiurus muricatus</i>							0.1				
<i>Torilis nodosa</i>							0.1				
<i>Viola sp.</i>							0.1				
<i>Trifolium stellatum</i>							0.1				
<i>Erica multiflora</i>							6.2				
<i>Cistus monspeliensis</i>							1				
<i>Carex hallerana</i>									0.1		
<i>Juniperus oxycedrus</i>									0.1		
<i>Brachypodium sylvaticum</i>			18					3	0.25		26
<i>Quercus suber</i>								10	5		90
<i>Carex flacca</i>									0.1	0.25	
<i>Carex sylvatica</i>			0.5						0.1		4
<i>Sorbus domestica</i>										0.5	
<i>Quercus frainetto</i>										10	
<i>Malus sylvestris</i>										0.25	
<i>Viola suavis</i>										0.25	
<i>Pteridium aquilinum</i>										0.25	26
<i>Helleborus bocconeii</i>											15
<i>Lathyrus venetus</i>											15
<i>Quercus dalechampii</i>											22
<i>Festuca exaltata</i>											35
<i>Melittis albida</i>											15
<i>Ulmus minor</i>											2.2
<i>Cytisus villosus</i>											22
<i>Clinopodium vulgare</i>											12
<i>Telime monspessulana</i>											2.3
<i>Teucrium siculum</i>											0.5
<i>Scutellaria gussonei</i>											14
<i>Viola alba subsp. dehnhardtii</i>											8.3
<i>Symphytum bulbosum</i>											4.3
<i>Asperula laevigata</i>											0.5
<i>Calicotome infesta</i>											6
<i>Pyrus amygdaliformis</i>											0.5
<i>Buglossoides purpureoerulea</i>											8
<i>Selaginella denticulata</i>											0.5
<i>Ranunculus neapolitanus</i>											2

	DAC	CIT	MAG	AAP	PEN	MAR	FIN	MRU	CAP	CIR	ANG
	(Average coverages for each species %)										
<i>Alnus glutinosa</i>			104								
<i>Circaea lutetiana</i>			17								
<i>Stachys sylvatica</i>			0.7								
<i>Carex pendula</i>			12								
<i>Angelica sylvestris</i>			3								
<i>Scrophularia nodosa</i>			0.1								
<i>Sambucus nigra</i>			17								
<i>Humulus lupulus</i>			18								
<i>Solanum dulcamara</i>			1.4								
<i>Cardamine impatiens</i>			0.5								
<i>Agropyrum caninum</i>			0.1								
<i>Asperula taurina</i>			0.5								
<i>Rubus caesius</i>			30.5								
<i>Salvia glutinosa</i>			7								
<i>Carex remota</i>			4								
<i>Alharia petiolata</i>			0.6								
<i>Athyrium filix-foemina</i>			0.6								
<i>Salix alba</i>			1								
<i>Lamium galeobdolon</i>			1								
<i>Populus nigra</i>			1								
<i>Salix purpurea</i>			4.5								
<i>Salix elaeagnos</i>			8.4								
<i>Aegopodium podagraria</i>			11								
<i>Geranium nodosum</i>			5.7								
<i>Geum urbanum</i>			3								
<i>Acer campestre</i>			2								
<i>Corylus avellana</i>			8								
<i>Geranium robertianum</i>			1,3								
<i>Melissa officinalis</i>			2								
<i>Viola reichenbachiana</i>			0.7								
<i>Dryopteris filix-mas</i>			0.7								
<i>Euonymus europaeus</i>			0.6								
<i>Campanula trachelium</i>			0.1								
<i>Mycelis muralis</i>			0.1								
<i>Euphorbia dulcis</i>			0.1								
<i>Arum italicum</i>			0.1								
<i>Euphorbia amygdaloides</i>			0.1								
<i>Rosa canina</i>			0.1								
<i>Pulmonaria officinalis</i>			0.6								
<i>Ranunculus lanuginosus</i>			1			0.1					
<i>Veronica montana</i>			0.1								
<i>Chaerophyllum temulum</i>			1.1								
<i>Prunus spinosa</i>			0.1								
<i>Senecio nemorensis</i>			0.6								
<i>Ostrya carpinifolia</i>	25		0.5								
<i>Oxalis acetosella</i>			0.5								
<i>Stellaria nemorum</i>			3.3								
<i>Equisetum arvense</i>			9								
<i>Eupatorium cannabinum</i>			6.8								
<i>Petasites hybridus</i>			17.3								
<i>Ranunculus repens</i>			3.4								
<i>Mentha aquatica</i>			0.7								
<i>Torilis japonica</i>			0.2								
<i>Parietaria officinalis</i>			1.2								
<i>Galium aparine</i>			0.1								
<i>Chaerophyllum hirsutum</i>			1.7								
<i>Lycopus europaeus</i>			0.1								
<i>Urtica dioica</i>			0.6								
<i>Poa trivialis</i>			3.3								
<i>Equisetum ramosissimum</i>			0.1								
<i>Galeopsis tetrahit</i>			1.2								
<i>Lonicera japonica</i>			3.4								
<i>Robinia pseudoacacia</i>			0.6								
<i>Primula veris</i>			0.6								
<i>Polygonum persicaria</i>			1.1								
<i>Lythrum salicaria</i>			0.1								
<i>Bidens tripartita</i>			0.1								
<i>Helianthus tuberosus</i>			0.1								
<i>Bromus ramosus</i>			0.1								
<i>Silene alba</i>			0.1								
<i>Calystegia sepium</i>			1.1								
<i>Polygonum mite</i>			0.5								
<i>Festuca heterophylla</i>			0.6								
<i>Potentilla reptans</i>			0.6								

DAC: *Quercetum ilicis* Br.-Bl. 1915
 CIT: *Quercetum ilicis galloprovinciale pistacietosum* Br.-Bl. 1952
 MAG: *Alno-Praxinetum oxycarpae* (Br.-Bl. 1915) Tchou 1946
 AAP: *Quercetum ilicis* Br.-Bl. 1915
 PEN: *Quercion pubescenti-petraeae* Br.-Bl. 1931 (original relevés)
 MAR: *Orno-Quercetum ilicis* Horvatic (1956) 1958
 FIN: *Oleo-Ceratonion* Br.-Bl. 1936 (original relevés)
 MRU: *Quercion pubescenti-petraeae* Br.-Bl. 1931 (original relevés)
 CAP: *Asplenio-Quercetum ilicis* Rivas-Martinez 1974
 CIR: *Asplenio-Quercetum ilicis* Rivas-Martinez 1974
 ANG: *Helleboro-Quercetum suberis* Signorello 1984

Table 4. Plant taxa in the study areas: the average values of species coverages are reported.

In some cases, the sum of the specific coverages exceeds 100% because of the overlapping of arboreal, shrub and herbaceous layers.

	Thermophilous species			Thermophilous species in common		Thermophilous climatic species	
	coverage	%	number	coverage	%	coverage	%
DAC	629	74.3	20	442	52.2	411.5	48.6
CIT	582.5	94.2	24	382.5	61.8	483	78.1
MAG	395	4.8	4	0	0	0	0
AAP	1106	99.6	27	403.5	36.4	351	31.6
PEN	479.4	94.3	18	154.2	30.3	372.1	73.2
MAR	122.6	66.5	5	141.7	77	112	60.8
FIN	502.7	96.6	39	166.5	51.2	77.1	14.8
MRU	80	47.3	13	52	30.8	66.5	39.3
CAP	580.5	95.7	18	293.5	48.4	456.5	75.4
CIR	328.5	81.6	18	251.5	62.5	294	73
ANG	1810	62.3	36	333	11.5	627.5	21.6
MEAN	601.47		20.18	238.21		295.56	
SD*	485.77		11.06	146.57		203.68	
VC**	80.76		59.71	63.04		68.91	

	Life forms					
	PH %	H %	T %	G %	CH %	(T-H) PH
DAC	75	18.70	0	6.30	0	-1402.50
CIT	63.60	27.30	0	6.05	3.05	-1736.30
MAG	38.50	38.50	19.20	3.80	0	-743.00
AAP	50	21.90	6.30	3.10	18.70	-780.00
PEN	68.20	5.40	0	21.40	5	-368.30
MAR	75	16.70	0	8.30	0	-1252.50
FIN	39	26.60	25	7.80	1.60	-62.40
MRU	77.30	9.10	0	9.10	4.50	-703.40
CAP	74.07	11.03	0	14.90	0	-823.90
CIR	80	10	0	10	0	-800.00
ANG	40	36.70	6.70	13.30	3.30	-1200
MEAN	61.87	20.17	5.20	9.45	3.28	-897.48
SD	16.71	11.16	8.84	5.34	5.47	473.70

Table 4A. Plant indices (* standard deviation, ** variation coefficient).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
	CLIMATE					TYTO ALBA-MAMMALS						PLANTS				
DAC	7	6	8	9	6	7	3	6	8	8	7	10	6,5	4	10	10
CIT	10	7	5	5	10	6	3	7	7	3	5	2	3,5	3	11	4
MAG	9	9	10	8	8	10	8	8	5	5	8	11	11	11	4	11
AAP	11	11	11	7	11	11	9	10	10	9	9,5	3,5	1	7	5	1
PEN	8	8	7	10	7	8	10	9	9	10	9,5	7	6,5	9	2	6
MAR	2	5	1	6	3	4	3	1	1	2	1	8	10	1	9	8
FIN	3	4	2	2	4	3	6	4	2	1	2,5	1	5	5	1	3
MRU	5	10	9	11	9	2	11	11	11	11	11	9	9	8	3	9
CAP	1	2	3	4	1	1,5	3	2	4	7	4	3,5	2	6	7	2
CIR	6	3	6	3	5	5	3	3	3	4	2,5	5	8	2	6	5
ANG	4	1	4	1	2	1,5	7	5	6	6	6	6	3,5	10	8	7

Table 5. Ranked values of climate, "Tyto alba-mammals trophic systems" and vegetation indices.

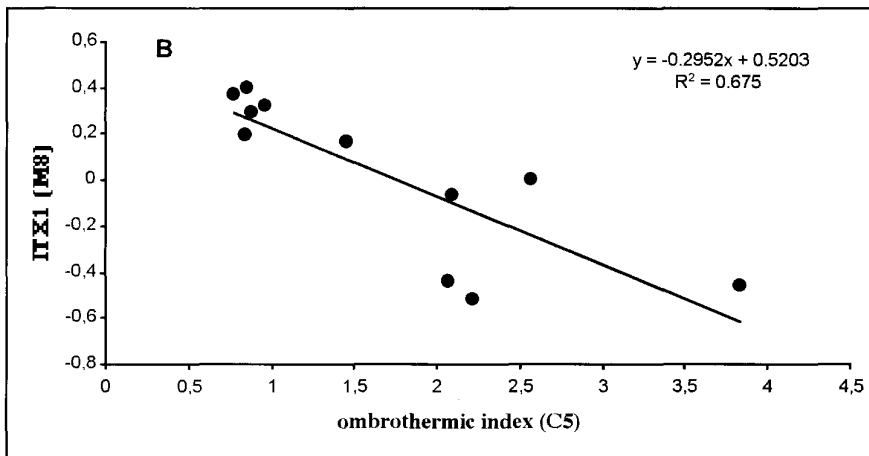


Figure 2B. Regression line between ombrothermic index and ITX1

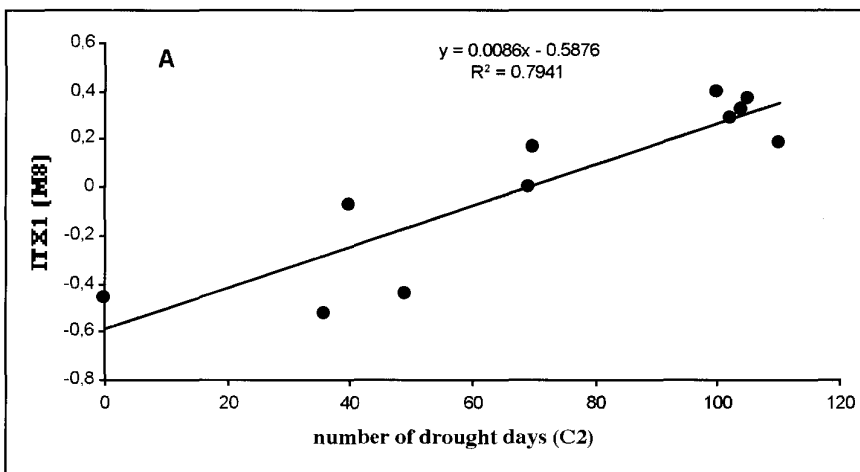


Figure 2A. Regression line between number of drought days and ITX1

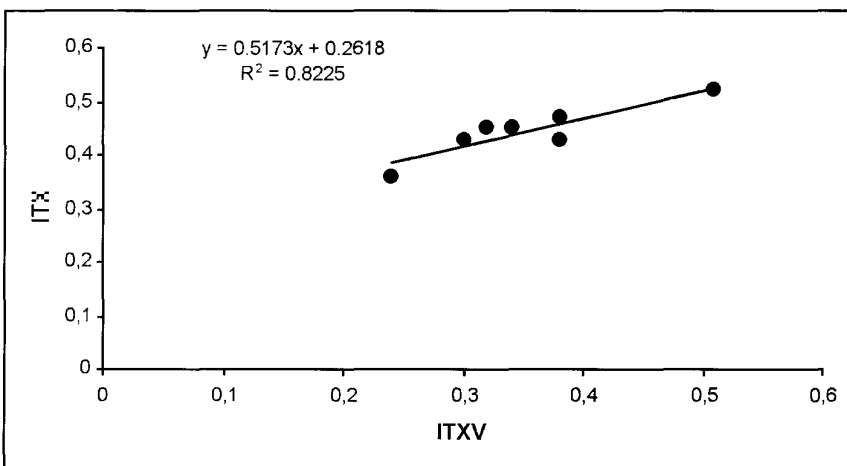


Figure 3. Regression line between ITXV and ITX in M. Rufeno (MRU) Reserve. ITXV = Thermoxerophily vegetation index; ITX = Thermoxerophily mammal index.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	-	<0.05	.01		<0.01	<0.01		<0.05								
2	<0.05	-	<0.05	.01	<0.01	<0.01	-	<0.01	-		<0.05					
3	<0.01	<0.01	-	-	.01	<0.01		<0.01	<0.01	<0.05	<0.01					
4		<0.01	<0.05	-		<0.05		-	<0.05	<0.05	<0.05	-				
5	<0.01	<0.01	<0.01		-	<0.01		<0.01	<0.05		<0.05					
6	<0.01	<0.01	<0.01	<0.01	<0.01	-	-	<0.01	<0.05		<0.05					
7		<0.05					-	<0.01	<0.05	<0.05	<0.01			<0.05	<0.05	
8	<0.05	<0.01	<0.01	<0.05	<0.01	<0.01	<0.01	-	<0.01	<0.05	<0.01					
9		<0.05	<0.01	<0.05	<0.05	<0.05	<0.05	<0.01	-	<0.01	<0.01					
10			<0.05	<0.05			<0.05	<0.05	<0.01	-	<0.01					
11		<0.05	<0.01	<0.05	<0.05	<0.01	<0.01	<0.01	<0.01	<0.01	-			<0.05		
12				<0.05								-	<0.05			<0.01
13												.01	-			<0.01
14							<0.01				<0.05			-		
15							<0.05								-	
16												<0.01	<0.01	-		

Table 6. Statistical significance of correlations among climate, Tyto alba-mammals trophic systems and vegetation, according to the Kendall (right-high half) and Spearmann (left-low half) tests

Sites	1	2	3	4	5	6	7	Thermoxerophily degree*
<i>Vegetation types</i>	%	%	%	%	%	%	%	
<i>Quercus cerris</i> coppice	63.4	41.7	51.9	37	57.8	66.7	48.1	1
<i>Castanea sativa</i> coppice					3.2			1
Broadleaves coppice	25.4	18.2	13.9	5.6	16.3	16.2	17.3	1
<i>Q.cerris, Q.pubescens</i> coppice		1.1	0.8					2
<i>Q.pubescens</i> coppice			2.4	7.1				2
Coniferous plantations	9.6	25	25.8	4.6	17.4	8.4	24.7	3
Sclerophyllous coppice						6.5		3
Shrublands	0.4	5	1.7	1.4	2.5	1.9	1.6	3
Abandoned pastures	0.4	2.3	1.7				1.2	4
Uncultivated land		0.9	0.5	0.5	1.4		1.2	4
Orchards	0.6		0.3	0.5	0.3			3
Rocks				1.9				
ITXV	0.24	0.38	0.37	0.5	0.32	0.29	0.34	
ITX	0.36	0.43	0.47	0.52	0.45	0.43	0.45	
ITX1	-0.61	-0.61	-0.48	-0.38	-0.45	-0.44	-0.5	
ITX2	0.01	0.07	0.03	0.07	0.06	0.07	0.02	
ITX3	0	0.02	0.03	0.03	0.02	0.01	0.005	

* 1 = high mesophily, 2 = moderate mesophily, 3 = moderate thermoxerophily, 4 = high thermoxerophily

Table 7. Extensions (in percentages) of vegetation types, thermoxerophily index values for vegetation and mammals in Tyto alba sites of M. Rufeno reserve.

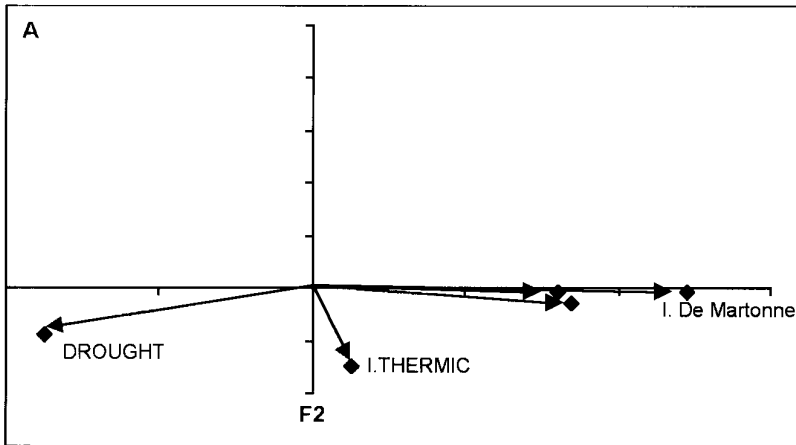


Figure 4. CCA ordination diagram with climate (A) and plant (B) indices (first axis horizontally, second axis vertically)

THSPCOV = Thermophilous species coverage
 THSPCL = Thermophilous climatic species
 THSPCOM = Thermophilous species in common
 PH = Phanerophytes
 H = Hemicryptophytes
 T = Therophytes
 G = Geophytes
 CH = Chamaephytes

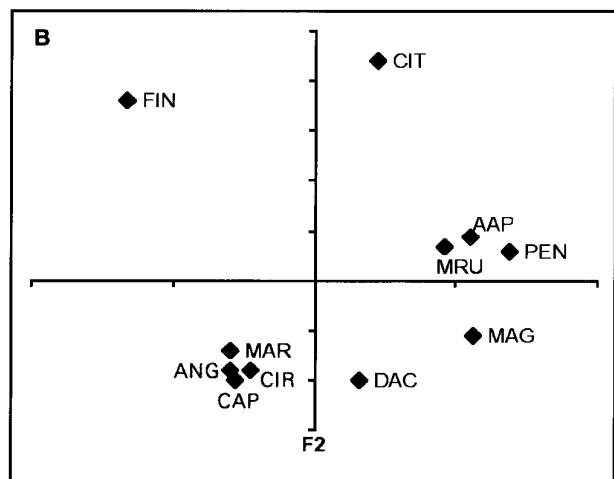
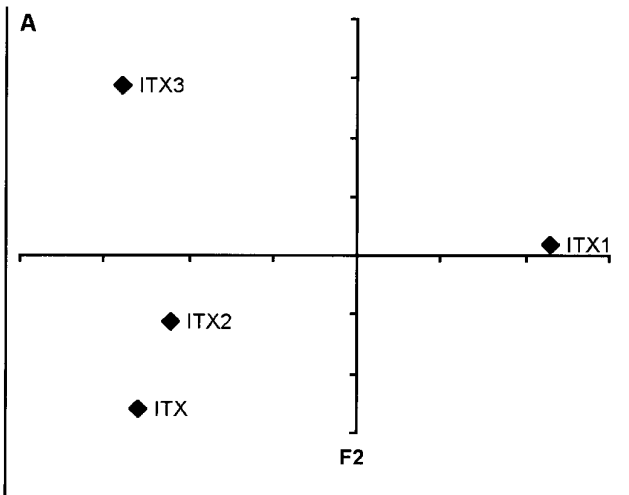
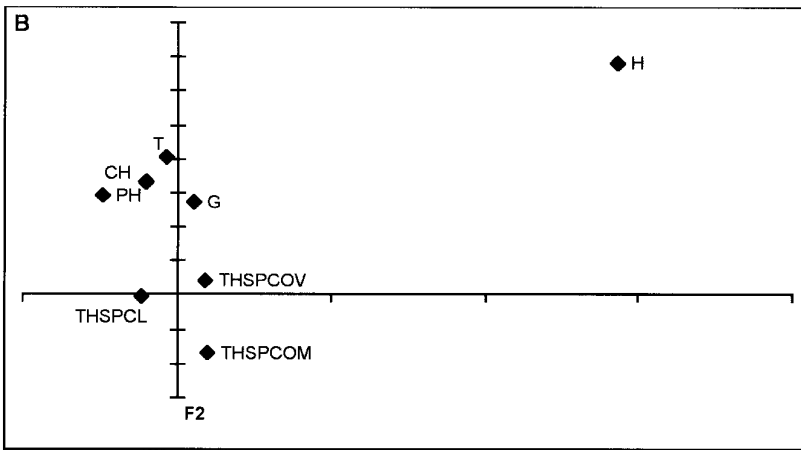


Figure 5. CCA ordination diagram with mammal indices (A) and sampling areas (B); first axis horizontally, second axis vertically

		Variance of the first factor		
		Climate	Mammals	Plants
Variance of the first and second factors	Climate	1	87.6	50.9
	Mammals	96.9	1	52.0
	Plants	75.1	70.9	1

Table 8. Values of variance for climate, mammals and plants by CCA analysis.

Statistical treatment

The climate ("C"), *Tyto alba*-mammals trophic systems ("M") and plant ("P") index values were expressed in ranks (table 5) and tested using to non-parametric tests (i.e. Kendall & Spearman tests) (Sokal & Rohlf, 1981). The significant results of these tests are reported in table 6. However overall data were also analyzed using several parametric tests. Moreover data were also subjected to Canonical Correspondence (CCA) Analysis (Prodon, *in litteris*), utilizing the CANOCO Programme (Ter Braak, 1985), to obtain an ordination of the fauna ("M") and plant ("P") matrices correlated at best with the environmental variables ("C") (Prodon & Lebreton, 1991; Mazzoleni *et al.*, 1992) and to represent them simultaneously (figure 4A, B; figure 5A, B).

RESULTS

Quite obviously, all indices of the same group (climate, plants, mammals) were strongly correlated to each other. There is less coherence within the "P" indices; even though the variation coefficient is considerably larger in the P indices than in the C and M indices ($p < .05$: "U" of Mann-Whitney and Kruskal-Wallis tests). Moreover, this difference is particularly evident in the comparison between the C and P indices or the components of the indices ($p < 0.01$; 2t) (table 6).

At least 20 out of 30 C-M correlations were significant at 0.05 (2t) or less, according to the Spearman test (all correlations were positive). In particular, M8 was strongly correlated to all C indices (table 6; figure 2: A, B). C-P correlations were always positive with the exception of five cases, but values were mainly non-significant, even if a trend can be detected. According to the Spearman test, only one of the total of 30 correlations was

significant at $p < 0.05$ (2t), regarding C4 vs. P12. P-M correlations were not significant, except for P14 vs. M7 and M11 (table 6). Nine correlations were negative, one even significantly (P15 vs. M7).

The CCA showed an overall high concentration of the variance in the first two axes (table 8) with the maximum (96.9) for the C-M relation, up to P-M relation (70.9). This analysis is still in progress; nevertheless some points can already be underlined.

Canonical correspondence analysis of "P" matrix constrained on climatic variables "C" showed a good correlation between thermophilous species vs. Drought and Thermic index (figure 4: A, B); the pattern of hemicryptophytes (H), expressing a more temperate climate, results properly separated from the "dry-warm" pole of environmental variables (Drought and Thermic index) and close to the "rain-cold" pole, well expressed by De Martonne index, Rain Summer and Omrothermic index.

In relation to "M" indices, the two above mentioned climatic poles (dry-warm and rain-cold) appear evident. Among "M" indices, ITX2, based on both Insectivores and Rodents, lies between ITX, based only on Insectivores and ITX3, based only on Rodents (figure 5A). Possibly, these two mammalian orders belonging to different trophic levels, reflect the influence of Mediterranean environments in quite a different way.

The pattern of the sampling areas (figure 5B) showed that the more humid areas (AAP, MRU, PEN and MAG) are well separated from the more thermoxerophilous areas (MAR, CAP, CIR, ANG).

DISCUSSION

The lesser coherence found within "P" indices when compared with greater coherence within C and M indices (see, for example, C6 vs. M11 in table 6 and M8 vs. C2

and C5 in figure 2: A, B) seems to confirm the greater heterogeneity shown by some structural and dynamic vegetation features. Particularly, the indices based on succession stages and life forms did not show significant intergroup correlations. This is probably due to the fact that, in phytocoenoses, the structural features (such as life forms) and dynamic features (such as evolutionary stages) are not linearly linked. The vegetation is a complex system depending on a high number of internal ecological variables affecting the coenoses in time and space, particularly in the Mediterranean environments subjected to strong historical anthropogenic influences (Schimel *et al.*, 1997; Naveh, 1987; Pignatti, 1978). This does not apply to mammal taxocoenoses because of their much lower inertia.

Among the "P" indices, some significant correlations found (table 6) seem very interesting:

P12 vs. C4 highlights the importance of cold winter stress on the bioclimatic characteristics of the phytocoenoses, influencing the distribution of the thermophilous evergreen species (Mitakos, 1980);

P15 vs. M7 is possibly due to the influence of the woody component on mammal communities (Pizzolotto *et al.*, 1991);

P14 vs. M7 depends on a fairly small group of species (*Quercus ilex* L., *Smilax aspera* L., *Asparagus acutifolius* L., *Rubia peregrina* L., *Myrtus communis* L., *Pistacia lentiscus* L., *Erica arborea* L., *Clematis flammula* L.); some of which (e.g. *Myrtus communis*, *Pistacia lentiscus*, *Erica arborea*) represent the most typical life forms of a Mediterranean vegetation, linked to degradation stages of the evergreen Mediterranean wood, e. g. after fire (Schimel *et al.*, 1997; Trabaud, 1981; De Lillis & Testi, 1992) and represent good indicators of a strong thermoxerophily.

C4 (correlated both to Plant index P12 and mammal indices 8,9,10,11 (table 6) appears linked to some central factor in the "C-P-M" relations. However, according to the Spearman test, both M7 and M11 seem significantly linked to the number of drought days (C2), Σ of the climate indices (C6) and the percentage of thermophilous species coverage shared in all areas (P14) (table 6), as was also expressed by the CCA results (figure 4 B). The bioclimatic data on the vegetation also support these relationships, according to the thermic and ombrothermic index values, as well as to the CCA results (figure 5 B). It is evident that the most thermoxerophilous areas (MAR, CIR, CAP) are well separated from the most humid ones (AAP, MRU) where, e. g., the ITX values (0.46 and 0.42) are the lowest and thermophilous species coverage is lower than in the other areas (table 4A). The Angitola area (ANG), even though characterized by the

highest thermic index value (table 2), does not show an elevated coverage value for thermophilous plant species. The local rainfall regime, together with the edaphic moisture of this area, influence the vegetation structure and the floristic composition more than the "M" trophic systems (the ITX value is 0.89), favouring the spread of a mesophilic cork-oak wood (*Helleboro-Quercetum suberis*) (Signorello, 1984; Testi & Lucattini, 1994).

The results suggest that the relatively poor correlation of "plant" indices may be mainly explained by:

(1) The different territorial size of the sampling areas. Climate data reflect territorial distances of the O.O.M. (order of magnitude) of 10^6 m². The same occurs for raptor hunting territory (Géroutet, 1965; Taberlet, 1983). Conversely, vegetation relevés are currently made on an O.O.M. of 10^2 - 10^3 m² areas clearly subjected to local influences such as exposure, slope, drainage, including very diversified small-scale anthropic pressures. As a result, each phytocoenosis should be considered as a peculiar system, characterized by local environmental and ecological factors and by their history, especially from the point of view of the human impacts (Federici & Pignatti, 1992). This is also linked with the typical inertia exhibited by long-living plant species.

(2) Methodological differences in data collecting. Climatic data are obtained in a standardised and automatic way, mammal trophic systems data, deriving from a single raptor species (*Tyto alba*), are obviously linked to a unique habitat but are collected and classified in a standardised way, while vegetation data, are linked to the subjective estimates of different researchers, even if automatic data processing reduces the degree of subjectivity. In the M. Rufeno reserve, where data were gathered by a single set of authors, correlation between the two biotic components, expressed by the ITX and ITXV, was more significant (figure 3). This happened despite the fact that M. Rufeno observations were made at a near micro-scale level. The high variance values from CCA (table 8) along with the fact that this value was higher in mammals than plants, confirm the general starting assumption. The mammal coenoses are probably less sensitive to landscape heterogeneity than plant coenoses. Thus, the trends in contradistency observed, suggest the hypothesis of a break of "climate-vegetation" equilibrium, particularly evident in fragmented and disturbed areas of the Mediterranean contexts, where vegetation is submitted to strong constraints (Pignatti *et al.*, 2000). The climate-plants relationship was well expressed by the pattern of hemicryptophytes (H), indicating a more temperate climate, properly separated from the "dry-warm" pole of environ-

mental variables (Drought and Thermic index) and close to the “rain-cold” pole (De Martonne index, Rain Summer and Ombrothermic index) (figure 4A, B). In relation also to “M” indices, the two above-mentioned climatic poles (dry-warm and rain-cold) are evident.

Among “M” indices, ITX2, based on both Insectivores and Rodents, lies between ITX, based only on Insectivores and ITX3, based only on Rodents (figure 5A). It is possible that these two mammalian orders, belonging to different trophic levels, reflect the influence of Mediterranean environments in quite a different way. Moreover, the sampling areas pattern (figure 5B) well supports the ecological gradients revealed by this analysis: the more humid areas (AAP, MRU, PEN and MAG) correspond to the “Rain” sector while the more thermoxerophilous areas (MAR, CAP, CIR, ANG), correspond to the “Dry-Warm” sector.

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CONCLUSIONS

Even at a meso-scale level, our data show a good correlation between C and M indices, no less than C-P and M-P relations. Very likely, the effects of geological and edaphic as well as historical and evolutive factors overlap more extensively with those of climate in plant than in animal communities. This could even be more clear at the meso than at the macroclimate level because stochastic events, fluctuations, and grain effects drive the differences among the relevant scale factors. This plays an important role in emphasising sampling problems and the linkage with abiotic factors strongly influence plant communities composed of sessile and long-living species.

In this light, the trophic systems studied express some climatic characteristics no less effectively than the plants: mammals are probably less sensitive to landscape heterogeneity and less dependent on the arbitrary choice of the observer. Thus, the results obtained could justify the use of a set of animals in bioclimatology.

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Negative effect of the wild boar (*Sus scrofa*) on the populations of snakes at a protected mountainous forest in central Italy

*Effet négatif du sanglier (*Sus scrofa*) sur les populations de serpents dans une forêt de montagne protégée en Italie centrale*

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Abstract

The potential effects of the wild boar (*Sus scrofa*) on the local abundance of the snakes was studied at two mountain plots, each 6 ha surface and apparently nearly identical in terms of habitat characteristics (mixed oak forest with clearings), inside the "Duchessa Mountains Natural Park" (central Apennines, Italy). Plot "A" was intensively used by wild boars for their usual rooting activities, whereas plot "B" was not. Although the two plots were surveyed for an identical time (21 days each, six to eight hours per day of research), it appeared that snakes were considerably more abundant in plot "B" than in plot "A". In particular, (i) the apparent abundance of *Vipera aspis* was approximately twice in plot "B" than in plot "A"; (ii) that of *Elaphe longissima* was approximately six times greater in plot "B" than in plot "A", and (iii) that of *Coluber viridiflavus* was approximately three times greater in plot "B" than in plot "A". *Natrix natrix* was captured only in plot "B". However, in both plots, *V. aspis* was the most common species, and *N. natrix* the least common species.

These data suggest that the presence of abundant populations of wild boars may have devastating effects on the local populations of snakes, because of (i) a direct predation effect, (ii) a potential indirect effect by reducing the abundance of prey communities for snakes, and (iii) a disturbance effect of the micro-habitats and shelters used by snakes.

Key-words

Mammals-Reptiles interactions, *Sus scrofa*, snakes, conservation, wildlife management, Apennines

RÉSUMÉ

Les effets potentiels du sanglier (*Sus scrofa*) sur l'abondance locale des populations de serpents ont été étudiés sur deux secteurs montagneux d'une superficie de 6 ha présentant un grande similitude en terme d'habitats (chênaies mixtes avec clairières), situés au sein du "Duchessa Mountains Natural Park" (Apennins, Italie). La parcelle "A" était intensivement fréquentée par les sangliers pour leur alimentation alors que la parcelle "B" ne l'était pas. Bien que les deux parcelles ont été suivies de façon identiques (21 journées chacune et six à huit heures par jour de recherche), les populations de serpents se sont avérées nettement plus abondantes dans la parcelle "B" que dans la parcelle "A". Cette étude a montré en particulier (i) que l'abondance apparente de *Vipera aspis* était approximativement le double dans la parcelle "B", comparée à la parcelle "A"; (ii) que les populations d'*Elaphe longissima* étaient environ 6 fois plus importantes dans la parcelle "B", comparée à la parcelle "A", et (iii) que *Coluber viridiflavus* était trois fois plus commune dans la parcelle "B" que dans la parcelle "A". *Natrix natrix* n'a été capturée que dans la parcelle "B". Cependant, dans les deux cas, *V. aspis* s'est avérée être l'espèce la plus commune, et *N. natrix*, la plus rare. Ces résultats suggèrent que la présence d'abondantes populations de sanglier peuvent avoir des conséquences drastiques sur les populations locales de serpents du fait (i) d'une prédation directe; (ii) de la réduction de l'abondance des proies de serpents, et (iii) d'une modification des micro-habitats et de la disponibilité en abris utilisés par les serpents.

Mots-clés

Interactions mammifères-reptiles, *Sus scrofa*, serpents, conservation, gestion de la faune, Apennins

INTRODUCTION

With an omnivorous diet consisting of both plant matters (e.g., tuberos, fruits, berries, seeds) and animal matters (earthworms, arthropods, small vertebrates), the wild boar *Sus scrofa* is certainly the Mediterranean ungulate with the greatest dietary plasticity (e.g., see Dardaillon, 1987), accomplished also with a remarkable adaptability to habitat variations and alterations (e.g., Marsan *et al.*, 1997). In mainland Italy, the Mediterranean wild boar race (*Sus scrofa majori*, which should be synonymous with *S. scrofa scrofa* according to Apollonio *et al.*, 1988; Randi *et al.*, 1989) has been genetically contaminated and nowadays practically replaced by a eastern European race, which was massively introduced for game reasons (Amori *et al.*, 1999). Unfortunately, this introduced race, which is known to attain a bigger size than the original Italian populations, proved to be extremely “aggressive”, and in fact has caused enormous damages to crops, plantations, and forestry conditions in wide areas of mainland Italy (Tosi & Toso, 1992). Indeed, the ecological control of wild boar populations is a management priority for many protected areas in mainland Italy, including national parks and natural reserves (e.g., Tosi & Toso, 1992). Wild boars represent a serious problem for mountainous forests of the central Apennines (central Italy), and thus it is not surprising that the institutions in charge with the protection and management of these protected areas have put special research attention to the field biology of wild boars, to their effects on the general ecosystem, and to the practical measures to be undertaken in order to limit their damages to agro-forest environments.

On behalf of the directorship of the “Duchessa Mountains Natural Park” (province of Rieti, Latium, central Italy), we conducted a field study to assess whether the excessive abundance of wild boars (which is known to occur within this protected area; Calò, 2000) may be a negative factor for the presence, abundance, and diversity of the snakes of this area. This study case is likely very important because (i) it may well be generalized to wide areas of central Italy, where, as in our study area, mixed oak forests are dominant at the altitude ranges of 800-1500 m a.s.l. (Filippi & Luiselli, 2000a), and because (ii) the snake-fauna of the study area is very rich, and includes also *Vipera ursinii* (Filippi & Luiselli, 2000a), which is certainly the most threatened snake species of Italy (Filippi & Luiselli, 2000b). In the present paper, we report the main experimental results of our investigation.

MATERIALS AND METHODS

Study area

The field research was conducted at a protected area of the central Apennine massif (Duchessa Mountains Natural Park, lat. 42° 12' N, long. 13° 20' E), situated approximately 80 km east of Rome and 30 km west of L'Aquila. This area is characterized by a montane massif up to 2184 m a.s.l. (Monte Murolungo), and represents the westernmost part of the Velino Massif, which is one of the highest mountains in central Italy. The climate is cool temperate, with Mediterranean influences of the type reduced; annual rainfall (1886-1986) was 1090 to 1173 mm, and annual mean temperature (1886-1986) was 11.3 to 12.7 °C (Ministero dei Lavori Pubblici, Servizio Idrologico 1886-1986). The area is characterized by an exceptional diversity of vegetation types, including alpine grasslands (*Festuca nigricans nigricans*, *Trifolium thalii*, *Ranunculus apenninus*, *Plantago atrata*, *Poa alpina*) at the upper elevations beyond the wooded surface, and forests of *Fagus sylvatica*, *Quercus pubescens*, *Q. cerris*, *Fraxinus ornus*, *Ostrya carpinifolia*, *Acer obtusatum*, *A. monspessulanus*, *Sorbus aria*, covering the most part of the massif at the intermediate and low elevations (i.e. 800-1600 m a.s.l.; cf. Petriccione, 1993).



Example of a devastated area by wild boar's (*Sus scrofa*) rooting tracks in the area of Duchessa mountains Natural Park (Italy).

The species

The snake-fauna of the Duchessa Mountains has been carefully studied during the recent years (see Filippi & Luiselli, 2000a), and consists of two viperids (*Vipera aspis* and *V. ursinii ursinii*), and four colubrids (*Natrix natrix*, *Coluber viridiflavus*, *Elaphe longissima*, and *Coronella austriaca*). Apart for *V. ursinii*, confined to the grasslands at the upper elevations (1700 to 2000 m a.s.l.), all the other species are found in the wide forests at the lower elevations (800-1500 m a.s.l.) (Filippi & Luiselli, 2000a). Wild boars are abundant in the area (Calò, 2000), and are found from the wooded areas at the lower elevations to the grassland at the upper elevations (Calò, 2000; Filippi & Luiselli, 2000a). Their abundance may place locally serious threats to the cultivations and the forest ground micro-habitats, especially in consideration of the fact that about 30% of the whole pasture surface is currently devastated by boar's grooming tracks (Calò, 2000).

METHODS

Field research was conducted from March to October 2000, and in March to May 2001. A total of 42 days were spent in the field, and at least six to eight hours of field effort per day of research were done.

Two study plots, both SW facing slopes, and nearly identical in terms of habitat characteristics, elevations, and climate, were surveyed for snakes. Plot "A", six hectares surface, 940-980 m a.s.l., was a mixed oak forest with clearings, situated just above the village "Cartore". Plot "B", six hectares surface, 920-960 m a.s.l., was also a mixed forest with clearings, situated along the path connecting the place "Casali di Collepizzuto" with "Cartore". The centers of the two plots were approximately 2.3 km of linear distance each another. In both areas the ground available to snakes consisted of grass (respectively 52% and 50%), stones or rocks (8% and 14%), cut tree-branches (4% and 5%) and leaf litter (36% and 31%) (for the methods used to assess the typological composition of the ground, see Filippi & Luiselli, 2001). The type of potential terrestrial preys for snakes were the same in the two plots, i.e. lizards (*Podarcis muralis*, *P. sicula*, *Lacerta bilineata*, *Anguis fragilis*), toads (*Bufo bufo*), and small mammals (*Apodemus sylvaticus*, *A. flavicollis*, *Clethrionomys glareolus*, *Crocidura* sp.), but their local abundance was not known (Filippi & Luiselli, 2000a).

Although apparently almost identical in terms of macro-ecological characteristics, the two plots differed in that "A" was characterized by a strong presence of wild boars, whereas "B" was not affected by the same problem. The strong presence of wild boars in plot "A" but not "B" was ascertained (i) by careful studies of the dispersal and home range use of these large mammals at the study area (Calò, 2000), and (ii) by the abundant tracks and signs of their presence on the soil of plot "A" but not of "B" (Filippi & Luiselli, 2000a). Human intrusion into the two surveyed plots, apart for the authors, was limited to a few excursionists walking along the paths crossing the two plots. In any case, the frequency of human intrusion was low and similar in the two plots (0.116 people x hour of field research in plot "A", and 0.123 people x hour of field research in plot "B"). Two snake corpses (a young *Elaphe longissima* and an adult male *Vipera aspis*), killed by excursionists, were found at plot "B", and no dead specimen was found at plot "A". An identical research effort was conducted in both study plots (21 field days at each plot). Moreover, to avoid that seasonality of samples may have biased data for the two plots (Bonnet & Naulleau, 1996; Bonnet *et al.*, 1999), we always maintained a constant sampling, which was to survey plot "A" at a given day, and plot "B" the day after, during the whole period of the research. Snakes were searched along standardized routes conducted along both the study plots. Each snake eventually captured was measured for snout-vent length (SVL, to the nearest ± 0.1 cm), and individually marked by ventral scale clipping for future identification. They were also palpated in the abdomen until regurgitation of ingested food or defecation occurred, and prey items were identified to the lowest taxon possible. For females, eventual pregnancy status and numbers of eggs were determined by abdominal palpation. In addition, the two specimens found already dead during our surveys were collected, dissected, placed in alcohol and deposited in the collections of the "Duchessa Mountains Natural Park" (Corvaro, Borgorose, province of Rieti).

RESULTS

A total of 10 snakes was captured in plot "A": 3 were *C. viridiflavus* (an adult male, an adult female, and one juvenile), 2 were *E. longissima* (one adult male, one juvenile), and 5 were *V. aspis* (three adult males, two adult females). On the other hand, 36 snakes were captured in plot "B": 9 were *C. viridiflavus* (four adult males, four adult

females, one juvenile), 12 were *E. longissima* (six adult males, four adult females, two juveniles), 1 was *N. natrix* (a juvenile), and 14 were *Vipera aspis* (six adult males, seven adult females, one juvenile) (figure 1). Considering that the field effort was the same in the two plots, the numbers of captured snakes (all species cumulated) differed significantly from the null hypothesis of an equal number of captures in the two plots (χ^2 test with $df = 1, P < 0.001$). Although the numbers of captured specimens differed significantly between the two plots (as well as, most probably, also the overall snake density, which was not calculated here due to the too small numbers of recaptures), nonetheless the snake-fauna composition was nearly identical, with *V. aspis* being the most common species, and *N. natrix* the least common species. In any case, it is noteworthy that: (i) the apparent abundance of *V. aspis* was approximately twice in plot "B" than in plot "A"; (ii) that of *E. longissima* was approximately six times greater in plot "B" than in plot "A", and (iii) that of *C. viridiflavus* was approximately three times greater in plot "B" than in plot "A" (Figure 1). On the other hand, the numbers of marked *N. natrix* were too low to stress anything on this matter. *Coronella austriaca*, a small secretive colubrid which

was captured at higher elevations (1500 to 1800 m a.s.l.) in the same mountainous area (Filippi & Luiselli, 2000a), was never encountered at our two study plots, but we could not exclude its presence here, although, in the case, it should certainly be extremely rare. No specimen captured in a given plot was recaptured in the other plot.

It is noteworthy that *V. aspis* occurred in the study plots with three different coloration morphs: (1) "normal *francisciredi*" (as in types 1 and 2 in Fig. 66 of Bruno, 1984), (2) "striped *francisciredi*" (as in types 5 and 6 in Fig. 66 of Bruno, 1984), and (3) melanistic (*sensu* Naulleau, 1973); *C. viridiflavus* occurred in a melanotic morph, black or dark-black on the back, and brownish to yellowish on the ventral side.

DISCUSSION

The present study provides clear evidence that the two surveyed plots differed significantly in terms of local abundance of snakes, which is a very interesting (and surprising) result if we consider that the two plots were almost

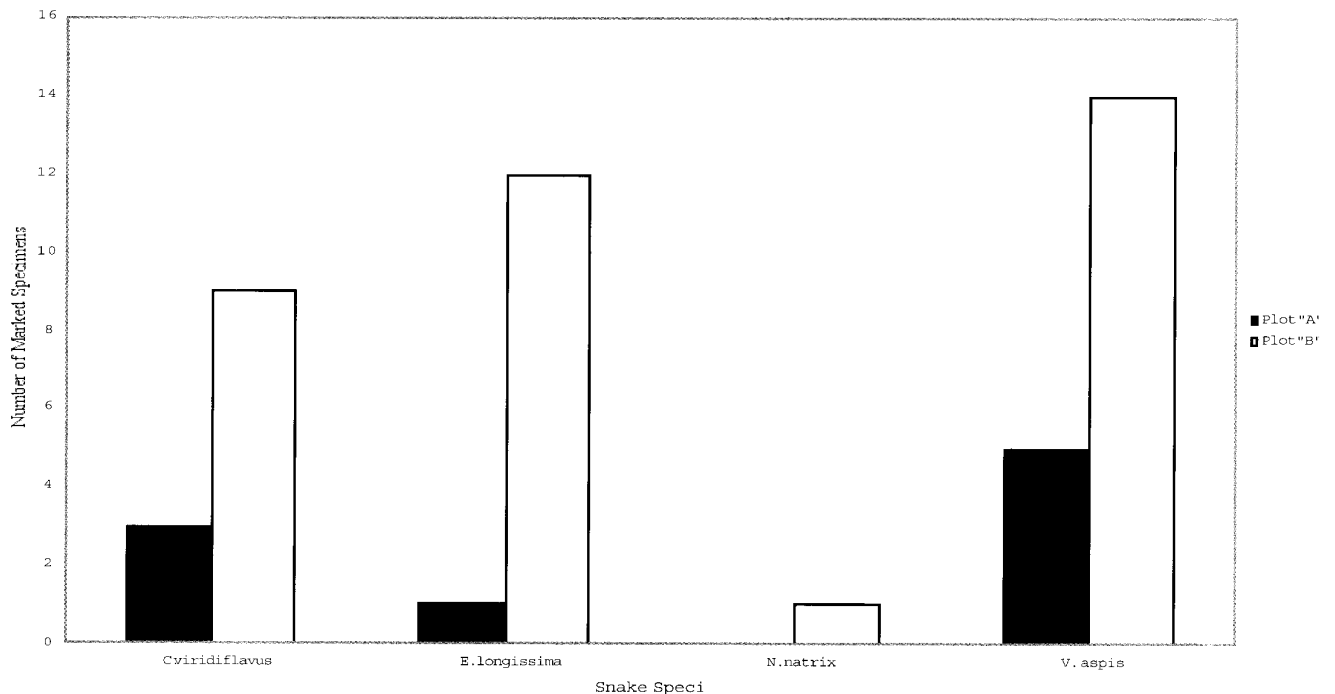


Figure 1. Numbers of snake specimens captured and marked in the two study plots at the study area. Note that snakes were significantly more abundant in the plot where wild boar activity signs were not found (plot "B"). For statistical details, see the text.

adjacent, and identical (at least to a human observer) in terms of general habitat characteristics, and potential prey resource composition. Moreover, the density of human intruders was similar in the two plots (and even a little higher in plot "B"), which is a good indication that no effects of differential disturbance by humans may be invoked to explain the above-mentioned differences in snake abundance observed between plots. Thus, the only apparent factor for the evident reduction of the snake abundance in plot "A" appears to be the strong presence of wild boars, whose "rooting" activities produced considerable removal of grass, leaf litter, and musks, as well as removal of many stones which may constitute shelters for small snakes. In this regard, at the actual state of our knowledge, it is not possible to exclude that the higher snake density at plot "B" can be caused in part also by the higher relative density of stones and rocks. Wild boar activity may be a detriment factor for the local abundance of snakes because of (i) a direct predation effect (wild boars are known to eat on snakes [e.g. see Cattaneo & Capula, 2000; Cattaneo & Carpaneto, 2000], and snakes should most probably be a part of their dietary spectrum in the study area, although no data on this issue are available), (ii) a potential indirect effect by reducing the abundance of prey communities for snakes, and (iii) a disturbance effect of the micro-habitats and shelters used by snakes. Therefore, based on the data presented in this paper, it may be assumed that an excessive density of wild boars (*sensu* Marsan *et al.*, 1997) may have devastating consequences on the local snake-fauna abundance, other than on many other forestry attributes (Tosi & Toso, 1992). Thus, it is strongly recommended that wild boar populations should always be carefully monitored by competent authorities when the protection of an endangered snake species is planned. Their negative effect on snake populations is probably indifferently strong in every season, and thus may considerably affect also the reproductive periods of snakes (which, in Mediterranean central Italy occur between April and May). To our knowledge, no previous experimental research has demonstrated any negative impact of the wild boar on free-ranging Mediterranean snakes. Nevertheless, wild boars have been seldom supposed to be among the threatening factors for particular snake species in the Mediterranean ecosystems (Capula & Luiselli, 2000).

It is also noteworthy that local farmers, interviewed by us during the execution of the present research project, also claimed that the abundance of snakes has declined evidently in the study area in the last two decades, and that this decline was most apparent after the increasing of the population abundance of wild boars, which

were actively hunted before the formal establishing of the Natural Park, but that cannot be freely hunted in this time.

ACKNOWLEDGEMENTS

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Seasonal and spatial distribution of butterflies (*Lepidoptera-Rhopalocera*) in “Evolution Canyon”, Lower Nahal Oren, Mt. Carmel, Israel

Distribution saisonnière et spatiale des papillons (Lepidoptera-Rhopalocera) dans le “Canyon de l’Évolution”, Nahal Oren inférieur, Mont Carmel, Israël

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Abstract

Twenty five species recorded from the microsite “Evolution Canyon” (“EC”), Lower Nahal Oren, Mt. Carmel, Israel represent 18% of the 138 butterfly species known in Israel. The majority of the species from “EC” are widely distributed in the Palearctic region, or even beyond its border. Only the distribution of *Pseudotergumia pisidice* and *Thymelicus hyrax* and six subspecies (*Anthocharis cardamines phoenissa*, *Gonepteryx cleopatra taurica*, *Lasiommata maera orientalis*, *Polyommatus icarus zelleri*, *Melitaea trivia syriaca*, and *Neohipparchia fatua sichaea*) is limited to the East Mediterranean sub-region. Our results indicate that species distributed over larger geographic areas might have larger local occurrences in comparison with species geographically less distributed. At “EC”, a significantly higher number of species was recorded on the “savanna-like” south-facing slope which is warmer, drier and microclimatically more fluctuating than the north-facing slope covered by a typical Mediterranean dense maquis. Apart of a general tendency for higher butterflies occurrence at the tops of both slopes, changing the biotope preferences was recorded during the year in *Artogeia rapae*, *Colias croceus*, *Pieris brassicae* and *Pontia daplidice*. The distribution of butterflies was significantly negatively correlated with the tree and bush cover. Differences in the possibility for butterflies of sun basking or in their host plant accessibility and quality seem to be interesting factors that might influence butterfly distribution and which are waiting for future evaluation.

Key-words

Lepidoptera, Israel, habitat differentiation, ecology, Middle East

Résumé

Les vingt-cinq espèces de papillons dénombrées dans le “Canyon de l’Évolution” (“EC”) à Nahal Oren, Mt. Carmel, Israël, représentent 18 % des 138 espèces connues en Israël. La majorité des espèces recensées dans le Canyon est largement distribuée dans la région paléarctique et même au-delà de ses limites. Seule la distribution de *Pseudotergumia pisidice*, celle de *Thymelicus hyrax*, ainsi que celle de six sous-espèces (*Anthocharis cardamines phoenissa*, *Gonepteryx cleopatra taurica*, *Lasiommata maera orientalis*, *Polyommatus icarus zelleri*, *Melitaea trivia syriaca* et *Neohipparchia fatua sichaea*) est limitée à la sous-région de la Méditerranée orientale. Nos résultats semblent indiquer que les espèces distribuées sur de grandes aires géographiques pourraient être localement plus largement représentées que les espèces à distribution géographique moindre. Dans l’“EC”, un nombre significativement plus élevé d’espèces a été observé sur le versant exposé au sud qui a une végétation de type savane, est plus chaud, plus sec et présente plus de fluctuations sur le plan microclimatique que le versant exposé au nord qui est couvert d’un maquis dense typiquement méditerranéen. À part une tendance générale à une occurrence plus élevée de papillons au sommet des deux versants, des modifications des préférences au niveau du biotope ont pu être observées au cours de l’année pour *Artogeia rapae*, *Colias croceus*, *Pieris brassicae* et *Pontia daplidice*. La distribution des papillons était corrélée négativement de façon significative à la couverture arborée et arbustive. Les différences au niveau de la possibilité pour les papillons de “se dorner” au soleil ou celles relevant de l’accessibilité et de la qualité des plantes-hôtes semblent être des facteurs intéressants pouvant influencer sur la distribution des papillons et qui devraient faire l’objet d’une étude plus poussée.

Mots-clé

Lepidoptera, Israël, différenciation au plan de l’habitat, écologie, Moyen-Orient

INTRODUCTION

Butterflies are not a species-rich group of Lepidoptera. In fact, just less than one tenth of the Lepidoptera world fauna belongs to the Rhopalocera (Larsen, 1974). Nevertheless, butterflies are often used in different kinds of biodiversity research since they can be easily identified in the field.

The research described in this paper forms part of a long-term biodiversity project aiming to reveal the underlying factors causing microsite differentiation in species and populations (Nevo, 1995, 1997, 2001). Butterflies were chosen to verify the differentiation pattern obtained earlier at the microsite in the other phylogenetic taxa, ranging from cyanobacteria up to mammals (reviewed in Nevo, 1995, 1997, 2001, and publications afterwards). The three following hypotheses about differentiation of butterflies at the microsite, "Evolution Canyon", Lower Nahal Oren, Mt. Carmel, Israel ("EC"), were proposed: 1. The species richness of Rhopalocera will be higher on the drier, climatically more fluctuating, African-like savanna south-facing slope (SFS) in comparison to the number of species recorded on the opposite, more humid,

climatically less fluctuating north-facing slope (NFS) covered by dense maquis. Previously, the same trend, i.e. higher species richness at SFS than NFS, was shown in Bacteria (Cyanobacteria and soil bacteria), Chlorophyta, Mollusca, scorpions, insects, reptiles, birds and rodents (summarized in Nevo, 1995, 1997, 2001). 2. The number of species and their occurrence will be positively correlated with the difference in the amount of solar radiation received by each slope during the year. 3. Species of the northern provenience, i.e., species distributed mainly in the East Mediterranean, Europe, and Central and Northern Palearct will prefer NFS, whereas species of the southern provenience, i.e., species distributed mainly in the Southern Mediterranean, Arabian Peninsula, and Southern Palearct will prefer SFS. Similar interslope differences were previously obtained at "EC" in vascular plants (Nevo *et al.*, 1999). Besides, it was shown previously that some animal taxa of African origin (i.e. rodent and lizard genera *Acomys* and *Agama*) prefer SFS whereas the taxa of European origin (e.g. rodent and lizard genera *Apodemus* and *Acomys*) prefer NFS (Nevo, 1995, 1997; Blaustein *et al.*, 1996).



Figure 1. A view of "Evolution Canyon", Lower Nahal Oren, Mt. Carmel, Israel – from the East.

MATERIAL AND METHODS

The Nahal Oren microsite

Lower Nahal Oren, Mt. Carmel, Israel (32°43'N; 34°58'E) designated by us as "Evolution Canyon" ("EC": Nevo, 1995) is located 14 km south of Haifa (figure 1). "EC" is a valley, dry in summer, through which the waters from Mt. Carmel are drained east-west into the Mediterranean sea. Opposed south-facing (SFS) and north-facing (NFS) slopes are 100 m apart at the valley bottom and 400 m apart at the top. SFS, covered by open park forest of evergreen *Ceratonia siliqua*-*Pistacia lentiscus*, with dominant savanna-like grassland, dramatically contrasts with NFS, covered by dense maquis-forest (brushwood forest) with dominant evergreen *Quercus calliprinos* and deciduous *Pistacia palaestina* (Nevo, 1997; Nevo *et al.*, 1999). The two slopes share an identical evolutionary history (Plio-Pleistocene canyon, presumably 3-5 MA: Nevo, 1995), geology (Upper Cenomanian Limestone: Karz, 1959), regional Mediterranean climate (mean annual rainfall ca. 600 mm, potential evapotranspiration 1700 mm, and mean August and January temperature 28 °C and 13 °C, respectively: Atlas of Israel, 1970), and pedology (Terra Rossa: Nevo *et al.*, 1998). By contrast, the opposite slopes diverge in topology (SFS dips 35° and NFS dips 25°: Nevo, 1997) and in geographic orientation. These two differences result in different inputs of solar radiation, interslope microclimate differences, and, at least partly, in differences in biota (Nevo, 1995, 1997).

According to Ayyad (1971) and Rorison *et al.* (1986), differences in amount of received radiation between NFS's and SFS's in the northern hemisphere are more prominent in the winter period; they become gradually less significant in summer months, and again tend to be increasingly conspicuous during autumn. On the average, SFS's receive per year more radiation than the NFS's with the same inclination (Ayyad, 1971; Rorison *et al.*, 1986). Indeed, significant interslope microclimate differences were recorded at "EC" in: (a) radiation (SFS received few-fold more radiation than NFS measured in 98 days from August 1997 to March 1998); (b) average temperature (SFS 19.5 °C, NFS 18.6 °C, measured on 154 days from 2 April 1997 to 6 March 1998, 1 m above the ground surface); (c) relative humidity (SFS 69.4%, NFS 71.4%, measured on 173 days from 29 May 1997 to 4 March 1998, 1 m above the ground surface); and (d) microclimate variability (differences between daily maxima and minima of radiation, temperature, and humidity, measu-

red 1 m above the ground surface) (Pavliček *et al.*, in preparation).

Interslope biota differences are evident in the contrast in species presence and their distribution between NFS and SFS. Only 31-48% of vascular plant species are common to both slopes (Nevo *et al.*, 1999). Striking differences in other groups of organisms (reviewed in Nevo, 1995, 1997, 2001) appears also between them. The soil type on both slopes is the same (Terra Rosa), but the measured pH, amount of organic C, concentration of NH₄-N⁺, Mn²⁺, Na⁺, and K⁺ were significantly higher on NFS than on SFS (Nevo *et al.*, 1998). In all, we can conclude that SFS harbours higher species richness and that it is more stressful than NFS since it receives more solar radiation, is warmer, drier, and microclimatically more fluctuating. The less speciose NFS is less stressful since it is microclimatically less fluctuating, cooler and wetter than SFS.

Butterfly observation and identification

To estimate the butterfly species richness and occurrence, the canyon was divided into seven stations. On each slope (SFS and NFS), three stations were assigned, two at elevation of 120 m above sea level (SFS1 and NFS7), two at elevation 90 m asl. (SFS2 and NFS6) and two at elevation 60 m asl. (SFS3 and NFS5). Station 4 was assigned at the valley bottom 45 m asl. (VB4). We include VB4 only in part of our analysis since our project deals mainly with the interslope differences and since no hypothesis about relationship between slopes and bottom was proposed.

The abundance of butterflies was estimated according to their occurrence in a 30-minute period at each station. Butterflies were recorded at each station along a 400 m-long horizontal transect, and within a radius of 15 - 20 m. Observations were made twice a month from January to December of 1997 from 8.00 a.m. until 11.30 a.m. The exact dates of observations were as follows: January 8 and January 17, February 10 and February 15, March 5 and March 11, April 8 and April 25, May 10 and May 21, June 8 and June 19, July 12 and July 23, August 9 and August 21, September 11 and September 23, October 10 and October 19, November 13 and November 21, December 12 and December 20. For identification, *Benyamini's Field Guide* (1990) was used. The identification was also confirmed by consulting the National Insect Collection at the Department of Zoology, Tel Aviv University.

Statistical methods

The most probable station order under H_0 hypothesis predicting no interslope differences in number of species or occurrence is: SFS(x)-NFS(x)-SFS(x)-NFS(x)-SFS(x)-NFS(x), where x represents any station on SFS or NFS, respectively. The most extreme deviation from H_0 is: SFS(x)-SFS(x)-SFS(x)-NFS(x)-NFS(x)-NFS(x), or NFS(x)-NFS(x)-NFS(x)-SFS(x)-SFS(x)-SFS(x). The probability of obtaining one of the mentioned station extreme orders is less than $p = 0.05$ by use of the Kruskal-Wallis test. Therefore, if the above-mentioned extreme order was reached, then we regarded the H_0 hypothesis as rejected at $p < 0.05$. In addition, a binomial test was performed in order to show significant interslope differences, with help of statistical tables (Aiken, 1955). In contrast to the previous test, the binomial one does not take into consideration the station order. The Spearman Rank Order correlation (in text Spearman correlation) was used to check whether the chosen parameters are significantly correlated one with another (Siegel, 1956). The index of complementarity (distinctiveness, distance) was calculated according to the following formula (Colwell & Coddington, 1994):

$$C_{jk} = \frac{\sum_{i=1}^{S_{jk}} |x_{ij} - x_{ik}|}{\sum_{i=1}^{S_{jk}} \max(x_{ij}, x_{ik})},$$

where x_{ij} and x_{ik} are presence-absence (1,0) values for species i in the list j and k .

All calculations were performed by means of Microsoft®Excel 97 and Statistica Rel. 5.0 (StatSoft Inc.).

RESULTS

Interslope differences in species richness and occurrence

Twenty five butterfly species were recorded at “EC”. They were represented by 2766 occurrences (table 1). Both parameters, i.e. number of species and their occurrence were significantly positively correlated (Spearman correlation, $r_s = 0.83$, $p = 0.0008$). At SFS, 23 species were recorded in contrast with only 10 species recorded

from NFS. The station order regarding the number of species and their occurrence was extreme (respectively 17/18/17/4/4/8 species and 830/853/629/56/16/42 occurrences, were recorded at the SFS1/SFS2/SFS3/NFS5/NFS6/NFS7 stations - Table 1, 4) in comparison with the most probable order under the expectation of no interslope differences. This result allows us to reject the H_0 hypothesis assuming an equal distribution of species richness and butterfly occurrences on both slopes. By means of the same test, it was possible to reject the H_0 hypothesis of equal interslope occurrences in 10 single species, i.e. in 42% of the species occurring on the slopes. In all those species, their occurrences were higher on SFS than on NFS (Table 1). Besides, a binomial test, that is not sensitive to the station order, showed significant ($p < 0.05$) interslope differences in 22 species out of 24 (Table 1). In the eleven additional species that showed significant interslope differences in the binomial test, some occurrences were equal on the SFS and NFS stations and only the total sum was significantly higher on the preferred slope. The fact that butterfly species were not distributed homogeneously on SFS indicates a low rate of complementarity (see “Material and Methods”) between SFS1, SFS2, and SFS3 ranged from 28.6% (SFS1 x SFS2) to 52.3% (SFS1 x SFS3). The measurement of complementarity was not possible at NFS due to the low number of butterfly species recorded there.

According to the occurrence of individual species all over the year, the most frequent species (i.e. counted more than 100 times) were *A. rapae*, *C. croceus*, *C. cardui*, *L. megera*, *P. brassicae*, and *Y. asterope*.

Seasonal distribution of species

In the course of the year, the number of species and their occurrence at “EC” changed (figure 2). At SFS, the maximal number of species was reached in the period from March till May and again in October (figure 3). The number of species began to increase on both slopes simultaneously at two different periods of the year (February and July), but in both cases the process of increase of the species number terminated earlier at NFS than at SFS (figure 3). At NFS, the first maximal peak in species number was recorded in the period from February till March and the second peak was observed in August (figure 3). At SFS, there were at least a few species recorded throughout the year, but at NFS no butterfly presence was recorded in July and in the period from October till December (figure 3). Both slopes were the most similar in February and again in August. They were the most dis-

Species	SFS1	SFS2	SFS3	VB4	NFS5	NFS6	NFS7	SFS/NFS	RD
<i>P. machaon</i>	24	14	0	0	0	0	0	38/0	4
<i>A. apollinus</i> *	43	29	1	0	0	0	0	73/0	2
<i>P. brassicae</i> *	37	42	74	13	1	1	2	153/4	2
<i>A. rapae</i> *	64	102	135	92	8	1	11	301/20	5
<i>P. daphidice</i> *	11	8	25	7	0	0	0	44/0	3
<i>M. fausta</i>	33	5	0	0	0	0	0	38/0	4
<i>A. cardamines</i>	0	4	20	26	0	0	0	24/0	2
<i>C. croceus</i> *	51	38	84	18	0	0	1	173/1	2
<i>G. cleopatra</i>	0	3	0	39	25	0	0	3/25	2
<i>C. cardui</i> *	288	277	188	138	19	13	19	753/51	5
<i>L. reducta</i>	0	0	0	8	0	0	0	0/0	2
<i>M. trivialis</i>	8	0	0	0	0	0	0	8/0	2
<i>Y. asterope</i> *	90	150	20	0	0	0	0	260/0	3
<i>N. fatua</i>	4	9	0	0	0	0	2	13/2	2
<i>P. pisidice</i>	35	23	0	0	0	1	3	58/4	1
<i>M. telmessia</i>	0	2	2	0	0	0	1	4/1	2
<i>L. megera</i> *	101	73	27	2	0	0	2	201/2	2
<i>L. maera</i>	7	9	0	0	0	0	1	16/1	2
<i>A. acamas</i> *	25	49	17	0	0	0	0	91/0	3
<i>L. boeticus</i>	0	0	10	0	0	0	0	10/0	4
<i>L. pirithous</i>	1	0	15	0	0	0	0	16/0	3
<i>P. icarus</i>	0	0	5	0	0	0	0	5/0	2
<i>C. alceae</i> *	8	8	1	0	0	0	0	17/0	2
<i>P. thrax</i>	0	8	1	0	0	0	0	9/0	3
<i>T. hyrax</i>	0	0	4	0	0	0	0	4/0	1
Total	830	853	629	343	53	16	42	2312/111	

* equal occurrence of butterflies at both slopes rejected ($p < 0.05$) due to extreme station order. In the column SFS/NFS, figures showing equal interslope occurrence was rejected by a binomial test ($p < 0.05$) are marked in bold.

Table 1. Occurrence of butterflies at the stations of "EC" during the year 1997 and rank of the species distribution (RD).

Table 2. Butterflies occurrences at "EC" during the months of the year 1997.

Species	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	Total
<i>P. machaon</i>	0	2	1	3	6	1	0	2	4	18	1	0	38
<i>A. apollinus</i>	17	27	5	1	0	0	0	0	0	0	4	19	73
<i>P. brassicae</i>	21	41	36	17	24	9	1	5	11	5	0	0	170
<i>A. rapae</i>	29	68	72	64	67	34	6	2	20	26	20	5	413
<i>P. daphidice</i>	9	7	9	4	5	1	0	0	5	7	2	2	51
<i>M. fausta</i>	3	7	1	0	0	0	0	2	9	8	7	1	38
<i>A. cardamines</i>	0	4	21	16	9	0	0	0	0	0	0	0	50
<i>C. croceus</i>	17	24	36	42	35	0	0	0	3	13	18	4	192
<i>G. cleopatra</i>	0	12	25	15	14	1	0	0	0	0	0	0	67
<i>C. cardui</i>	14	127	530	151	86	15	1	0	0	6	10	2	942
<i>L. reducta</i>	0	0	0	0	0	0	1	5	2	0	0	0	8
<i>M. trivialis</i>	0	0	0	0	0	0	0	2	5	1	0	0	8
<i>Y. asterope</i>	0	5	21	32	47	71	21	7	36	17	3	0	260
<i>N. fatua</i>	0	0	0	0	0	4	8	3	0	0	0	0	15
<i>P. pisidice</i>	0	0	0	0	0	0	0	6	18	32	6	0	62
<i>M. telmessia</i>	0	0	0	0	0	1	2	2	0	0	0	0	5
<i>L. megera</i>	25	77	9	27	13	29	20	0	4	1	0	0	205
<i>L. maera</i>	0	9	0	0	0	4	3	1	0	0	0	0	17
<i>A. acamas</i>	0	0	0	0	1	24	36	12	17	1	0	0	91
<i>L. boeticus</i>	0	2	1	3	3	1	0	0	0	0	0	0	10
<i>L. pirithous</i>	1	1	0	6	1	0	0	0	0	0	2	5	16
<i>P. icarus</i>	0	0	1	3	1	0	0	0	0	0	0	0	5
<i>C. alceae</i>	0	0	3	2	0	7	1	0	2	2	0	0	17
<i>P. thrax</i>	4	0	0	0	0	0	0	0	0	1	2	2	9
<i>T. hyrax</i>	0	0	0	1	3	0	0	0	0	0	0	0	4
Total	140	413	771	387	315	202	100	49	136	138	75	402	766

(Roman numbers designate months of a year.)

similar in the period when no butterflies were recorded at NFS as indicated by the curve of interslope relative change of species richness (figure 3) with a lower limit at 5 (no interslope difference) and with an upper limit at 10 (100% of interslope difference).

There was a remarkable species replacement at “EC” between different periods of the year. Only *A. rapae* was active throughout the year. Four species (*Y. asterope*, *L. megera*, *P. brassicae*, and *P. machaon*) were active throughout the year with exception of the rainy and cold winter months. Two species (*C. croceus*, *C. cardui*) were active throughout the year with exception of the hottest and dry summer months. Two species (*N. fatua*, and *M. telmessia*) were on the contrary active only during summer. One species (*P. thrax*) was recorded only in the winter period and three species (*T. hyrax*, *P. icarus*, and *A. cardamines*) only in the spring. Some species with long period of activity had both spring and autumn peaks of occurrence during the year (*A. rapae*, *Y. asterope*).

As regards occurrence, it reached its maxima in the period from February till June with a peak in March.

Global and regional distribution of species recorded at “EC”

The recorded species at “EC” are distributed in Israel mainly in the northern and central mountain ranges and in the coastal plain (appendix 1), i.e. in the regions which constitute the main Mediterranean zone. However, *P. daphidice*, *C. croceus*, *C. cardui*, and *L. boeticus* are common in other parts of Israel too (appendix 1). The species recorded at “EC” are widely (i.e. cosmopolitan, Holarctic and Palearctic, Palearctic) or regionally distributed (e.g. European, East Mediterranean and Central Asian, Circum-Mediterranean, East Mediterranean, Ponto-Mediterranean, Irano-Turanian, South-east Mediterranean and Saharo-Arabian) (appendix 1). Unfortunately, our data set does not allow the study of

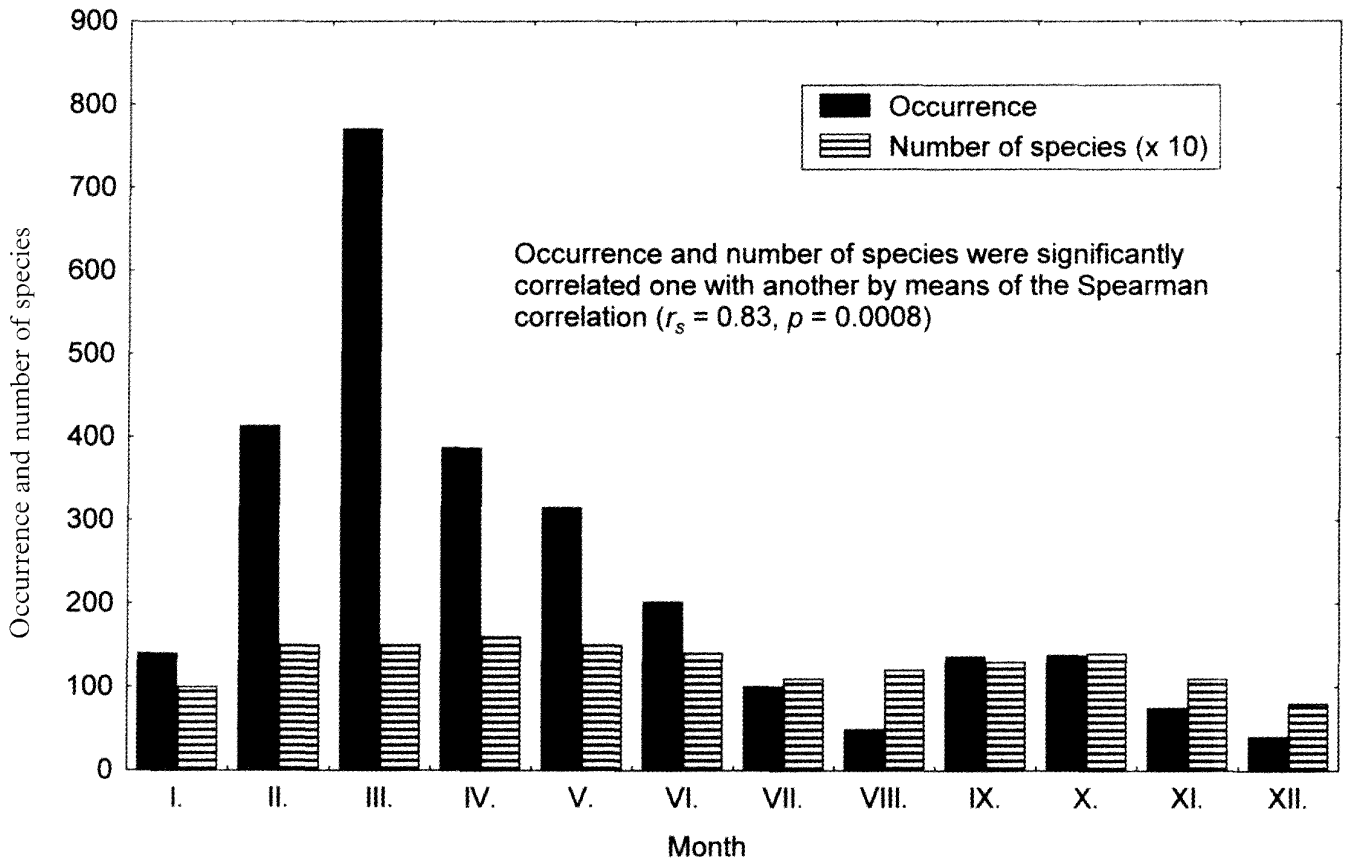


Figure 2. Monthly changes in butterfly occurrences and number of species at “EC”, Lower Nahal Oren, Mt. Carmel, Israel.

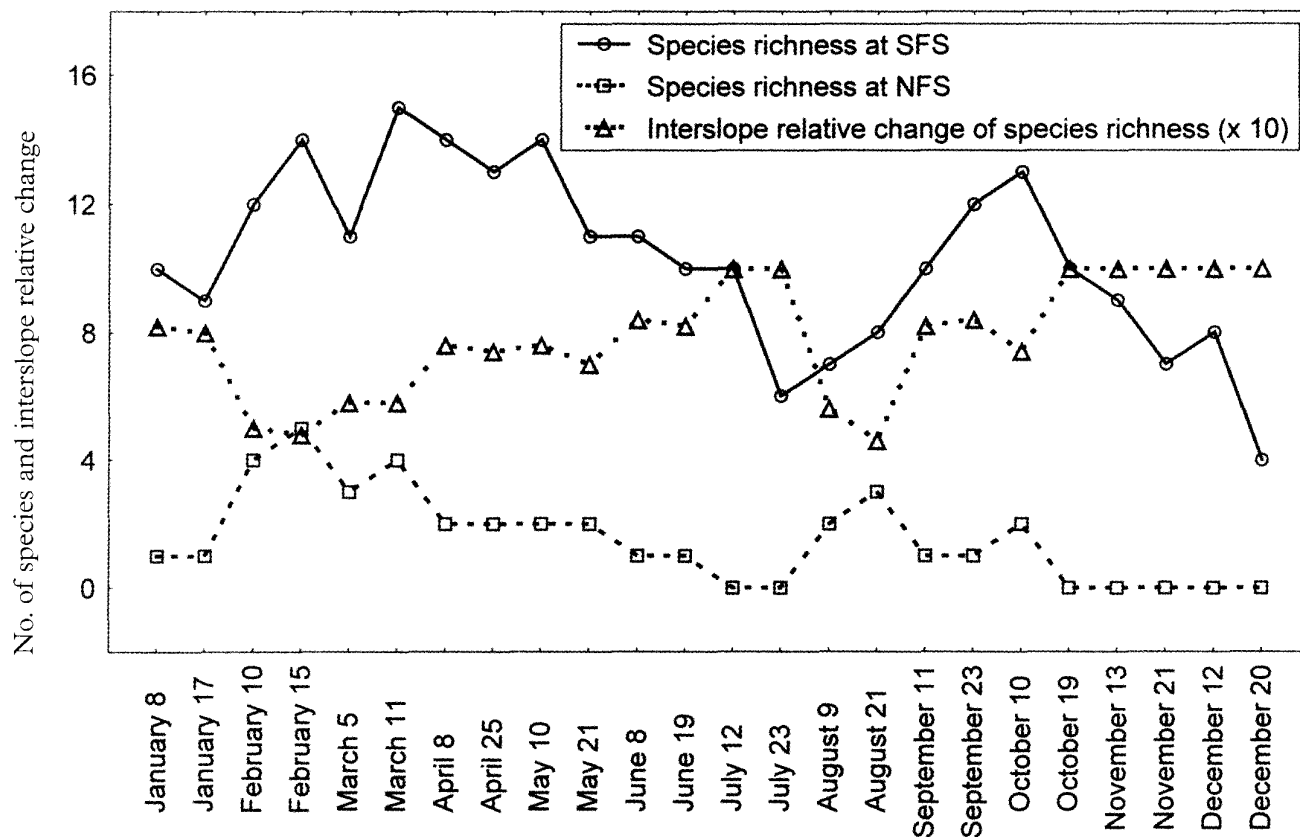


Figure 3. Changes in the number of butterfly species recorded at SFS and NFS and interval of the relative change of species richness between the slopes during the year. Note: The interval has its minimum at 5 (identical number of species on both slopes) and its maximum at 10 (butterfly species present on one slope and absent on the second one).

relationship between the global distribution of the species and the species interslope distribution at "EC", since all of them but one preferred SFS to NFS. On the second side, our data indicate that there might be a relationship between the species global distribution and its local occurrence at "EC". We ranked the species according to their global distribution as follows (table 1): (a) rank 1 - species distributed in 1 zoogeographic subregion, (b) rank 2 - species distributed in 2 or more subregions in one zoogeographic region, (c) rank 3 - species distributed in 2 zoogeographic regions, (d) rank 4 - species distributed in more than 2 zoogeographic regions, and (e) rank 5 - cosmopolitan species. The consecutive Spearman correlation between the butterfly occurrence at "EC" and their rank distribution was, $r_s = 0.35$, with nearly significant probability $p = 0.069$.

Host plants

Three of the recorded species (*L. reducta*, *M. fausta*, *G. cleopatra*) are monophagous (larvae feed on just one plant genus or one plant species) and 15 species are oligo- or polyphagous. For six species, the host plants are not recorded or are uncertain. As for *A. acamas*, it might not be a phytophagous species at all. It was observed in Oman and India that they may feed on ant larvae (Wynter-Blyth, 1957; Larsen, 1980). To understand the expected relationship between occurrence of adults and their caterpillar host plants, a large amount of data will have to be collected from the microsite and from the region. Unfortunately, the full host plant spectra of most caterpillars recorded at "EC" are not known either locally or in the area of their global distribution (appendix 1). Host plant species of

Station	<i>P. brassicae</i>	<i>A. rapae</i>	<i>P. daphidice</i>	<i>C. croceus</i>
	II-V/VIII-XI	II-V/VIII-XI	II-V/VIII-XI	II-V/VIII-XI
SFS1	15/13	27/28	0/9	15/26
SFS2	30/6	56/27	3/3	24/8
SFS3	58/2	105/8	14/2	82/0

Table 3. Change in station preference in the two periods of the maximal occurrence during the year in four Pieridae species.

some species recorded at “EC” are different at the micro-site from the ones mentioned in literature (i.e. in *L. boeticus* and *L. pirithous*, appendix 1) or the adults of mentioned species did not develop at “EC” and immigrated there from elsewhere. Three species (*A. appolinus*, *G. cleopatra*, and *M. fausta*) were recorded only in one slope, but their expected host plants were observed on both slopes of “EC”. The expected host plant of *L. reducta* was recorded on the other slope than the species itself (appendix 1, p. 109). All these uncertainties means that, at the present, it is impossible to analyze the relationship between the interslope distribution of butterflies and their host plants at “EC” due to the lack of data.

Spatial distribution of species and occurrence

The low level of complementarity showed that the intraslope distribution of butterflies was not homogeneous at least as SFS is concerned. The following groups of species were significantly (tested by means of a binomial test) preferring one of the SFS stations: (a) Eight species preferred SFS1 to the lower part of the slope (SFS3) (*P. machaon*, *A. appolinus*, *M. fausta*, *P. pisidice*,

L. megera, *C. cardui*, *M. trivialis*, *C. alceae*). (b) Six preferred SFS3 to the upper part of the slope (SFS1 or SFS2) (*P. brassicae*, *A. rapae*, *P. daphidice*, *C. croceus*, *L. boeticus*, *L. pirithous*). In the first four mentioned species, the preference for a specific SFS station changed during the year. Their higher occurrence at SFS3 (and at VB4) than at SFS1 was from February till May. Later on, in August–November, their higher occurrence was at SFS1 (and SFS2) rather than at SFS3 (and VB4) (table 2). On the whole, they significantly occurred more at SFS3 than at SFS1 because of their higher abundance in spring and their lower occurrence in summer (Table 3). (c) Three species preferred SFS2 rather than SFS1 or SFS3 (*Y. asterope*, *A. acamas*, *P. thrax*). In addition to the above mentioned preferences at the SFS stations, two species (*G. cleopatra*, *L. reducta*) preferred VB4 in comparison with any of the SFS or NFS stations. In the species that did not show any significant preference for any station it was not possible to distinguish between two possibilities, i.e. either statistics were not able to detect any significant difference due to the small data set or they occurred equally on the compared stations.

The Spearman correlation analysis showed negative significant or nearly significant correlations between gene-

tation	Number of species	Occurrence	General plant cover	Cover made of perennial plants	Cover made of annual plants	Cover made of trees and shrubs	Stones and rock cover
SFS1	17	830	45%	27.5%	12.5%	7.5%	45%
SFS2	18	853	55%	25%	26.5%	7%	37.5%
SFS3	17	629	90%	35%	37.5%	30%	20%
VB4	9	343	84.5%	17.5%	65%	5%	1.5%
NFS5	4	53	100%	82.5%	12.5%	57.5%	5%
NFS6	4	16	150%	95%	5%	85%	17.5%
NFS7	8	42	70%	55%	3.5%	60%	15%

Table 4. Number of species, their occurrence (presented work), and covers made of plants, rock and stones (Nevo et al., 1999) at the stations at “EC”.

ral plant cover and number of species or number of occurrences at stations ($r_s = -0.75$, $p = 0.054$ and $r_s = -0.71$, $p = 0.071$, respectively), between cover made of perennial plants and number of species or number of occurrences at stations ($r_s = -0.764$, $p = 0.046$ and $r_s = -0.750$, $p = 0.052$), between cover made of trees and shrubs and number of species or number of occurrences at stations ($r_s = -0.79$, $p = 0.036$ and $r_s = -0.79$, $p = 0.036$) (table 4). Only positive but not significant correlations were found between number of species on slopes (or occurrence) and cover made of annual plants and cover made of stones and rocks (table 4).

DISCUSSION

Species richness and zoogeographical origin of the butterflies recorded at "EC"

The twenty-five species recorded from "EC" represent 18% of the 138 known Israeli butterfly species (Benyamini, 1983). By contrast, 142 species are known from Lebanon (Larsen, 1974), 103 from Syria (Sanetra, 1999), 82 from Jordan (Larsen & Nakamura, 1983; Bozano, 1990), and only 58 species from Egypt including the Sinai (Larsen, 1990). These data indicate that in the East Mediterranean region the species richness decline from the mesic eastern part to the more arid southern part of the area; similarly, and that the species numbers decrease from the mesic north to the arid south of Israel. Considering the incomplete inventory of butterflies, especially in Syria and Jordan, the contrast between the northern mesic and southern arid regions might be even greater. The number of butterfly species collected at "EC" compared to the number of species known in Israel is similar to that of the various other studied groups of insects (i.e. 13%-20% in different beetle families: Chikatunov *et al.*, 1997, 1999, 2000; Háva *et al.*, 2001, and Volkovitsh *et al.*, 2000).

All the butterfly species recorded in the "EC" are widely distributed in the Palearct, and in some cases even beyond the Palearct. The most restricted distributions were the ones of *Pseudotergumia pisidice* and *Thymelicus hyrax* and of six subspecies (*Anthocharis cardamines phoenissa*, *Gonepteryx cleopatra taurica*, *Lasiommata maera orientalis*, *Polyommatus icarus zelleri*, *Melitaea trivialis syriaca*, and *Neohipparchia fatua sichaea* restricted to the East Mediterranean sub-region (appendix 1). About half of

the "EC" species penetrate Israel's southern desert regions (*Papilio machaon*, *C. croceus*, *A. acamas*, *P. pisidice*, *C. alceae*, *M. fausta*, *P. daphidice*, *L. boeticus*, *L. pirithous*, *M. trivialis*, *C. cardui*, *Y. asterope*, and *P. thrax*), but only the first five of these have been recorded from Arabia (Larsen, 1983). It was not possible to study the relationship between their slope preferences and their global distribution since only one butterfly species preferred NFS than SFS. Nevertheless, the relationship at "EC" between the species global distribution and the amount of local occurrences was near to the significant level and therefore might be a promising topic for a future study.

Local inter- and intraslope differences

In general, the adult butterfly significantly preferred SFS than NFS in both criteria, number of species and occurrence. Only *G. cleopatra* occurred significantly more at NFS than at SFS, but its maximal occurrence was at VB4, from where it probably penetrates NFS. The recording of occurrence at "EC" might be biased in spite of the fact that transects and time intervals were of the same length. Since the average temperature is higher at SFS (Pavliček *et al.*, in preparation) and since the ground there is not shaded, butterflies might be more active, i.e., flying more, especially in the morning hours and in the cold but sunny days. In addition, it might be easier to register resting or flying butterflies at the open "savanna-like" SFS than at NFS covered by a dense maquis. The fact that we recorded higher occurrences of butterflies at SFS than at NFS also in summer, with no indication of declining magnitude of interslope differences, in the period when interslope differences in the amount are minimal (Ayyad, 1971; Rorison *et al.*, 1986), indicates that the error due to different behavior of butterflies caused by differences in microclimates on the slopes, if any, was not very serious. We avoided a second error by limiting the size of the recording radius to 15-20 m along the assigned transects.

The fact in itself that the more radiated and "savanna-like" slope harbours more species and higher occurrence of butterflies than the one covered by dense maquis would probably not surprise the majority of insect collectors. Nevertheless, the fact that this phenomenon is of more general nature is exciting. At "EC", the higher number of species at SFS than at NFS was observed in the following terrestrial taxa (taxa in which gamete fusion usually takes part in body liquid): Bacteria (Cyanobacteria and soil bacteria), Chlorophyta, Mollusca, Scorpions, Insects (grasshoppers, beetles), reptiles, birds, and rodents (summarized in Nevo, 1995, 1997, 2001). The opposite trend, i.e., higher species

richness at NFS than SFS was observed in the less speciose water-dependent taxa (the taxa in which gamete fusion or large part of their life cycle depends on availability of water in their surrounding environment) such as Euglenophyta, Bacillariophyta, lichens, fungi (lichenicolous fungi, Micromycetes, Agaricales), and mosses (summarized in Nevo, 1995, 1997).

The interslope pattern at "EC" in number of species is similar to the pattern of general decrease in species richness from tropical to temperate latitudes (Schall & Pianka, 1978), especially to tropical savanna richer in terrestrial species than the temperate zone which abounds with water-dependent cryptogamic plant and fungi (Nevo, 1997).

Regarding "EC", there is probably no direct relationship between the amount of solar radiation and the slope number of butterfly species and their occurrences since in summer, when the expected interslope differences in amount of solar radiation received by both slopes are about zero (Ayyad, 1971; Rorison *et al.*, 1986), the magnitude of interslope difference in species number and occurrence did not decline.

Nevertheless, another important factor connected with the slopes and the solar radiation might be the possibility of sun basking. To fly, butterflies, as well as other insects, need to maintain their thoracic muscles, in a high temperature of about 35 °C to 42 °C (Bartholomew & Casey, 1997; Watt & Kohane, 1999). They have to keep their thorax temperature high enough by sun basking in order to be "ready to take off" at any time, in case of predator attacks or to protect territories against invaders (Dreisig, 1995; Stutt & Wilmer, 1998). The option of sun basking constitutes bring advantage especially in the morning hours and in cold sunny days when the ambient temperature is relatively low. Sun basking, in comparison with metabolically costly endothermic warm-up, allows quicker increase of thoracic temperature and is metabolically less costly (Auerswald *et al.*, 1988). For example in the butterfly species *Pachliopta aristolochine*, the thorax temperature increases due to sun basking from 25 °C to 46 °C in just 30 seconds (Heinrich, 1996). Our analysis showed that the butterfly occurrence and number of species were negatively significantly correlated with the cover made by trees or bushes that at NFS, covered by dense maquis, limits sun basking to small openings in the maquis or to an above tree canopy layer. In contrast, sun basking is possible at SFS near of the ground, above or on the stones, rocks and leaves and flowers of perennial and annual plants. Since the thoracic temperature equilibrium depends on habitat choice, convective cooling and flight metabolism (Dreisig, 1995), higher irradiance at SFS than at NFS in the hot hours of the day

might not be a problem. At least in Danaine butterflies, thoracic temperature excess was not positively correlated with solar irradiance, body mass or wing loading (Dreisig, 1995), and butterflies of hot regions might be adapted to the high daily summer temperature by an increased upper limit of thoracic temperature, as it was the case in *Maroglossum stelaratum* in which the thoracic temperature upper limit is 46 °C (Harrera, 1992). Perhaps the connection with the possibility of sun basking and guarding of a territory might explain the hill-topping (the tendency of certain species to accumulate on the top of hills) observed in males of many butterfly species and known from the "EC" assemblage in males of *P. machaon* and *L. megera* (Larsen, 1974; Dennis, 1987). Hill-topping can possibly explain why at SFS and NFS the highest intraslope butterfly occurrences were observed at the upper stations on both slopes (SFS1 and NFS7).

Nevertheless, the species plant composition and the accessibility to certain plants might be another important factor influencing the butterfly occurrence on the slopes. It might in fact be difficult to explain by the possibility of sun basking all aspects of butterfly occurrence at "EC", in particular the pattern of occurrence changes observed at SFS in the course of the year. The majority of the host plant of the butterfly species recorded from "EC" are annuals and perennials (appendix 1). In spite of the fact that almost the same number of species of annuals and perennial plants (168 and 173, respectively) was recorded at SFS and NFS and that the cover made by them was larger at NFS (42.3%) than at SFS (27.4%) (Nevo *et al.*, 1999), they might be more visible, accessible and of different quality at SFS than at NFS because of interslope difference in radiation and cover made of trees and bushes. As a matter of fact, even butterfly species in which caterpillars develop on bushes occurred more frequently at SFS than at NFS, i.e. they preferred the slope where bushes are less abundant. The major problem, that makes the problems of the relationship between butterflies and their host plants at "EC" unsolvable at the moment, is that we have no data about the occurrence of caterpillars and the distribution and preferences of their host plants. This aspect will need to be studied in the future. The changes in the plant host quality might explain the observed changes in occurrence at SFS in four Pieridae species. In spring, caterpillars of the species feeding on *Capparis* sp. (mainly *P. brassicae*) occurred mainly at the lower part of SFS, and later in September and October, when the plants on the lower parts of SFS were almost dry, the larvae were recorded on still green plants at the upper part of SFS (Kravchenko, unpublished data).

APPENDIX 1. List of species collected at "EC", their distribution and their host plants.

Abbreviations: C - Central, E - East(ern), N - North(ern), S - South(ern), W - West(ern); for the number codes of zoogeographic areas in Israel see fig. 4.

1. Family Papilionidae

1.1. *Archon apollinus* (Herbst, 1798) - E Mediterranean and Irano-Turanian species (Israel, Syria, Turkey, Iran, Iraq, Jordan, Lebanon) barely penetrating the Balkans (Larsen, 1974). Zoogeographic areas in Israel: 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 15, 19. Comment: The previously recognized subspecies (or varietas) *A. a. bellargus* Staudinger 1892 was synonymized with the nominate subspecies (DeFreina, 1985). Larval host plants: *Aristolochia* spp. (Higgins & Riley, 1970; Larsen, 1974). At "EC", *A. parvifolia* was recorded on both slopes (Nevo *et al.*, 1999).

1.2. *Papilio machaon syriacus* Verity, 1905 - Levantine and Arabian (Israel, Lebanon, Syria, Jordan, Hasa oasis in Saudi Arabia; Larsen, 1983) subspecies of Holarctic species (Larsen, 1974). Zoogeographic areas in Israel: 1, 2, 3, 4, 5, 6, 7, 8, 9, 11, 10, 11, 15, 17, 19. Larval host plants: different genera and species of Daucaceae, and *Ruta* (Père Tomb in Larsen, 1974).

2. Family Pieridae

2.1. *Anthocharis cardamines phoenissa* Kalchberg, 1894 - E Mediterranean subspecies of W European and temperate Asian species (Larsen, 1974). Zoogeographic areas in Israel: 1, 2, 3, 4, 6, 11, 18, 19. Larval host plants: different genera and species of Brassicaceae. *Sisymbrium*, if available, seems to be the preferred host plant in Lebanon (Larsen, 1974).

2.2. *Artogeia rapae leucosoma* (Schawerda, 1905) - E Mediterranean subspecies of Palearctic species (species introduced in N America, Australia, etc.). Zoogeographic areas in Israel: 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 15, 19. Larval host plants: different genera and species of Brassicaceae, as well as *Tropaeolum* and *Capparis* sp.

2.3. *Colias croceus* (Geoffroy, 1785) - W Palearctic including Arabia (Larsen, 1983). Zoogeographic areas in Israel: all areas. Larval host plants: different genera and species of family Fabaceae.

2.4. *Gonepteryx cleopatra taurica* Staudinger, 1881 - E Mediterranean subspecies of Mediterranean species. Zoogeographic areas in Israel: 1, 2, 3, 4, 6, 11, 18, 19. Larval host plants: *Rhamnus* spp. (Oberthür, 1915; Barragu, 1954), in Lebanon *Rhamnus alaternus* (Larsen, 1974). At "EC", *R. lycioides* was recorded on both slopes and *R. alaternus* only at NFS (Nevo *et al.*, 1999).

2.5. *Madais fausta* (Olivier, 1804) - Eremic Africa, Asia (incl. India). Zoogeographic areas in Israel: all areas. Comment: Lebanon (occasionally Turkey) represents the NE border of the species distribution (Larsen, 1974). Larval host plants: *Capparis* sp. (Larsen, 1974). At "EC" *Capparis* sp. grows on SFS, VB and NFS7 (Pavliček, unpublished).

2.6. *Pieris brassicae* (Linnaeus, 1758) - W & S Palearctic. Zoogeographic areas in Israel: 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 15, 19. Comments: Feltwell (1981) did not find support for regarding Levantine populations of *P. brassicae* as a separate subspecies *P. b. catoleuca* Röber, as was postulated earlier. The species has its southern border of distribution (where it still reproduces) in Negev. Larval host plants: different genera and species of Brassicaceae and *Capparis spinosa* (Larsen, 1974; Rungs, 1981).

2.7. *Pontia daphidice* (Linnaeus, 1758) - Palearctic with extension to Ethiopia (Asir Mts.: Larsen, 1990). Zoogeographic areas in Israel: all areas. There is the genetic evidence (Geiger *et al.*, 1988) that the populations of *P. daphidice* are composed of two sibling species, *P. daphidice* (L., sensu Wagener, 1988) and *P. edusa* (Fabricius, 1777, sensu Wagener, 1988). The populations from Israel, Canary Islands, Morocco and France belong to the nominal species *P. daphidice*, whereas the populations from Switzerland, Italy, Yugoslavia and Greece belong to *P. edusa*. Larval host plants: different genera and species of Brassicaceae and Resedaceae.

3. Family Lycaenidae

3.1. *Apharitis acamas* (Klug, 1834) - Ethiopian and S Palearctic (also recorded from Arabia: Larsen, 1983), E Mediterranean and Irano-Turan. Zoogeographic areas in Israel: 1, 2, 3, 6, 18, 19. Larvae myrmecophilous (Wynter-Blyth, 1957; Larsen, 1980).

3.2. *Lampides boeticus* (Linnaeus, 1767) - Ethiopian, S Palearctic, Australian. Zoogeographic areas in Israel: all areas. Migratory species. Larval host plants: inside of the seedpods of different genera and species of Fabaceae, but recorded in Israel on leaves of *Sesbania aegyptiaca* (Halperin & Sauter, 1991). In Lebanon preferred host plant is *Cohutea arborescens* (Larsen, 1974). Either *C. arborescens* or *S. aegyptiaca* were not recorded at "EC" (Nevo *et al.*, 1999).

3.3. *Leptotes pirithous* (Linnaeus, 1767) - Ethiopia with extension to S Europe and E Mediterranean. Zoogeographic areas in Israel: all areas. Larval host plants: Different genera and species of Fabaceae, Fagaceae, Viciaceae, Lythraceae, and Ericaceae (Tennent, 1996). In Israel: on *Acacia albida* and *Spartium junceum* (twigs) (Halperin & Sauter, 1991). Neither *A. albida* nor *S. junceum* were recorded at "EC" (Nevo *et al.*, 1999).

3.4. *Polyommatus icarus zelleri* Verity, 1919 - E Mediterranean subspecies of European and S Palearctic species. Zoogeographic areas in Israel: 1, 2, 3, 4, 5, 6, 8, 9, 10, 11, 13, 18, 19. Larval host plants: different genera and species of Fabaceae. In Israel: *Astragalus pinetorum* (Benyamini, 1993), but this species was not recorded at "EC" (Nevo *et al.*, 1999).

4. Family Nymphalidae

4.1. *Lasiommata maera orientalis* Heyne, 1894 - E Mediterranean subspecies of Palearctic species. Zoogeographic areas in Israel: 1, 2, 3, 4, 6, 11, 18, 19. Larval host plants: different genera and species of Poaceae including *Hordeum*, *Glycerina*, etc. (Larsen, 1974).

4.2. *Lasiommata megera lyssa* (Hübner, 1829) (= *L. m. emilyssa* Verity, 1919; DeFreina, 1991) - E Mediterranean and Irano-Turanian subspecies of Palearctic species. Zoogeographic areas in Israel: 1, 2, 3, 4, 6, 11, 19. Comment: The species prefers cattle pastures (Henning *et al.*, 1997). Larval host plants: different genera and species of Poaceae.

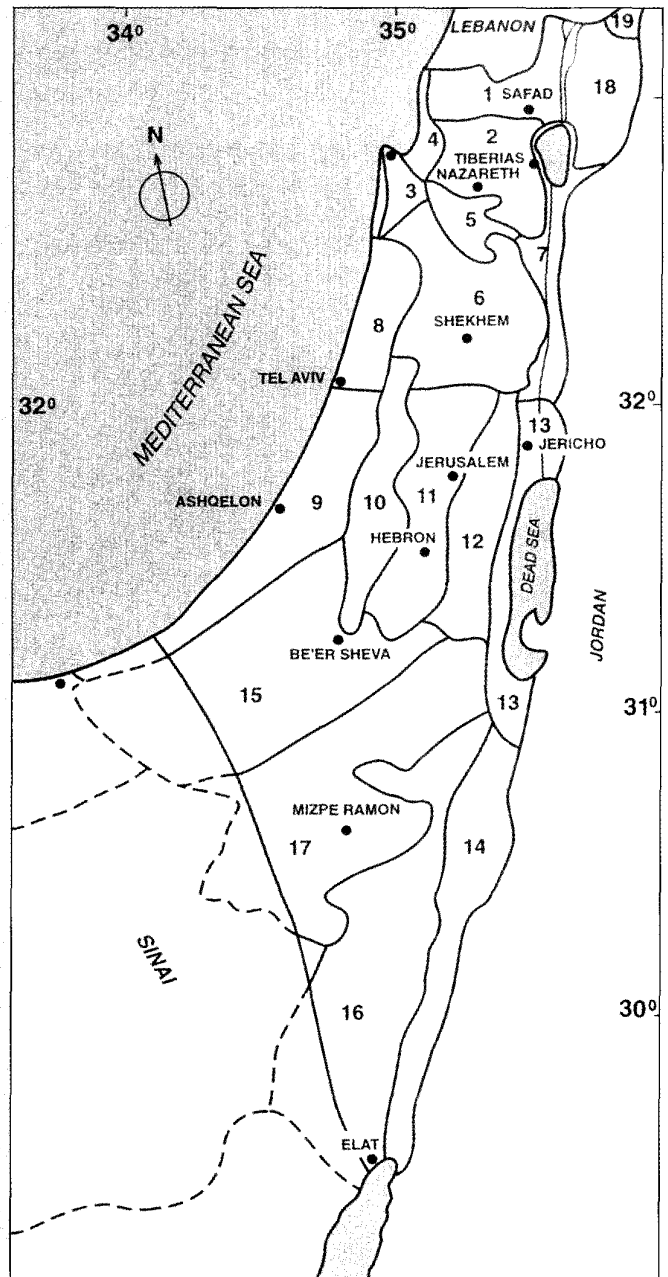
- 4.3. *Limenitis reducta* Staudinger, 1901 - SW European, E Mediterranean, and Irano-Turanian species. Zoogeographic areas in Israel: 1, 3, 4, 6, 11, 18, 19. Larval host plants: *Lonicera* sp. (Larsen, 1974). At "EC", *L. etrusca* was recorded on NFS only (Nevo *et al.*, 1999).
- 4.4. *Maniola telmessia* (Zeller, 1847) - W Asian (Larsen, 1974). Zoogeographic areas in Israel: 1, 2, 3, 4, 6, 11, 18, 19. Larval host plants: Poaceae?
- 4.5. *Melitaea trivia syriaca* Rebel, 1905 - E Mediterranean subspecies of S Palearctic species. Zoogeographic areas in Israel: 1, 2, 3, 4, 5, 6, 7, 8, 10, 11, 12, 13, 15, 17, 19. Larval host plants: Scrophulariaceae, mainly *Verbascum* sp. (Larsen, 1974). At "EC" *V. tripolitanum* was recorded on SFS and VB, and *V. orientale* was recorded on SFS (Nevo *et al.*, 1999).
- 4.6. *Neohipparchia fatua sichaea* Lederer, 1857 - E Mediterranean subspecies of Ponto-Mediterranean species. Zoogeographic areas in Israel: 1, 2, 3, 4, 6, 11, 18, 19. Larval host plants: Poaceae?
- 4.7. *Pseudotergumia pisdice* (Klug, 1832) - E Mediterranean species with the S border of distribution in the Sinai Peninsula (Larsen, 1990) and Saudi Arabia (Hejaz Mts., Pittaway, 1985). Zoogeographic areas in Israel: 1, 2, 3, 6, 10, 11, 8, 9, 15, 17. Larval host plants: Poaceae?
- 4.8. *Cynthia cardui* (Linnaeus, 1758) - Cosmopolitan species. Zoogeographic areas in Israel: all areas. Larval host plants: different genera and species of Cucurbitaceae, Vitaceae, Viciaceae, Boraginaceae, Asteraceae, Brassicaceae and Malvaceae.
- 4.9. *Ypthima asterope* (Klug, 1832) - Ethiopian and S Palearctic. Zoogeographic areas in Israel: 1, 2, 3, 4, 5, 6, 7, 8, 10, 11, 12, 13, 19. Larval host plants: Larval host plants: Poaceae?

5. Family HesperIIDae

- 5.1. *Carcharodus alceae* (Esper, 1780) - S Palearctic species extending to Arabia (*C. a. swinhoei*; Larsen, 1983). Zoogeographic areas in Israel: 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 12, 13, 15, 18, 19. Larval host plants: Malvaceae, such as *Malva*, *Althaea*, *Hibiscus* (Larsen, 1974).
- 5.2. *Pelopidas thrax* (Hübner, 1821) - Ethiopian & S Palearctic. Zoogeographic areas in Israel: 1, 2, 3, 4, 5, 6, 7, 8, 10, 12, 13, 18, 19. Larval host plants: Poaceae including cereals (Larsen, 1974).
- 5.3. *Thymelicus hyrax* Lederer, 1861 (= *T. pfeifferi* Bytinski-Salz & Brandt, 1937) - E Mediterranean: Greece (Poorten, 1990), Syria. Zoogeographic areas in Israel: 1, 2, 3, 4, 6, 11, 18. The southern border of the species distribution in Israel is probably somewhere in the Judean Mts.

Figure 4. Zoogeographic areas in Israel (according to Fishelson, 1985; modified).

1. Upper Galilee,
2. Lower Galilee,
3. Mt. Carmel,
4. Northern Coastal Plain,
5. Yizre'el Valley,
6. Samaria,
7. Jordan Valley and Southern Golan,
8. Central Coastal Plain,
9. Southern Coastal Plain,
10. Judean Foothills,
11. Judean Hills,
12. Judean Desert,
13. Dead Sea Area,
14. Arava Valley,
15. Northern Negev,
16. Southern Negev,
17. Central Negev,
18. Golan Heights,
19. Mount Hermon.



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Cape plants. A conspectus of the Cape flora of South Africa

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National Botanical Institute of South Africa, Pretoria & Missouri Botanical Garden, Saint Louis: 743 p. (2000).
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Parmi les vingt-cinq points chauds de biodiversité identifiés à la surface de la Terre, la région du Cap, zone méditerranéenne située dans la partie méridionale de l'Afrique du Sud, se place sans conteste dans le peloton de tête, sur le plan de la richesse en végétaux vasculaires et en endémiques. En effet, ce territoire de taille assez restreinte (90 000 km²) abrite environ 9 000 plantes vasculaires dont 69 % d'endémiques. La Région Floristique du Cap représente donc une entité biogéographique bien définie, mais le faible nombre de familles endémiques (5) incite toutefois Cox (2001) à ne pas la considérer comme un empire floristique en tant que tel, contrairement à bon nombre de ses prédécesseurs.

Depuis plus de trente ans, les recherches floristiques et phyto-écologiques se sont multipliées en Afrique du Sud (cf. notamment les travaux de Cowling, Goldblatt, Linder, Richardson et Taylor), afin de mieux définir et circonscrire cette extraordinaire diversité végétale et d'en décrypter les processus responsables. Après le premier catalogue dressé par Bond & Goldblatt (1984), ce nouveau bilan permet de disposer de données actualisées sur l'ensemble des végétaux vasculaires de la région. En fait, ce travail se positionne à l'interface d'une flore classique et d'une simple énumération d'espèces.

Dans l'introduction, les auteurs dressent, en une trentaine de pages, un panorama des caractéristiques physiques de la région du Cap, puis ils traitent de la composition et de la diversité floristiques en comparant fréquemment les données locales à celles d'autres régions du globe, grâce à l'emploi de plusieurs tableaux très utiles pour le phytogéographe. Enfin, en trois pages, sont synthétisées de manière exemplaire les diverses explications pouvant rendre compte de cette richesse floristique exceptionnelle et de cette unicité phytoécologique. La plus grande diversité régionale de la province floristique du Cap par rapport au bassin méditerranéen trouve en partie son origine dans des processus de spéciation par radiation adaptative plus intenses, rapides et récents (Richardson *et al.*, 2001), en réponse à des fluctuations environnementales pas-

sées, à un isolement reproducteur de populations végétales se dispersant peu et soumises à des feux récurrents dans des habitats contrastés, et à une spécialisation poussée des insectes pollinisateurs. Cette introduction est enrichie par 12 planches photographiques en couleur, qui donnent un bref aperçu du kaléidoscope floristique sud-africain.

Le corps du texte (700 p.) est consacré à l'énumération de toutes les plantes vasculaires (ptéridophytes et phanérogames) indigènes et des principales xénophytes naturalisées. La classification des familles suit le travail de l'*Angiosperm Phylogeny Group* (1998) qui incorpore de nombreuses données moléculaires dans l'objectif d'une classification plus monophylétique. Pour chaque famille, existe une clé détaillée des genres (ce qui n'était pas le cas dans le catalogue de Bond & Goldblatt, 1984), puis, au sein de chaque genre, l'utilisation de quelques caractères morphologiques simples autorise le regroupement des taxons qui sont brièvement décrits en 3-4 lignes. Une caractérisation de l'habitat principal de l'espèce, ainsi que sa répartition dans les six centres phytogéographiques définis en début d'ouvrage complètent l'ensemble. Il est dommage que la classification pratique des types biologiques de Raunkiaer n'ait pas été retenue, mais la plupart des auteurs anglo-saxons sont toujours curieusement réticents à l'employer, alors qu'elle a une réalité biologique indéniable...

D'intéressantes notes taxonomiques, qui justifient la plupart des choix opérés par les auteurs, terminent l'ouvrage.

Cape Plants. A conspectus of the Cape flora of South Africa constitue donc une synthèse précieuse pour tout botaniste et phytogéographe intéressé par la diversité végétale du Monde méditerranéen, mais les recherches en systématique, phylogéographie, et écologie évolutive ne manquent encore pas en Afrique du Sud, si l'on veut tenter d'expliquer précisément, par exemple, la fabuleuse radiation adaptative du genre *Erica* (658 taxons dont 635 endémiques !) dans les fynbos de la région du Cap...

.....

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Threatened birds of the World

A. J. Stattersfield & D. R. Capper (eds)

Lynx Edicions, Barcelone & Birdlife International, Cambridge : 852p. (2000) (70 £).

Ce volumineux ouvrage dépasse de très loin son prédécesseur (*Bird to watch 2*, 1994), tant du point de vue de la masse impressionnante d'informations qu'il propose, que de celui de la qualité et de la quantité des illustrations qu'il recèle.

À parcourir les pages de ce volume, même le plus optimiste et insouciant des ornithologues se sentira progressivement submergé par un sentiment de crainte et d'effarement à la vue de cet interminable catalogue d'espèces d'oiseaux globalement menacées. En effet, d'après cette compilation, 1 186 espèces d'oiseaux (soit 1/8^e des espèces de la planète) sont considérées comme étant sérieusement menacées d'extinction au cours du XXI^e siècle et 103 espèces ont déjà disparu depuis l'an 1800. Après un rappel des critères de rareté et de vulnérabilité de l'UICN, cet ouvrage présente en 600 p. la longue liste des espèces menacées à l'échelle mondiale. Pour chacune d'entre elles, figurent sur une demi-page une illustration couleur, une carte de distribution, la catégorie de vulnérabilité, les effectifs mondiaux, les tendances et les principaux éléments de sa chorologie, de son écologie, des menaces et des objectifs ou moyens de conservation, et enfin, les principales références bibliographiques spécifiques. Ce livre passe ensuite plus succinctement (80 p.) en revue les espèces appartenant aux autres catégories de l'UICN "near threatened" (NT), "least concern" (LC), "data deficient" (DD), "not evaluated" (NE) et "extinct" (E). Enfin, cette masse de données est ensuite synthétisée et restituée par pays ou par territoire, et l'ouvrage se termine par une quarantaine de pages de références bibliographiques. Si, bien évidemment, les espèces des forêts tropicales et des milieux insulaires figurent nettement parmi les plus nombreuses, celles des zones méditerranéennes présentent malheureusement de nombreux cas extrêmement préoccupants. Citons

en particulier pour le bassin méditerranéen la situation catastrophique ("critical") de l'Ibis chauve *Geronticus eremita* et du Courlis à bec grêle *Numenius tenuirostris*, et le cas très préoccupant ("endangered") de l'Eristature à tête blanche *Oxyura leucocephala*. Une vingtaine d'autres espèces méditerranéennes classées en "vulnerables" ou "near threatened" achèvent de compléter ce triste bilan.

L'ouvrage, fruit d'un travail collectif colossal, constitue sans nul doute une mise au point et une synthèse indispensables, à même d'attirer efficacement l'attention des décideurs et des pouvoirs publics sur le délabrement progressif de l'avifaune mondiale.

ÉRIC VIDAL.

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Éloge de la plante : pour une nouvelle biologie

Francis Hallé

Éditions du Seuil, Paris : 352 p. (1999)

Bien qu'il ne traite pas spécifiquement de la région méditerranéenne ou même de l'écologie, le livre de Francis Hallé *Éloge de la plante* doit être lu par tous les chercheurs, étudiants, naturalistes ou simple curieux du monde des plantes. Cet ouvrage constitue en effet une véritable révolution dans la perception du monde végétal et plus particulièrement des plantes supérieures. Admirablement rédigé, l'auteur, dans un effort pédagogique remarquable, rend accessible au plus grand nombre des notions de biologie pourtant quelquefois complexes. Cet effort est complété par des dessins et schémas certes simples mais réalisés avec humour, ce qui accentue encore notre entrain à lire l'ouvrage comme un roman.

Francis Hallé revient sur des notions simples mais fondamentales du statut des végétaux dans le monde vivant car ceux-ci, d'après lui, sont encore trop perçus au travers d'une vision zoocentriste qui empêche de percevoir la véritable identité et le fonctionnement des plantes. Ainsi, en vrac, plusieurs véritables hérésies à des connaissances érigées quelquefois en dogme, sont énoncées : les plantes ne sont pas des individus mais des colonies dont l'unité est la cellule végétale, ces colonies sont potentiellement immortelles car elles se reproduisent de manière préférentielle par voie végétative. Elles peuvent perdre certaines parties ou se réitérer à l'infini car elles reproduisent un échantillon de base élaboré dès le stade de l'embryon. De nombreuses plantes pérennes se

construisent sur des symétries axiales avec leurs propres déchets : la lignine. L'organisation des plantes serait plus proche de celle des cristaux, des coraux ou des sociétés de fourmis que de tout autre forme animale. Nous n'irons pas plus loin afin de réserver au lecteur d'autres surprises de taille. Afin d'étayer ses affirmations, Francis Hallé utilise toutes les disciplines scientifiques de la biologie, de la biologie cellulaire à l'écologie, en réhabilitant la morphologie et l'anatomie comparée qui viennent souvent à point pour mesurer la distance qui sépare les végétaux des animaux. Pour renforcer des affirmations quelquefois hardies, Francis Hallé a fait appel à de nombreuses sources bibliographiques puisées dans des résultats de recherches novatrices et publiées dans de nombreuses revues scientifiques de haut niveau.

En conclusion, le livre de Francis Hallé devrait tenir une bonne place dans la rénovation des enseignements de botanique. En permettant certaines assertions, il fait partie des ouvrages qui permettent de dépoussiérer une science qui reste bien souvent trop descriptive de la diversité des formes rencontrées dans la nature, sans rechercher les mécanismes responsables de leurs mises en place.

THIERRY DU TOIT

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*Guide d'identification des charbons
de bois préhistoriques et récents
Sud-ouest de l'Europe : France,
Péninsule ibérique et îles Canaries*

Jean-Louis Vernet et coll.

CNRS Éditions, Paris : 395 p. (2001)

En dépit des nombreuses études anthracologiques publiées à ce jour dans le sud-ouest de l'Europe (France, Espagne, Portugal, îles Canaries), il n'existait pas jusqu'alors de guide d'identification propre aux charbons de bois à l'usage des archéo-anthracologues. L'ouvrage de J.-L. Vernet vient combler en grande partie cette lacune, en fournissant un catalogue suffisamment complet pour satisfaire la plupart des anthracologues travaillant en région méditerranéenne, qu'ils soient spécialistes ou débutants,

Dans un bref avant-propos l'auteur place les limites de l'ouvrage, lequel s'adresse principalement aux spécialistes des charbons archéologiques et rappelle les grands principes de l'archéoanthracologie. Un lexique (de 7 pages) explique les termes utilisés dans les fiches descriptives des taxons. Les définitions des caractères diagnostiques sont simples et vont à l'essentiel, mais

des petits schémas explicatifs complémentaires auraient parfois été très utiles.

Une clé de détermination est ensuite proposée, fondée principalement sur l'observation du plan transversal, en général toujours bien observable sur des charbons de taille pluri-millimétrique. La présence de cette clé, qualifiée modestement par l'auteur de « tentative d'orientation pour la détermination des taxons », vient au contraire renforcer le côté didactique de cet ouvrage. Des tableaux, au nombre de cinq, s'attachent tout particulièrement à la distinction de groupes difficiles : les genres *Pinus*, *Quercus* et *Prunus*, la distinction des genres *Phillyrea* et *Rhamnus*, et enfin les principaux genres de Rosacées Maloïdées. L'ouvrage se termine par un index des taxons cités, sous leur nom latin, mais aussi français, anglais, espagnol et portugais.

Le corps de l'ouvrage est entièrement consacré aux fiches descriptives des taxons. 171 taxons ont été sélectionnés à partir de la synthèse de l'ensemble des travaux d'analyse archéo-anthracologiques réalisés par l'auteur et son équipe ces trente dernières années. Ces taxons ont été choisis parmi ceux les plus fréquemment rencontrés en Europe sud-occidentale. Pour chaque taxon figure la période à partir de laquelle le taxon a pu être identifié (du paléolithique au Moyen Âge), mais il est dommage que les références des travaux qui mentionnent ces identifications ne soient pas clairement indiquées.

Chaque fiche rappelle les principaux critères diagnostiques observables sur les trois plans ligneux. Il est regrettable cependant que la lecture de ces fiches, qui devrait être rapide et aisée, soit rendue difficile par la petite taille de la police de caractères choisie par l'éditeur.

Enfin, et c'est l'intérêt de cet ouvrage, une planche photo illustre chaque fiche descriptive. Ces clichés noir & blanc ont été pris au microscope électronique à balayage (MEB). Chaque plan ligneux est représenté, sauf très rare exception. Disons, le tout de suite, ce sont les clichés des plans transversaux qui seront les plus utiles aux utilisateurs de ce guide, car les plus proches de ce qu'ils pourront observer dans leur propre microscope. Les photos des plans tangentiels sont de qualité inégale. Celles des plans radiaux sont en grande majorité inutilisables du point de vue diagnostique en raison du faible grossissement utilisé, empêchant de distinguer le détail des structures, ou au contraire d'un grossissement trop fort, illustrant un point d'anatomie précis mais impossible à observer soi-même sur un microscope optique de routine. Ces maladresses, inévitables dès qu'il s'agit de faire des photos de charbons de bois, viennent du fait que le MEB permet des observations plus fines et surtout beaucoup plus esthétiques qu'un microscope optique équipé d'objectifs ne dépassant pas x 250. Elles proviennent également de la difficulté d'exprimer, par un seul cliché pris à un seul grossissement, toute la complexité du plan radial, très riche du point de vue diagnostique. Ces photos ont au moins le mérite de montrer à quoi ressemble un charbon de bois vu au microscope, avec cette impression de relief si caractéristique, mais aussi cette difficulté à obtenir un

plan d'observation satisfaisant, contrairement à ce qui peut être fait sur des lames xylologiques.

Par ailleurs, contrairement à ce que précise l'auteur dans son avant-propos, l'ouvrage n'est pas présenté comme une flore traditionnelle. Les 149 premières fiches concernent les Angiospermes dicotylédones. Puis vient la description des Monocotylédones (4 fiches), des Gymnospermes (17 fiches) et des Ptéridophytes (1 fiche). Les taxons ne sont pas classés par famille mais par ordre alphabétique, ce qui empêche d'apprécier les similitudes anatomiques de certains genres au sein d'une même famille.

Malgré ces imperfections, en partie explicables par l'ampleur de la tâche que représente la mise au point d'un tel ouvrage, ce

« *Guide d'identification des charbons de bois préhistoriques et récents* » est un manuel qui deviendra vite indispensable à tous les anthracologues dont l'aire d'étude est comprise dans celle décrite par cet ouvrage, à savoir la région méditerranéenne septentrionale. Plus généralement, il s'adresse à toutes les personnes, enseignants ou étudiants, que l'anthracologie et l'anatomie du bois intéressent.

BRIGITTE TALON

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Résumés de thèses de doctorat en sciences

Labauve Corinne

L'invasion de la région méditerranéenne française par l'escargot *Xeropicta derbentina* : mécanismes, conséquences écologiques et agronomiques

Thèse de doctorat en sciences soutenue le 19 septembre 2001 à l'Université d'Aix-Marseille III, Faculté des sciences de Saint-Jérôme (UMR, 6116 IMEP, équipe Écologie du paysage et biologie de la conservation, case 461, 13397 Marseille Cedex 20, France)

Jury

Jacques Cabaret, directeur de recherches, INRA-Nouzilly, rapporteur ; Luc Madec, maître de conférences, Rennes, rapporteur ; Frédéric Magnin, chargé de recherche CNRS, Univ. Aix-Marseille III, co-directeur ; Marcel Barbero, professeur, Univ. Aix-Marseille III, co-directeur ; Robert Cameron, professeur, Sheffield, examinateur ; Markus Pfenninger, maître de conférences, Francfort, examinateur.

Xeropicta derbentina est un escargot dont l'invasion est spectaculaire car il constitue de nombreuses populations très denses. Originaire de Méditerranée orientale, il a été introduit en France dans les années 1940. Limitée à la région d'Aix-en-Provence dans les années 1960, l'invasion concerne aujourd'hui toute la Provence, et atteint même les Hautes-Alpes et la rive droite du Rhône. *X. derbentina* colonise les pelouses sèches, les friches, les pâturages et les milieux anthropisés jusqu'à 900 m d'altitude. L'extension de l'invasion semble favorisée par sa capacité de dispersion active (18 m en six mois) et par son aptitude à être dispersé par les activités humaines. En été, ces escargots forment des grappes sur des supports verticaux. Lorsqu'ils tombent au sol, à cause d'un véhicule, d'un promeneur ou d'un animal, il ne leur faut que 3 à 8 minutes pour se repercher sur n'importe quel objet qui les transportera plus ou moins loin : la distribution de *X. derbentina* au sein du paysage est ainsi largement dépendante de l'organisation des voies de communication. La plasticité adaptative de son cycle de vie, qui, sous l'influence de facteurs démographiques (forte densité) ou environnementaux (microclimat) peut être annuel ou bisannuel, est aussi susceptible de contribuer à son succès dans les processus de colonisation. Les conséquences de l'invasion par *X. derbentina* sont principalement dues aux densités élevées de certaines populations (jusqu'à 10 350 individus/m²). La diversité spécifique des communautés malacologiques diminue lorsque l'abondance de *X. derbentina* augmente. *X. derbentina* est également un hôte intermédiaire efficace dans la transmission de la pneumonie vermineuse des petits ruminants. En conditions expérimentales et semi-naturelles il semble moins efficace que *Ceratomyxa*

virgata ; cependant, la forte densité des populations de *X. derbentina* dans les pâturages lui conférerait une plus grande efficacité dans la transmission de cette maladie.

Gerbaud Eric

Dynamique des communautés végétales en écosystèmes perturbés : le cas des espèces adventices des cultures extensives du Parc naturel régional du Luberon

Thèse de doctorat en sciences avec label européen soutenue le 4 janvier 2002 à l'Université de Provence, Faculté des sciences de Saint-Charles (UMR, 6116 IMEP, équipe Écologie du paysage et biologie de la conservation, case 461, 13397 Marseille Cedex 20, France)

Jury

Jacques Mailler (prof. ENSA Montpellier), président ; Peter Poschold (prof. Univ. Regensburg, Allemagne), Alain Peeters (prof. Univ. Louvain, Belgique) et Maurice Roux (prof. Univ. Aix-Marseille III), rapporteurs ; Phil Wilson (dr. Plantlife, Grande-Bretagne), examinateur ; Gilles Bonin (prof. Univ. Provence) et Thierry Dutoit (MCF Univ. Provence), co-directeurs de thèse.

Peu d'études ont été réalisées sur les communautés d'adventices des écosystèmes de grandes cultures dans le bassin méditerranéen à l'exception des travaux des malherbologues visant à leur éradication ou des phytosociologues pour la classification typologique de ces communautés. Nos travaux ont donc eu pour objectifs une première approche de la dynamique des communautés d'adventices dans un contexte d'agriculture extensive maintenue par une mesure agri-environnementale sur le territoire du Parc naturel régional du Luberon. Nous nous sommes particulièrement intéressés aux rôles des lisières, de la rotation culturale, mais aussi à la compétition entre adventices et l'espèce cultivée (le blé) ainsi qu'à la recherche d'interactions positives entre communautés d'adventices et le système d'exploitation agricole.

Nos résultats montrent que, contrairement aux systèmes d'agriculture intensive du nord-ouest de l'Europe, les bords de champs ne constituent pas des refuges pour les adventices typiques des champs de céréales (messicoles). De même, ces communautés possèdent une faible mémoire séminale et la majorité des espèces disparaissent après une dizaine d'années d'introduction d'une prairie semi-naturelle dans la rotation culturale. Certaines messicoles rares sur le territoire national entrent fortement en compétition avec le blé et réduisent son rendement agricole. Cependant la valeur nutritive des adventices, notamment leurs teneurs en élé-

ments minéraux, constitue un élément majeur pour le maintien du pâturage ovin de parcours. Ces résultats sont ensuite discutés pour la mise en place de mesures de gestion conservatoire compatibles avec les objectifs de production agricole.

Brewer Simon

Recolonisation postglaciaire de quelques taxons tempérés en Europe : une approche spatiale et temporelle

Thèse de doctorat en sciences soutenue le 25 janvier 2002 à l'Université d'Aix-Marseille III, Faculté des sciences de Saint-Jérôme (UMR, 6116 IMEP, équipe Paléoécologie, case 451, 13397 Marseille Cedex 20, France).

Jury

Gilles Bonin, examinateur ; Richard Bradshaw, rapporteur ; Rachid Cheddadi, examinateur ; Eric Faure, examinateur ; Brian Huntley, rapporteur ; Rémy Petit, examinateur.

Les changements climatiques entre périodes glaciaires et interglaciaires ont engendré des modifications à grande échelle dans la distribution des arbres forestiers. L'analyse pollinique peut être utilisée pour reconstruire ces changements de façon temporelle à l'échelle d'un site et de façon spatiale en utilisant un réseau de sites. Basées sur un ensemble de sites polliniques, des cartes isochrones représentant la propagation de dix taxons forestiers sont présentées. Ces cartes permettent l'identification de refuges et routes de recolonisation. Parallèlement, les taux de propagation ont été calculés. Malgré certaines similitudes dans l'histoire de la recolonisation les taxons montrent des réponses individuelles aux changements environnementaux de la transition jusqu'à l'époque actuelle. Ceci renforce la théorie des communautés comme structures temporaires. L'impact de ces changements pour la conservation est discuté dans ce travail. Information concernant la recolonisation peut également être obtenue à partir d'une étude de marqueurs génétiques obtenus dans les populations actuelles. Par conséquent, l'intégration des deux ensembles de données offre la possibilité d'étudier ces changements de distribution de façon précise.

Des études comparatives basées sur les pollens et les données génétiques sont présentées pour deux parmi les dix taxons. Dans le premier cas, l'information à partir d'une étude extensive de l'ADN chloroplastique de l'ensemble des chênes blancs est utilisé, pour mieux définir la propagation postglaciaire observée à

partir des cartes polliniques. Dans le second cas, une étude des marqueurs isozymes de *Fagus sylvatica* est comparée avec des paramètres quantifiés du processus de recolonisation (vitesse de propagation, temps d'arrivée, distance au refuge). Des relations significatives ont été trouvées entre ces paramètres historiques et la richesse allélique et la diversité génétique. Ceci suggère qu'au niveau génétique, la diversité soit largement dictée par l'histoire de l'espèce. Ces approches comparatives offrent par conséquent la perspective d'une plus grande compréhension des changements de distribution des arbres forestiers dans le passé, savoir vital pour le futur.

Ortu Elena

Reconstruction sur base pollinique de la dynamique de la végétation tardiglaciaire et holocène dans les Alpes maritimes italiennes

Thèse de doctorat en sciences en co-tutelle italo-française soutenue le 13 mars 2002, à l'Université de Pavie (Italie)

Jury

F. Montacchini, directeur de thèse, co-directeur de thèse : J.-L. de Beaulieu, rapporteur ; C. Alberta Accorsi, rapporteur ; H. Richard, examinateur ; M. Barbero, examinateur ; R. Caramiello, examinateur ; F. Bracco.

Le travail présenté comprend une étude de la végétation actuelle et une étude palynologique effectuées dans les Alpes maritimes italiennes. L'étude de la végétation actuelle se base sur 43 relevés phytosociologiques des tourbières d'altitude et des pelouses environnantes ; elle a permis d'évaluer l'impact anthropique actuel et de le comparer au passé. Le contenu pollinique des bryophytes récoltées sur les tourbières a été comparé à la végétation actuelle et aux spectres fossiles, dans le but de faciliter la compréhension des diagrammes paléo-palynologiques. L'étude de l'histoire de la végétation est basée sur l'analyse palynologique de 6 carottes sédimentaires (dont 3 atteignent le Tardiglaciaire) provenant de six zones humides dans l'aire comprise entre le Vallon de St-Anna di Vinadio et la Vallée Ellero. Leur étude a permis d'avancer des hypothèses sur les étapes de la dynamique végétale depuis le Tardiglaciaire, sur la localisation des refuges glaciaires, sur la migration des essences arborées et sur l'influence de l'action humaine sur la dynamique végétale et la limite supérieure des forêts.

Instructions aux auteurs

Ecologia Mediterranea publie des travaux de recherche originaux et des mises au point sur des sujets se rapportant à l'écologie fondamentale ou appliquée des régions méditerranéennes, à l'exception des milieux marins. La revue exclut les articles purement descriptifs ou de systématique. *Ecologia Mediterranea* privilégie les domaines scientifiques suivants : bioclimatologie, biogéographie, biologie de la conservation, biologie des populations, écologie génétique, écologie du paysage, écologie microbienne, écologie végétale et animale, écophysiologie, paléoclimatologie, paléoécologie. La revue accepte également la publication d'actes de colloques, d'articles de synthèse, de notes méthodologiques, de comptes-rendus d'ouvrages, ainsi que des commentaires sur les articles récemment parus dans *Ecologia Mediterranea*.

Les manuscrits sont soumis à des lecteurs spécialistes du sujet, ou à des membres du Comité de rédaction, ou aux Editeurs. La décision finale d'accepter ou refuser un article relève des Editeurs. L'article proposé doit être envoyé en triple exemplaire à l'adresse de la revue. Une fois leur article accepté, les auteurs devront tenir compte des remarques des lecteurs, puis ils renverront leur texte corrigé au secrétariat de la revue, sous 3 mois, imprimé en un exemplaire et informatisé (disquette 3.5'), si possible PC et au format Word 7 ou RTF). Les auteurs devront s'assurer de la correspondance entre le texte imprimé et le texte informatisé. Les illustrations originales seront jointes à l'envoi. Les épreuves corrigées doivent être retournées au secrétariat de la revue sans délai. Les livres et monographies devant être analysés seront envoyés aux Editeurs.

Préparation du manuscrit

Les articles (dactylographiés en double interligne, en format A4) doivent être rédigés de préférence en français ou en anglais, mais les travaux en espagnol ou en italien sont aussi acceptés. Si l'article soumis n'est pas rédigé en anglais, il est demandé (en plus des résumés) une version anglaise abrégée ainsi qu'une traduction en anglais des titres des figures et tableaux.

L'article doit être complet : titres français et anglais, auteur(s) et adresse(s), résumés en français et anglais (au minimum), version anglaise abrégée (si le texte n'est pas en anglais), mots-clés, texte, puis remerciements, bibliographie, figures et tableaux. Le texte des articles originaux de recherche devrait normalement comporter quatre parties : introduction, méthodes, résultats, discussion.

En ce qui concerne la saisie du texte, il est simplement demandé aux auteurs de distinguer clairement les titres des différents paragraphes. Les titres ne seront pas numérotés. Pour numéroter les sous-titres, éviter les lettres. Attention, l'emploi de mots "soulignés" est à proscrire. Les noms d'auteurs cités figureront en minuscules dans le texte comme dans la bibliographie. En français, n'utilisez les majuscules que pour les noms propres, sauf exception justifiée. Les ponctuations doubles (: ; ? !) sont précédées d'un espace insécable, contrairement aux ponctuations simples (, .). En revanche, toutes les ponctuations sont suivies d'un espace. La mise en forme définitive du texte sera assurée par la revue. L'adresse de chaque auteur sera indiquée. Dans le cas où la publication serait le fait de plusieurs auteurs, il doit être précisé lors du premier envoi la personne à qui doit être retourné l'article après lecture.

Résumés, mots-clés et version abrégée

Les résumés doivent comporter 300 mots au maximum et la version anglaise abrégée 1000 mots (environ une page). Le nombre de mots-clés est limité à six, dans la langue des résumés ; ils ne doivent généralement pas figurer dans le titre.

Bibliographie

La bibliographie regroupera toutes les références citées et elles seules. Les références seront rangées dans l'ordre alphabétique des auteurs et de façon chronologique. Les abréviations internationales des titres des revues doivent être utilisées (sauf en cas de doute). Vérifier attentivement le manuscrit pour s'assurer que toutes les références citées dans le texte apparaissent bien en bibliographie et inversement. La mise en forme doit suivre les exemples suivants :

— **article** : Andow D.A., Karieva P., Levin S.A. & Okubo A., 1990. Spread of invading organisms. *J. Ecol.*, 4 : 177-188.

— **ouvrage** : Harper J.L., 1977. *Population biology of plants*. Academic Press, London. 300 p.

— **article d'ouvrage** : May R.M., 1989. Levels of organization in ecology. In : Cherret J.M. (ed.), *Ecological concepts*. Blackwell Scientific Public., Oxford : 339-363.

— **actes d'un colloque** : Grootaert P., 1984. Biodiversity in insects, speciation and behaviour in Diptera. In : Hoffmann M. & Van der Veken P. (eds), *Proceedings of the symposium on "Biodiversity : study, exploration, conservation"*, Ghent, 18 November 1992 : 121-141.

Citations et renvois appelés dans le texte

Les mots "figure" et "tableau" annoncés dans le texte sont écrits en toutes lettres et en minuscules. Indiquer le nom d'auteur et l'année de publication (mais indiquer sous les auteurs dans la bibliographie). Exemples : "Since Dupont (1962) has shown that...", or "This is in agreement with previous results (Durand *et al.*, 1990 ; Dupont & Dupont, 1997)...". Le numéro de page de la citation n'est mentionné que dans le cas où elle est entre guillemets. Si la publication est écrite par plus de deux auteurs, le nom du premier doit être suivi par *et al.*

Abréviations, nomenclature et mots latins

L'usage d'une abréviation technique doit être précédé de sa signification lors de sa première apparition. Les codes de nomenclature doivent être respectés selon les conventions internationales. Les mots latins doivent être mis en italiques (*et al.*, *a priori*, *etc.*), et en particulier les noms de plantes ou d'animaux. Lors de la première apparition du nom d'une espèce, il est demandé d'y faire figurer le nom d'auteur (exemple : *Olea europaea* L.).

Figures et tableaux

Les figures (précédées de leurs légendes) doivent être remises séparément du texte, sur fichiers séparés Adobe Illustrator ou Adobe Photoshop, prêtes à l'impression, sans nécessiter de réduction (donc au maximum : format 16 x 22 cm ou 8 x 22 cm).

Les tableaux doivent être saisis soit en texte, **avec une seule tabulation entre chaque occurrence**, soit sur Excel, mais toujours sur fichiers séparés.

Un fichier "Légendes tableaux" et un fichier "Légendes figures" doivent être fournis séparément.

Important : ne pas intégrer figures, tableaux et diagrammes dans les fichiers Word.

Tous les documents destinés être insérés dans le texte doivent y être annoncés, numérotés dans l'ordre croissant. Les tableaux informatisés ne doivent pas comporter de signes (: ou |) pour marquer les colonnes. Un original papier de chaque document est exigé.

Tirés-à-part

Il est fourni 25 tirés-à-part par article, même lorsqu'il y a des auteurs multiples. Des tirés-à-part supplémentaires peuvent être obtenus à la demande : ils seront facturés.

Instructions to authors

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Manuscripts are reviewed by appropriate referees, or by members of the Editorial Board, or by the Editors themselves. The final decision to accept or reject a manuscript is made by the Editors. Please send 3 copies of the manuscript to the editors. When an article is accepted, the authors should take the reviewers' comments into consideration. They must send back to the journal Editorial Office their corrected printed manuscript (one copy) and include the corresponding floppy disk (as far as possible: 3.5" PC, Word 7 or .RTF) within 3 months. The authors are asked to check the conformity between printed and computerised versions. Enclose the original illustrations. Corrected proofs must be returned to the journal Editorial Office without delay. Books and monographs to be reviewed must be submitted to the Editors.

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Manuscripts (typewritten with double spacing and A4 paper size) should preferably be written in French or English, but Spanish and Italian are accepted. If the language is not English, you should include an English short version and English titles for figures and tables.

The manuscript must be complete: French and English titles, author(s) and address(es), French and English abstracts (at least), an English short version (only if it is not the language used in the article), key-words, text, references, acknowledgements, figures and tables. For research papers, the text should normally consist of 4 sections: introduction, methods, results and discussion.

When typing the manuscript, please distinguish titles clearly from other paragraphs. Titles and subtitles should not be numbered. Avoid using letters to number subtitles. Use lower-case letters for names. Do not underline any words. In English, there is one space after punctuation, none before.

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Each author's address should be specified. The first time, please state the complete address of the correspondent author to whom the proofs should be sent.

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Abstracts should be no longer than 300 words. The English abridged version should not exceed one page (1000 words). Do not use more than six key-words (translated in the abstract's language). Key-words should not be present in the title.

References

All publications quoted in the text should be presented in a list of references following the text. The list of references should be arranged alphabetically by author and chronologically per author. You should abbreviate the titles of periodicals in the list of references (except if you are not sure of it). Make sure that all citations and references correspond. Use the following system for references:

— journal article:

Andow D.A., Karieva P., Levin S.A. & Okubo A., 1990. Spread of invading organisms. *J. Ecol.*, 4 : 177-188.

— book:

Harper J.L., 1977. *Population biology of plants*. Academic Press, London. 300 p.

— book section:

May R.M., 1989. Levels of organisation in ecology. In: Cherret J.M. (ed.), *Ecological concepts*. Blackwell Scientific Public., Oxford : 339-363.

— conference proceedings:

Grootaert P., 1984. Biodiversity in insects, speciation and behaviour in Diptera. In: Hoffmann M. & Van der Veken P. (eds.), *Proceedings of the symposium on "Biodiversity: study, exploration, conservation"*, Ghent, 18 November 1992 : 121-141.

Citations in-text

The words "figure" and "table" announced in-text should be written *in extenso* and in lower-case letters. In the text, refer to the author's name and year of publication (followed by pages only if it is a quotation). If a publication is written by more than two authors, the name of the first author should be used followed by "et al." (this indication, however, should never be used in the list of references: first author and co-authors should be mentioned). Examples: "Since Dupont (1962) has shown that...", or "This is in agreement with previous results (Durand et al., 1990; Dupont & Dupont, 1997)...".

Abbreviation, latin words

Explanation of a technical abbreviation is required when first used. International convention codes for nomenclature should be used. Latin words should be in italics (*et al.*, *a priori*, etc.), particularly for taxonomic classifications (the first time, please state the author's name: for example, *Olea europaea* Linné).

Figures and tables

Figures should be submitted **separately** (Adobe Illustrator or Adobe Photoshop) and they should be preceded by the figure legend. Figures should be sent "ready to be printed", without need to be reduced (so their size should be 16 x 22 cm or 8 x 22 cm maximum).

Tables should be submitted **separately** (Word, with only one tabulation between occurrences), or (Excel).

"Legends Tables" and "Legends Figures" should be submitted **separately**.


Important: Don't integrate figures and tables into Word.

All the illustrations being should be quoted in text, numbered in sequence and should have a legend. Computerised tables' columns should not be represented by signs (: or |).

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