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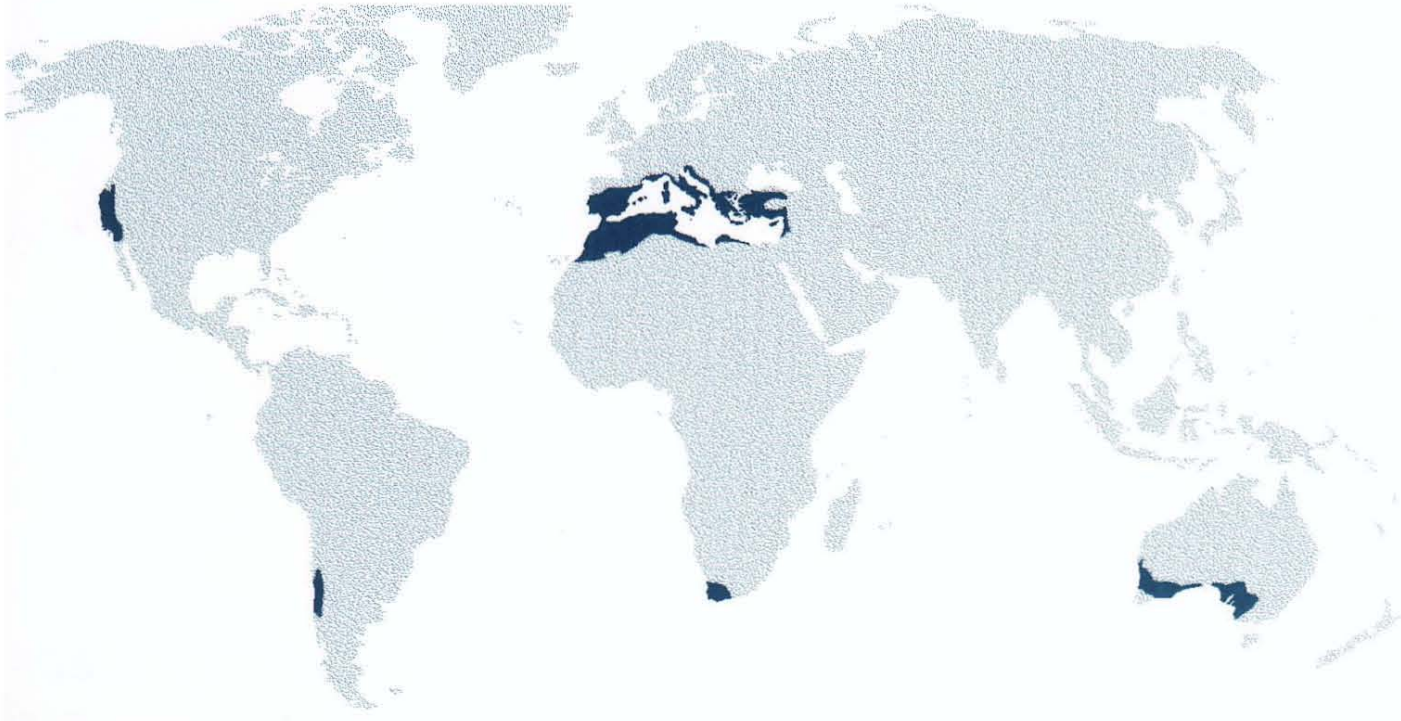

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Faculté des Sciences et Techniques de Saint Jérôme
Institut Méditerranéen d'Ecologie et de Paléoécologie, case 461
F - 13397 MARSEILLE Cedex 20 FRANCE

Tél. : + 33 4 91 28 85 35 - Fax : + 33 4 91 28 80 51
E-mail : ecologia.mediterranea@botmed.u-3mrs.fr
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Vegetation-environment relationships in Lefka Ori (Crete, Greece): ordination results from montane-mediterranean and oro-mediterranean communities

Relations végétation-environnement dans le massif des Lefka Ori (Crète, Grèce) : résultats d'une ordination des communautés des étages montagnard-méditerranéen et oro-mediterranéen

I.N. Vogiatzakis & G.H.Griffiths

Department of Geography, The University of Reading, Whiteknights, Reading, UK. RG6 6AB. Tel. +44 118 9318733, Email: i.vogiatzakis@reading.ac.uk

ABSTRACT

The extensive Lefka Ori massif on the island of Crete supports more than 100 endemic plant species and is of considerable ecological importance internationally. However, little is known or understood about plant community distribution in the massif. Montane-mediterranean and oro-mediterranean vegetation was sampled at two study sites and the relationships between a range of environmental variables and plant community distribution were investigated. Classification of the floristic data was performed with Two Way Indicator Species Analysis (TWINSPAN) resulting in five distinct vegetation communities. Canonical Correspondence Analysis (CCA) suggested that the two main compositional gradients were associated with altitude, pH, organic matter and slope. Rocky slopes, screes and karstic depressions were identified from field observations as the main habitats. Separate ordination analysis was performed only for the first two groups since the third supported only one community. Altitude and bare rock percent cover control vegetation patterns on rocky slopes, whereas on screes ground cover and pH are the most important factors.

Key-words: ordination, Lefka Ori, endemic plants, conservation

RESUME

L'imposant massif montagneux des Lefka Ori sur l'île de Crète (Grèce), abrite plus d'une centaine de plantes endémiques. L'importance de cette richesse floristique et écologique est reconnue à l'échelle mondiale. Cependant, peu de choses sont connues en ce qui concerne la distribution des communautés végétales dans ce massif. Des relevés de végétation ont été réalisés sur deux sites d'étude, au niveau des étages montagnard-méditerranéen et oro-meditérranéen, dans le but d'étudier l'influence possible de plusieurs variables environnementales sur la distribution des communautés. Une classification des données floristiques a été établie à l'aide du logiciel TWINSPAN, et a permis de définir cinq communautés de végétation distinctes. Une analyse canonique des correspondances (ACC) indique que les deux principaux gradients de composition floristique sont associés à l'altitude, au pH, à la matière organique et à la pente. Les observations de terrain ont permis d'identifier comme principaux habitats, les pentes rocheuses, les éboulis, et les dolines. Une analyse d'ordination séparée a été menée uniquement sur les deux premiers groupes, car le troisième ne comptait qu'une seule communauté. Sur les pentes rocheuses, l'altitude et le pourcentage de la roche nue déterminent le type de couverture végétale. Par contre, sur les éboulis, la couverture du sol ainsi que le pH constituent les paramètres les plus importants dans la détermination du couvert végétal.

Mots-clés : ordination, Lefka Ori, plantes endémiques, conservation

INTRODUCTION

Worldwide, the destruction of natural habitats or their conversion to other uses is resulting in rapid species loss. From an estimated global total of 270,000 plant species, 12.5 percent are considered to be threatened (Walter & Gillet, 1998). The expansion of forestry and agriculture, habitat loss and fragmentation, soil and water pollution and global climate change are all contributing to the destruction of habitats and the loss of plant species. Despite the severity of the problem a recent IUCN report (Walter & Gillet, 1998) stresses that there is insufficient knowledge of the taxonomy, habitat requirements and distribution of many plants to identify potential threats, and therefore, to assess their vulnerability to extinction.

These problems are particularly well illustrated by the situation in the Mediterranean Basin, despite its recognition as a reservoir of plant biodiversity (Gomez-Campo, 1985; Heywood, 1995; Médail & Quézel, 1997). In recent decades, agricultural intensification, overgrazing, afforestation and tourist development have destroyed and continue to threaten important habitats and their associated plants. The present extinction rate of the Mediterranean higher plants is 0.15 percent of the total, representing 37 species presumed to be extinct. Moreover, there are 4251 plant taxa under threat in the Mediterranean (Greuter, 1994).

Conflict between development pressures and conservation priorities is a major problem in many parts of the world but is particularly acute on the island of Crete. The varied topography, geology and climate of the island give rise to a wide variety of ecological niches; this is reflected, in turn, in a diverse flora. The island contains 1706 native plant species (Turland et *al.*, 1993), of which 180 (species and subspecies) are wholly or mainly confined to Crete (Montmollin & Iatrou, 1995). Crete, therefore, is a place of considerable ecological and botanical interest. This is reflected in various phytosociological (Zohary & Orshan, 1965; Barbero & Quézel, 1980; Zaffran, 1990), floristic (Barclay, 1986; Turland *et al.*, 1993) and landscape studies (Grove & Rackham, 1993; Rackham & Moody, 1996). The importance of the Cretan flora in a global context has also been highlighted; the IUCN (Heywood & Davis, 1994) include Crete within one of the Centres of Plant Diversity where immediate conservation action is suggested. According to Delanoë *et al.* (1996), 11 percent of the island's species belong to globally threatened taxa, while 13 percent of the total taxa are locally threatened (Table 1).

Despite the importance of the Cretan flora in a regional and global context, human modification of both natural and cultural landscapes continues to threaten the survival of endemic species on the island. According to Grove & Rackham (1993), these threats are: tourism, urbanisation, road building, intensification of cultivation, changes in grazing pressure, abandonment of cultivation, the increase in tree cover and increased fire frequency.

Although knowledge of the taxonomy of the Cretan flora is considered to be satisfactory, the understanding of species ecology and distribution is relatively poor. The most important sources of distribution data for the Cretan flora can be found in Turland *et al.* (1993), Chilton & Turland (1997), Strid (1986), Strid & Tan (1991) and Jalas & Suominen (1972-1996). There are also numerous publications on individual Cretan species (e.g. Greuter *et al.*, 1985). All these sources use different mapping schemes, making comparisons between species' distributions from different sources difficult. There is only one National Park on the island, the Samaria Gorge. The Samaria Park is 48.5km^2 in area and contains stands of pine-cypress forest and associated endemic species. The islands of Dia and Theodorou to the north of Iraklion and Chania respectively are Nature Reserves. These are managed mainly for the population of the Cretan ibex, an endemic mammal transferred from Samaria. Along a coastal valley at Vai in the N.E. of the island, the largest Cretan date palms (*Phoenix theophrastii* Greuter) are protected and monitored by the Forest Service. At least 30 sites in Crete have also been proposed for inclusion in the NATURA 2000 network of protected sites within the European Union (Council of Europe, 1992). There is also a presidential decree (No. 67/1981) on the protection of rare plant and animal species (Kassioumis, 1994). With the exception of Samaria, which is mostly below the sub-alpine and alpine zones, there is limited floristic information relating

IUCN Categories	Globally threatened taxa	Locally Threatened Taxa
Extinct	-	-
Endangered	11	14
Vulnerable	61	73
Rare	118	146
Insufficiently documented	3	5
Total	**193**	**238**
% of taxa threatened	**11**	**13**

Table 1. Threatened plants on Crete (source: Delanoë *et al.*, 1996).

specifically to the high mountain area of the Lefka Ori and this region is currently offered no protection. However, Lefka Ori is proposed as one of the 296 sites in Greece to be protected under the pan-European NATURA 2000 network comprising Special Areas of Conservation (SACs) for threatened habitats and species (Council of Europe, 1992). A recent analysis (Papastergiadou, 1998), suggests that Lefka Ori ranks in the top nine of NATURA 2000 sites proposed for Greece, on the basis of the number of Red Data List and threatened plants in Greece and other relevant criteria. There is a new proposal to extend the Samaria National Park to include Lefka Ori. It is particularly critical therefore, that a baseline of current distribution patterns is established and that the environmental factors controlling patterns of distribution are well understood.

Two types of habitat are especially rich in endemic plants within Crete: the gorges and the high mountain areas. This study focuses on those plant species of the high mountain zone of the Lefka Ori, which are vulnerable to new road building and changes in grazing pressure. Since detailed species distribution maps for Crete are unavailable, it is not possible to develop an effective conservation strategy for endemic plants in the Lefka Ori. The objectives of the study therefore are to:

- contribute to the knowledge of species distributions, notably for rare and endemic plants;

- use this knowledge to develop and apply GIS techniques to predict plant distribution patterns;

- identify conservation priorities in the Lefka Ori, from knowledge of distribution patterns and potential threats;

- assist with the development of a European-wide typology of habitats of importance for nature conservation as part of the Pan-European Biological and Landscape Diversity Strategy (ECNC, 1999).

This paper reports only on the first of these objectives: the development of the model to describe community patterns across the sub-alpine and alpine zones of the Lefka Ori.

MATERIALS AND METHODS

Study area

The Lefka Ori massif (Figure 1) is the most extensive mountain massif on the island: 38,500 ha are above 1000 m asl. with 15 peaks above 2200 m asl., including Pachnes, the highest peak at 2453 m. Lefka Ori is a rugged marble and dolomite massif rich in rock debris and karstic formations. The western part consists mainly of phyllite and quartzite, giving a more rounded landscape of smoothly shaped summits. Shallow calcareous *lithosols* and *rendzina* soils dominate throughout much of the massif. They often represent degraded soil profiles with limited water supply. Calcareous woodland is extensive in the Lefka Ori massif. *Cupressus sempervirens* L. covers the eastern slopes above the Askifos plain, as well as above the Imbros gorge to the south, often occurring in ravines down to sea level. It also grows in association with *Acer sempervirens* L. and *Quercus coccifera* L. On mountain sides with northerly aspects, the endemic *Zelkova abelicea* (Lam.) Boiss. is present. *Pinus brutia* Ten. occurs on drier substrates, notably the southern slopes, together with

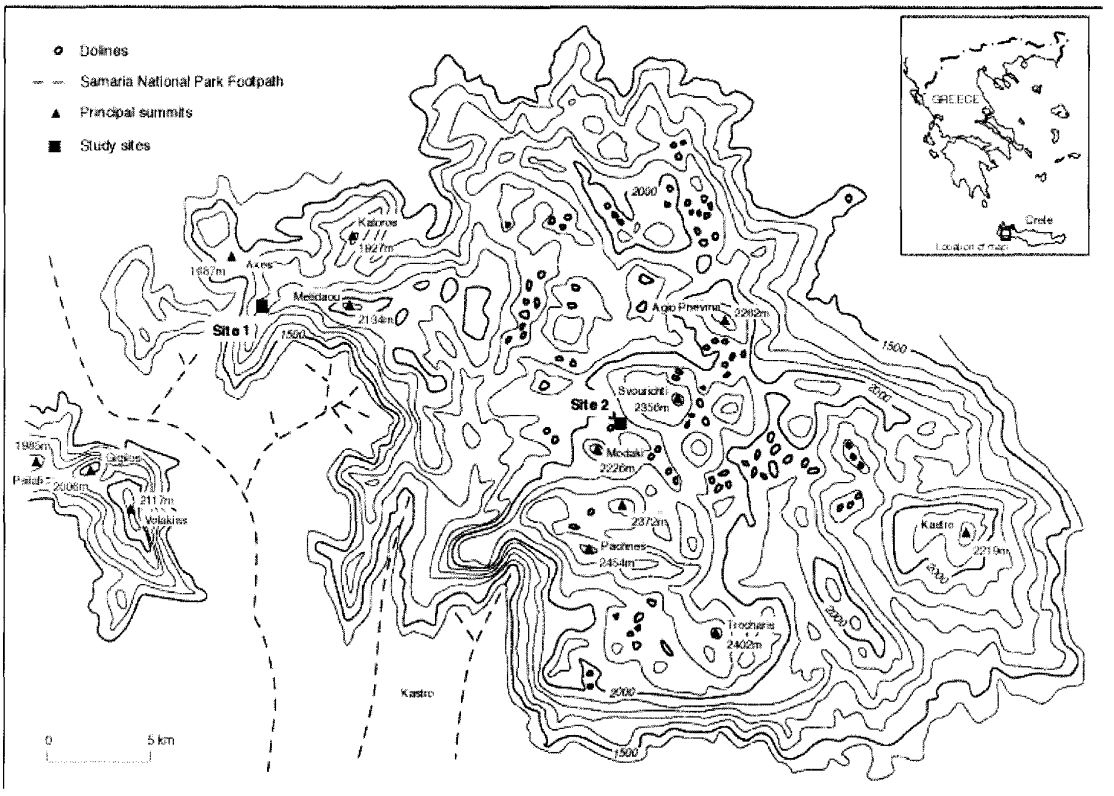

Figure 1. Map of the study area and the location of the study sites (modified from Zaffran, 1990).

Cupressus sempervirens and *Quercus coccifera* up to 1200 m asl. (Turland *et al.*, 1993). The upper limit of forest growth on the southern side of the Lefka Ori is at 1600-1650 m asl., while on the northern side the limit is up to 150 m higher.

Lefka Ori is ecologically important with more than 100 endemic plant species occurring across the massif. Out of the 263 taxa included in the Red Data Book for threatened and rare plant species of Greece, 23 occur only in the Lefka Ori (Phitos *et al.*, 1995). Some of the endemic plants are rare and localised species such as *Myosotis solange* Greuter & Zaffran, *Centaurea baldacii* Degen ex Haláksy, *Nepeta sphaciotica* P.H.Davis, *Ranunculus radinotrichus* Greuter & Strid, all of which are restricted to Lefka Ori above 1800 m asl.

On the basis of field observations, the most characteristic habitats of Lefka Ori above the tree line are mountain pasture, karstic dolines, and scree slopes.

Mountain pasture is the dominant habitat of the high mountain tops of Crete above the tree line. This habitat is predominantly covered with spiny, cushion-like xerophytes. Grazing is still one of the main impacts in these high altitude areas and many of the typical plants are adapted to heavy grazing pressure. *Astragalus angustifolius* Lam., *Verbascum spinosum* L. and *Berberis cretica* L. are spiny and *Daphne oleoides* Schreb. has a pungent taste. The main plant on these slopes is the endemic *Sideritis syriaca* L. subsp. *syriaca*.

An exceptional and important habitat of Lefka Ori is dolines. These karstic depressions, in which clay soil has accumulated as a result of decalcification, are variable in size (10-100 m in diameter) and more vegetated than screes, mainly with *Berberis cretica*.

The latter which cover most of the mountain summits above 1900 m asl. are relatively homogeneous in phytosociological terms. Some of the commonly found endemic species on screes in Lefka Ori include *Alyssum fragillimum* (Bald.) Rech.f., *Silene variegata* Boiss. & Heldr. and *Dianthus spacioticus* Boiss & Heldr.

Field Data

120 plots were sampled within two sites (Figure 1). The two sites, each approximately 11.5 km^2, were selected to be representative of the montane-mediterranean and oro-mediterranean zone of the massif. The precise location of each site was partly determined by their accessibility and proximity to water to facilitate fieldwork in a remote and rugged region. The size of each plot (10 m x 10 m) was selected according to the species-area curve principle (Kent & Coker, 1993). For estimating percent plant cover the DOMIN scale (1-10) was adopted. Apart from a species list and a quantitative abundance measure, additional environmental information for each of the plots was also recorded, including altitude, aspect, slope, and percentage of visible rock and percentage of bare ground. The range of altitude sampled was from 1500-2400 m asl. Soil samples and soil depth measurements were also taken at each plot for subsequent analysis (pH, organic matter content and soil texture). The first field season was in June, July and August 1997 and the second was in July and August 1998. The sampling dates were considered to be appropriate given the phenology of the plants of interest, notably the endemic species.

For species identification the *Mountain Flora of Greece* (Strid, 1986; Strid & Tan, 1991) and the *Flora Europaea* (Tutin *et al.*, 1964-1980) were used. Nomenclature of the plant taxa given in this paper is according to Turland *et al.* (1993) and Chilton & Turland (1997). The plant species that were recorded in the study area were collected and thoroughly preserved, both to assist with later identification (where problematic) and to provide specimens for the herbarium at the Mediterranean Agronomic Institute at Chania (MAICh).

Classification and Ordination

The use of multivariate techniques in combination with numerical methods is frequently employed by ecologists to answer problems on vegetation community patterns and distribution (Brown *et al.*, 1993; Smith, 1995).

Canonical Correspondence Analysis (CCA; ter Braak, 1986) and Two Way Species Indicator Analysis (TWINSPAN: Hill, 1979) were used in order to identify and determine the relative contribution of the environmental variables that explain the distribution of plants at the two field study sites.

First, the vegetation samples collected in the field were classified using TWINSPAN. TWINSPAN is a polythetic divisive classification technique, which classifies vegetation communities according to their floristic similarity. This classification of vegetation samples into distinct community types provided the framework within which to interpret the results of the ordination analysis. Ordination (CCA) was subsequently applied to describe compositional gradients.

CCA is a direct gradient analysis technique that relates community variation (composition and abundance), to environmental variation enabling the significance of environmental variables on community distribution to be determined. This was performed both for the whole data set and separately for the field samples falling within each vegetation community, to determine the differences in the contribution of environmental variables between community types.

Both classification and ordination analyses presented here were carried out using PC-ORD version 3.18 for Windows (McCune & Mefford, 1997). On the ordination diagrams presented in this paper, points represent samples while vectors represent environ mental variables. The length of a vector is proportional to its importance and the angle between two vectors reflects the degree of correlation between variables. The angle between a vector and each axis is related to its correlation with the axis (Kent & Coker, 1992).

RESULTS

Vegetation classification

TWINSPAN classification of the vegetation data on the basis of floristic composition resulted to five distinct communities (Figure 2).

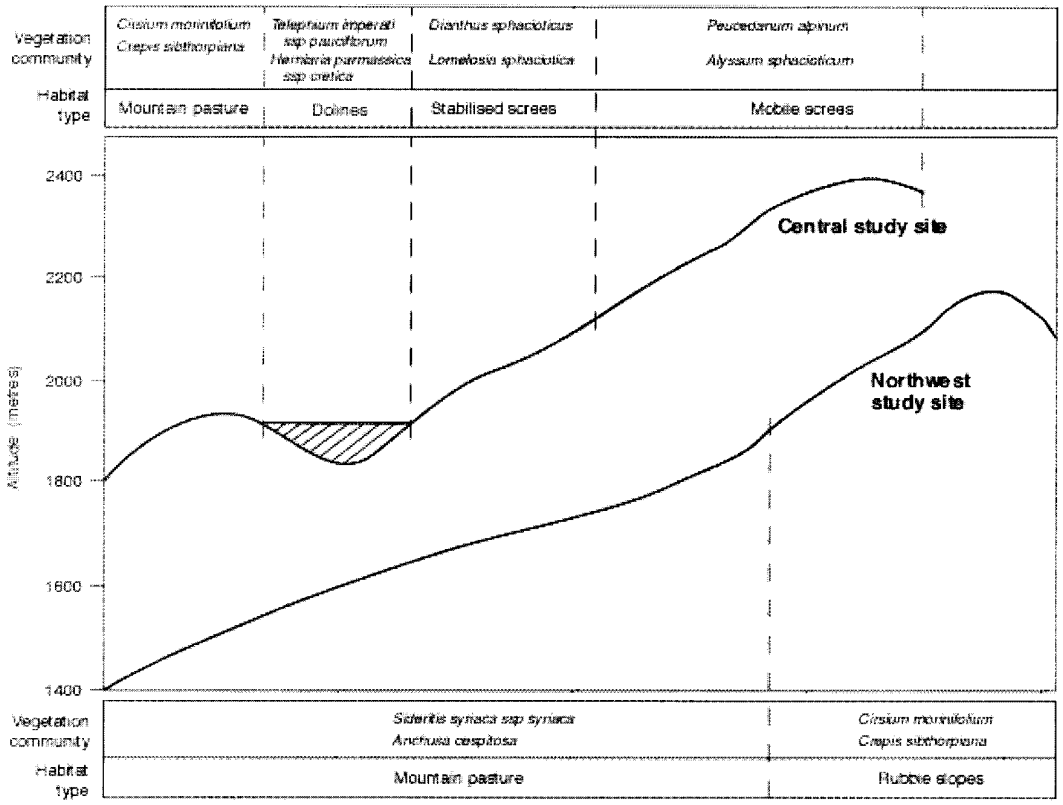

Figure 2. Schematic sections of the two study sites showing the variation in vegetation and habitat types with altitude

1. *Sideritis syriaca* L. subsp. *syriaca* - *Anchusa cespitosa* Lam. community. This community is probably the most common one in Lefka Ori above the treeline. It mainly occupies rocky mountain pastures in the most arid zones of the massif. The 28 samples belonging to this community have a wide altitudinal range (1500-1900 m) and are characterised by the endemic species *Anchusa cespitosa* and *Sideritis syriaca* subsp. *syriaca*.

2. *Cirsium morinifolium* Boiss. & Heldr. - *Crepis sibthorpiana* Boiss. & Heldr. community. There were 27 samples identified within this community on mountain slopes characterised by the presence of the endemics *Cirsium morinifolium* and *Crepis sibthorpiana*. The vegetation comprises many spiny, prostrate, cushion-like plants adapted to harsh grazing conditions.

3. *Telephium imperati* L. subsp. *pauciflorum* (Greuter) Greuter & Burdet - *Herniaria parnassica* Heldr. & Sart. ex Boiss. subsp. *cretica* Choudri community. This distinct group of samples was found on dolines (karstic depressions) from 1800-2100 m. These were more vegetated in comparison to the rest of the sites from which samples were taken within the study area. *Telephium imperati* subsp. *pauciflorum*, *Herniaria parnassica* subsp. *cretica* and *Hypericum kelleri* Bald. are three of the endemic species found in this community.

4. *Peucedanum alpinum* (Sieber ex Schult.) B.L. Burdtt & P.H. Davis - *Alyssum sphacioticum* Boiss. & Heldr. community. This community comprises 20 sample plots on screes ranging from 2020-2400 m. The soil is thin or absent and highly alkaline, with only moderate organic matter content. The characteristic species of this community are, *Peucedanum alpinum, Cynoglossum sphacioticum* Boiss & Heldr., *Alyssum sphacioticum, and Silene variegata*, all of them endemic to Crete.

5. *Dianthus sphacioticus* - *Lomelosia sphaciotica* (Roem. & Schult.) Greuter & Burdet. community. Most of the 26 samples of this community were found on screes showing a preference for a N, NW aspect. Characteristic endemic species of the community are, *Dianthus sphacioticus* and *Lomelosia sphaciotica*.

Within these five communities 40 endemic species were recorded (Table 2).

The inclusion of Lefka Ori as a Natura 2000 site and the possible inclusion of the massif in the Samaria national park, will require the establishment of a management plan for the region to ensure that the most important botanic sites are adequately safeguarded. This will require maps showing the distribution of community types across Lefka Ori. At present there is insufficient knowledge of plant distribution to achieve this mapping from biological records. The long term objective of the project therefore is to develop a GIS-based system to predict distribution patterns by extrapolation following the establishment of a model relating plant distribution to environmental variables within the two selected study sites. In the following section the procedures for the development of the model are described, with an analysis of the critical environmental factors that determine plant distribution in this remote ecosystem.

Ordination

CCA was performed on the whole data set (all sample plots). The eigenvalues of the first two CCA axes for this set are 0.45 and 0.20 (Table 3). Table 3 also shows the canonical coefficients of all the environmental factors taken into account. Axis 1 is strongly correlated with altitude (r = 0.88), pH (r = 0.88) and percentage of ground cover (r = 0.76). Axis 2 is strongly correlated with organic matter (r = 0.66) and slope (r = - 0.55). These first two axes of CCA account for 14.5 percent of the total variance in the sample data. CCA axes were statistically tested with a Monte Carlo permutation test (99 permutations) and were proven to be significant (p = 0.01).

The samples-variables biplot (Figure 3) derived from 120 field samples, displays three distinct clusters:

1. Samples to the left of the biplot relate to rocky mountain slopes and are controlled by organic matter and bare rock;

2. Samples to the right of the biplot are strongly related to altitude, pH and percentage of bare ground cover. These correspond to samples on boulder fields and screes;

3. Dolines form their own cluster at the top of the plot.

These clusters thus relate to the three habitat types; mountain pasture, scree slopes and dolines.

Ordination of samples by habitat type

A separate ordination was performed for those samples falling in the two of the three clusters identified from the CCA of the whole dataset, to detect and interpret significant environmental variables operating within two of the habitat types. There was no separate ordination performed for the doline habitat group of samples because it only included one community: *Telephium imperati* subsp. *pauciflorum* - *Herniaria parnassica* subsp. *cretica*.

For mountain pasture the eigenvalues are 0.22 and 0.13 for axis 1 and 2 respectively. The variation in the species data explained by the first two axes is 18.5 percent. Axis 1 is highly correlated with altitude (r = - 0.85), soil depth (r = 0.54) and bare ground cover (r = - 0.49). Axis 2 is mainly influenced by bare rock cover (r = - 0.84), altitude (r = 0.51) and bare ground cover (r = - 0.54).

In Figure 4, there is a clear separation between the two communities characteristic of mountain pastures. On the top left side of the biplot samples belonging to the *Cirsium morinifolium* - *Crepis sibthorpiana* community are mainly found at higher altitudes with increased scree cover and shallow soils. The *Sideritis syriaca* subsp. *syriaca* - *Anchusa cespitosa* community by contrast, is found within the

Plant community	No. of species Recorded
Sideritis syriaca ssp. *syriaca* - *Anchusa cespitosa*	17
Cirsium morinifolium - *Crepis sibthorpiana*	15
Telephium imperati ssp. *pauciflorum* - *Herniaria parnassica* ssp. *cretica*	15
Peucedanum alpinum - *Alyssum sphacioticum*	11
Dianthus sphacioticus - *Lomelosia sphaciotica*	21

Table 2. Number of endemic species by community

	Complete data set		Mountain pasture		Scree slopes	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Eigenvalues	0.45	0.20	0.22	0.13	0.23	0.19
Coefficients of environmental variables						
Altitude	0.88	0.29	-0.85	0.50	-0.56	0.05
Slope	-0.09	-0.55	0.18	0.02	-0.25	0.28
Aspect	0.36	0.31	0.03	0.17	0.56	-0.01
Bare rock	-0.54	-0.44	0.11	-0.84	0.30	-0.27
Ground cover	0.76	-0.20	-0.49	0.54	-0.68	0.07
Soil Depth	-0.25	0.42	0.54	-0.11	0.40	-0.40
Organic Matter	0.43	0.66	0.10	-0.01	0.30	0.37
pH	0.88	0.42	-0.44	0.18	-0.35	-0.65

Table 3. Eigenvalues and canonical coefficients of the first two CCA axes for the three ordinations discussed

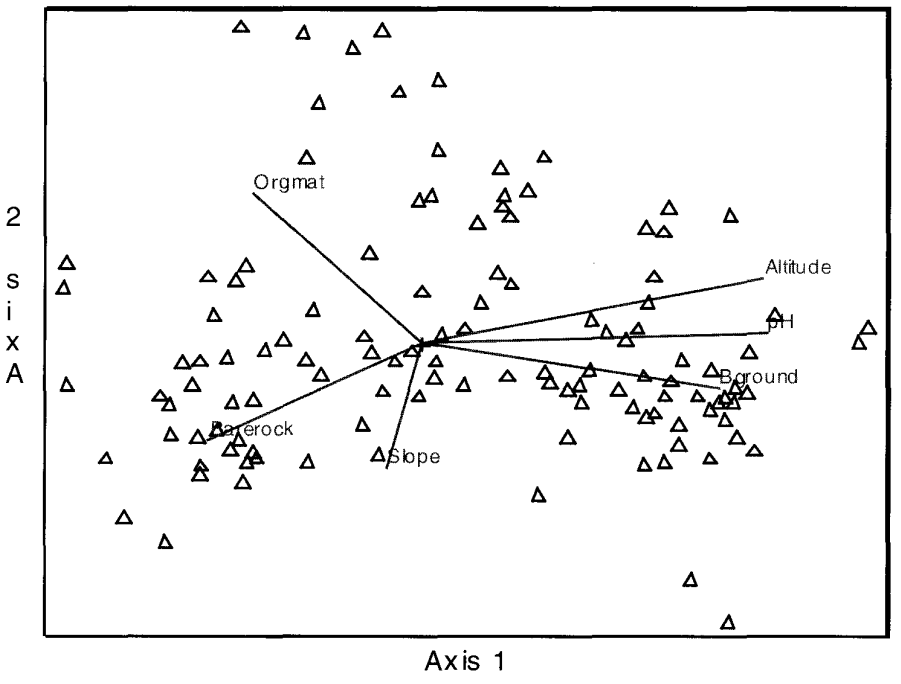

Figure 3. Ordination biplot for the complete dataset (a definition for each variable is also given)

Variable: Altitude - Aspect - Barerock (Bare rock) - Bground (Bare ground) - OM - PH - Sdepth - Slope

Definition: Elevation in metres - degrees off north - percentage of visible bedrock - percentage of unvegetated ground covered with - colluvial material - Organic matter - Soil depth in cm - Slope steepness

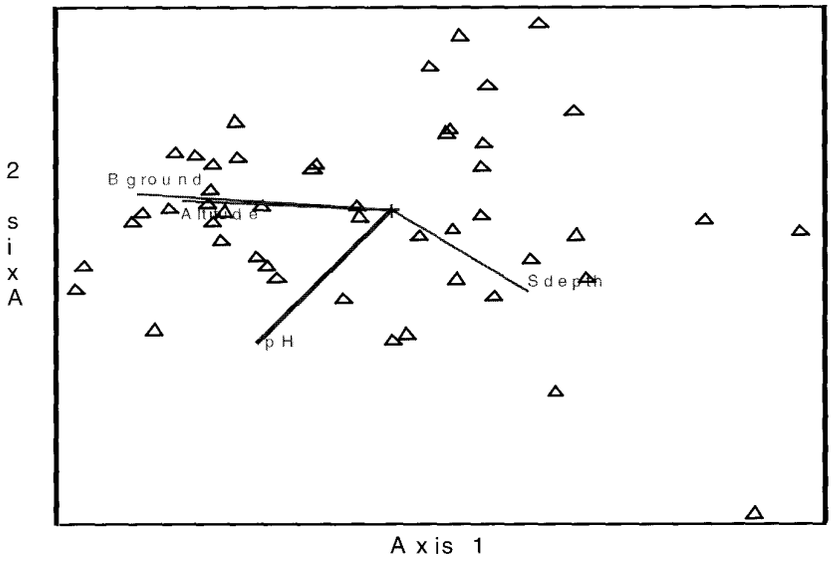

Figure 4. Ordination plot of samples on rocky mountain pastures.
Only the variables that have a correlation coefficient higher than 0.5 are shown

lower part of the biplot and corresponds to rocky pasture at lower altitude with better developed soils.

The ordination for those samples occurring within the scree slopes habitat type is presented in Figure 5. The variation in the species data explained by the first two axes is 14.8 percent. Axis 1 has an eigenvalue of 0.23 while Axis 2 has an eigenvalue of 0.2. Percentage of bare ground cover (r = - 0.68) and altitude (r = - 0.56) are the two variables that define the gradient on axis 1. pH (r = - 0.65) and soil depth (r = - 0.40) are the most significant variables for axis 2.

The community of *Peucedanum alpinum* - *Alyssum sphacioticum* forms a cluster to the left of the biplot (Figure 5) on scree-covered slopes at higher altitudes, while the *Dianthus sphacioticus* - *Lomelosia sphaciotica* community appears to be widely dispersed along both axes.

DISCUSSION

The purpose of this study was to determine which environmental factors explain the montane-mediterranean and oro-mediterranean community patterns in the Lefka Ori since there is a lack of quantitative analysis of vegetation-environment relationships. The data acquired on two intensive field seasons of vegetation sampling confirmed the richness of Lefka Ori as a location for Cretan endemic species.

Each of the five communities contains a considerable number of endemics, a proportion of which are unique to each community (Table 2).

Site 1 (Figure 1) is more vegetated than site 2 as it is confined to platey limestone that is more water retentive than crystalline limestone (Rackham & Moody, 1996). The first community *Sideritis syriaca* subsp. *syriaca* - *Anchusa cespitosa* is similar to *Anchuso-Picnomon acarnae* (including the sub-association *Galio–Taraxacum meghalorizon*) as described by Zaffran (1990). This community, which occurs across a wide range of altitude and aspect, dominates the most important summits of Lefka Ori providing moderate pasture for sheep. The second community *Cirsium morinifolium* - *Crepis sibthorpiana* mainly occurs above 1900m on the north west area of the massif, where scree formation is small scale compared to the rest of the massif. This community does not exhibit similarities with the associations identified by Zaffran (1990) who

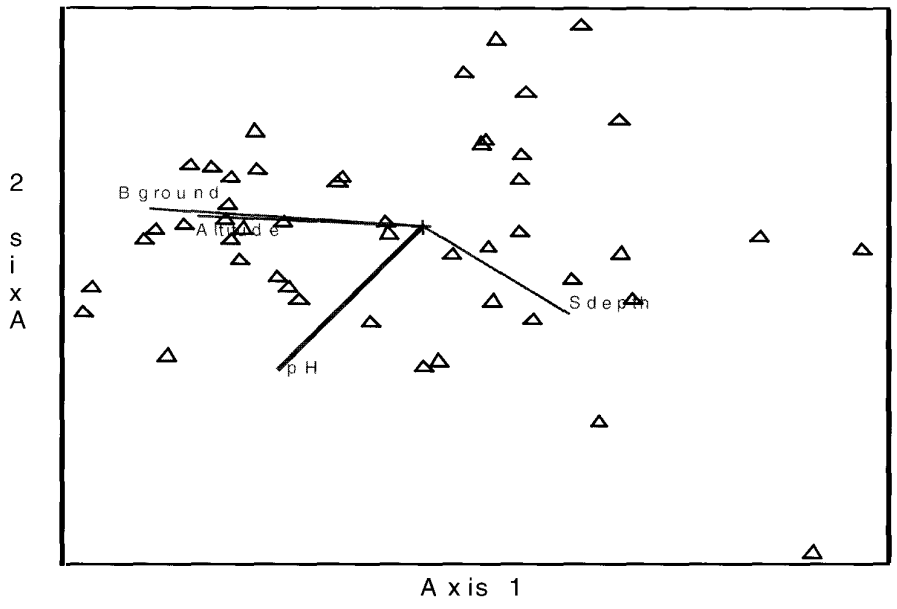

Figure 5. Ordination biplot of the group of samples on scree slopes.
Only the variables with a correlation coefficient more than 0.5 are presented.

recorded *Crepis sibthorpiana* forming an association with *Anthemis rigida.* Site 2 is more diverse floristically than site 1, due to its unique geomorphology. The scree slopes of the central Lefka Ori resulting from the break down of crystalline limestone cover most of the mountain summits above 1900 m and are relatively homogeneous in phytosociological terms. The *Peucedanum alpinum - Alyssum sphacioticum* community is found at higher altitudes on steep slopes, while *Dianthus sphacioticus - Lomelosia sphaciotica* community, exhibits a preference for gentler slopes and deeper soils. These communities correspond to the screes' associations described by Zaffran (1990); namely *Alysso-Silenetum variegatae* with the sub-association *Peucedanum - Cynoglossetum sphaciotici* and *Lomelosio - Centranthetum sieberi.*

Finally, on dolines, *Telephium imperati* subsp. *pauciflorum - Herniaria parnassica* subsp. *cretica* community was found, described by Zaffran (1990) as *Hyperico-Herniarietum parnassicae* association.

The vegetation community types classified by TWINSPAN were confirmed by the results from CCA. The CCA of all the field samples revealed the presence of two major gradients: altitude and pH along the first axis and organic matter and slope along the second axis.

The ordination performed on the samples cluster identified as the mountain pasture habitat, corresponded to an elevation and surface cover type gradient. Elevation affects the amount of precipitation, as well as temperature, while the nature of the soil surface is of utmost importance in arid environments for controlling moisture availability (Moustafa & Zaghloul, 1996). Of the two communities associated with this habitat *Cirsium morinifolium - Crepis sibthorpiana* shows a preference for higher altitudes and stony surfaces.

The ordination performed for the scree habitat samples revealed surface cover type and pH as dominant gradients. Again the nature of the soil surface is related to its water storage capacity while pH determines the nutrient availability. The *Peucedanum alpinum - Alyssum sphacioticum* community prefers loose screes on more alkaline soils than the *Dianthus sphacioticus - Lomelosia sphaciotica* community, more usually found on consolidated colluvial material.

Since only one community was associated with dolines the *Telephium imperati* subsp. *pauciflorum - Herniaria parnassica* subsp. *cretica* community, no separate ordination was performed. Dolines in the

Cretan mountains host a plant community of small prostrate herbs often with well-developed roots, with more perennials than annual plants. Egli (1991) distinguishes between wet and dry dolines in Crete pointing out that the common doline plants are found in both types.

Field observations, which were verified by the ordination procedure, demonstrated the importance of the various geomorphologic features within the area. Geomorphology is of fundamental importance as it is one of the driving forces of biological evolution and controls habitability (Drury, 1993). Screes, dolines and cliffs host their own vegetation communities that support significant numbers of endemic species.

Limestone is the dominant rock substrate in the mountains of southern and central Greece. The numerous regional and local endemics of Crete, Peloponissos and Sterea Ellas are generally found on this substrate (Strid, 1993). Lefka Ori is no exception as demonstrated by this study. Although dry rocky habitats on limestone host a lot of endemic species, scree slopes in particular have the highest concentration (Strid & Papanikolaou, 1985). According to Zaffran (1990) screes on Cretan mountains originate from the Tertiary and thus support a rich palaeo-endemic element. Dolines though, are relatively poor in endemic species compared to scree slopes and rocky mountain habitats.

CCA analysis explained relatively little of the total variance in the data. However this is typical of CCA analyses and can be attributed to high noise levels typical of species – abundance data (ter Braak after Richards *et al.*, 1995). Potentially a number of other variables of more importance e.g. climatic, were not included in the ordination and may contribute, to an unknown degree, to the variance. The lack of reliable rainfall and temperature data for the sub-alpine and alpine areas of Lefka Ori, precluded the inclusion of climatic data in the ordination. These areas though can be considered to be relatively uniform climatically with precipitation exceeding 1400 mm across the massif and a uniform temperature regime (Rackham & Moody, 1996).

It has also been difficult to quantify the impact of grazing on species diversity and abundance and their changes over time, especially in the context of rising livestock numbers encouraged by direct subsidies from the Common Agricultural Policy (CAP). The role of grazing has always been a controversial issue in community ecology. According to Phitos *et al.* (1996) grazing is the main threat for many of the rare plant species in Crete. However, Bergmeier (1998) contests this in a recent study on the phenology and grazing dynamics of vegetation in Lefka Ori. He suggests that fewer endemic species than assumed are actually threatened by grazing. In certain cases, for example dolines, grazing enables the survival of endemic plants since it results in the exclusion of plants with higher competitive ability (Egli, 1991).

The study has demonstrated the potential of ordination to detect the main environmental gradients that influence the distribution of plant communities identified by numerical classification. These two methods, whether used separately or in combination, have proven to be successful in mountain ecology throughout Europe. More specifically classification techniques have been used for defining land units in the Central Pyrenees using a range of measured landscape attributes (Del Barrio *et al.*, 1997), as well as identifying floristic resemblance within rock-cliff and scree vegetation communities in the Greek mountains (Dimopoulos *et al,* 1997). On the other hand multivariate techniques such as Canonical Correspondence Analysis (CCA) and Principal Component Analysis (PCA) have been employed for interpreting patterns in the Norwegian mountain flora (Birks, 1996) and alpine vegetation in the Lagorai range in Italy (Gerdol, 1990) respectively.

The ordination analysis conducted so far has generated basic hypotheses about the environmental controls which determine community distribution and endemic plant distribution patterns in Lefka Ori. This is the first step in the development of a procedure for predicting and mapping the distribution of vegetation communities across Lefka Ori.

Future work involves the mapping of these environmental variables within a GIS and the construction of a spatial model that will predict the vegetation composition across the landscape. This is now possible with GIS techniques that are increasingly being applied in conservation biology (Scott *et al.*, 1992; Kiester *et al.*, 1996).

The basic aim is to generate estimates at the regional level based on the appropriate extrapolation

of modelled results at the local level. Thus the use of a model developed at the field level is necessary in order to extrapolate across an entire region. This is now a critical issue given the proposal to include the Lefka Ori as part of the Samaria National Park and to designate the massif as a Natura 2000 site.

GIS will allow the testing of conservation options and scenarios based on the distribution maps that will enable the selection of sites for special protection. In particular, sites which are vulnerable to disturbance (e.g. from planned or existing roads, tourist development) or sites that are specially small or isolated, would be candidates for enhanced protection.

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Mediterranean phytoclimates in Turkey

Phytoclimats méditerranéens en Turquie

Javier María GARCIA LOPEZ

Dr. Ingeniero de Montes, Unidad de Ordenación y Mejora del Medio Natural, Servicio Territorial de Medio Ambiente, Junta de Castilla y León C/ Juan de Padilla s/n 09002-Burgos, Spain;
email: javier-maria.garcia@bu.jcyl.es

ABSTRACT

The aim of this study is to define a numeric/taxonomic model for Turkish phytoclimates based upon 375 meteorological stations belonging to the official Turkish network and a computer simulation process specially developed for this study. 10 phytoclimatic subtypes with Mediterranean, nemoro-Mediterranean or boreo-Mediterranean contents have been established, each with its factorial ambits of existence, abbreviated coordinates for phytoclimatic diagnosis of its stations, a qualitative phytoclimatic key, individual maps of geographic distribution of subtypes, and a computerised non-discrete general phytoclimatic model for Turkey in *"continuum"* conditions. We must underligne the originality on a world scale of Mediterranean phytoclimates in a transitional position tending to steppe conditions.

Key-words: Phytoclimatology, Mediterranean, Turkey, steppe

RESUMEN

Se establece un modelo numérico-taxonómico de los fitoclimas turcos mediante la consideración de 375 estaciones termopluviométricas de la red oficial y de un proceso de simulación informática especialmente desarrollado para este estudio. Se establecen así para Turquía 10 subtipos fitoclimáticos con contenido fitológico mediterráneo, nemoromediterráneo o boreomediterráneo, sus respectivos ámbitos factoriales de existencia, coordenadas abreviadas de diagnosis fitoclimática de sus estaciones, una clave fitoclimática cualitativa, mapas individuales de distribución geográfica de subtipos, y la materialización e informatización para Turquía del modelo fitoclimático general en condiciones de "*continuum*". Se hace especial hincapié en la originalidad a nivel mundial de los fitoclimas mediterráneos transicionales hacia condiciones estépicas.

Palabras clave : Fitoclimatología, Mediterráneo, Turquía, estépico

RESUME

Cette étude a pour objectif de mettre en place un modèle numérique et taxonomique pour les phytoclimats de Turquie. Elle se base sur l'examen de 375 stations météorologiques appartenant au réseau officiel de la Turquie et sur une simulation informatique développée dans le cadre de ce travail. 10 sous-types phytoclimatiques méditerranéens, némoro-méditerranéens ou boréo-méditerranéens ont été mis en évidence. Chacun a été caractérisé par : les conditions climatiques limites, une diagnose phytoclimatique de ses stations, une clé phytoclimatique qualitative, une carte individuelle de distribution géographique ; enfin, un modèle informatique phytoclimatique général non-discret a été dressé pour l'ensemble de la Turquie en conditions de « *continuum* ». Il faut souligner l'originalité, à un niveau mondial, de ces phytoclimats méditerranéens, en situation de transition par rapport à des conditions climatiques steppiques.

Mots-clés : phytoclimatologie, Méditerranée, Turquie, steppes

INTRODUCTION

In phytoclimatic terms, the geographical situation of the Anatolian peninsula as a Mediterranean appendix, or outpost, of the central Asian land mass is favourable to the entry of decidedly continental regimes. Moreover, it is open to steppe conditions unknown in the western Mediterranean, where continental characteristics are severely limited owing to the region's marginal position vis-à-vis the great Euro-Asiatic continental masses. Thus, Turkey is included in the Mediterranean (IV), nemoral (VI), steppe (VII), boreal (VIII) and arcticoid X(IX) phytoclimatic regions of Walter & Lieth (1960) and presents a wealth of intermediate transitional phases. Particularly interesting are the transitions between Mediterranean and steppe phytoclimates, which are highly original on a world scale.

The geographic area covered is roughly as given below (García-López, 1991) and excludes eastern Thrace, a very small part of the country situated in Europe on the west bank of the Bosphorus:

- A vast central area, the Anatolian Plateau. This is an ancient base covered in argillaceous sediments and volcanic formations, which gradually rises from west to east.
- A mountain chain to the north, the Pontic range. This borders the Black Sea from the Bosphorus to Georgia, where it links up with the Caucasus.
- A mountain chain to the south, the Taurus massif. This borders the Mediterranean littoral and links up with Kurdistan by way of the Antitaurus, a great crystalline mass rising apart to the south east, and with the Syrian and Lebanese coastal ranges by way of the Amanus massif.
- A group of high plateaux at over 2000 m and mountain ranges of over 3000 m, lying to the east of the central Anatolian plateau.

Geobotanic synthesis may be summarised as follows :

The north-facing slopes of the Pontic ranges contain coastal formations of *Carpinus betulus* L., *Quercus iberica* Steven ex Bieb. and *Castanea sativa* Mill., with lauroid elements in the easterly third of the massif (regions of Ordu, Trabzon, Giresun and Rize), beech-woods of *Fagus orientalis* Lipski. at higher altitudes, and conifer forests, principally of *Abies bornmuelleriana* Mattf., *Abies nordmanniana* (Siev.) Mattf. and *Picea orientalis* (L.) Link., crowned by Alpine pastures On the southern slopes, influenced by the Anatolian steppe, are mixed pre-Pontic oak woods of more xeric tendency, consisting chiefly of *Quercus dshorochensis* C. Koch., *Quercus syspirensis* C. Koch. and *Carpinus orientalis* Miller, with stands of *Pinus sylvestris* L. at the coldest locations.

The southern slopes of the Taurus range present typically Mediterranean littoral garrigue proper to *Oleo sylvestris-Ceratonion siliquae* Br.-Bl. *ex* Guinochet & Drouineau 1944 *em.* Rivas-Martínez 1975, with stands of *Pinus brutia* Ten., and kermes oak *Quercus calliprinos* P.B. Webb., giving way at high altitude to scanty marcescent formations of *Ostrya carpinifolia* Scop. and *Quercus pseudocerris*, stands of *Pinus pallasiana* Lamb., and at more humid locations cedar *Cedrus libani* A. Rich. or fir *Abies cilicica* Carr. At high altitude these formations give way to light savin *Juniperus excelsa* Bieb., cushioned alpinoid scrub and cryoxeric pasture. The northern slopes, influenced by the central Anatolian steppe, present largely xeric formations based on conifers like *Pinus pallasiana* and *Juniperus excelsa*.

The central Anatolian plateau is now covered to a large extent by crops and cushioned scrub belonging to several taxa of the *Astragalus* and *Artemisia* genera. Contact with the forested areas of the north (Pontus) and south (Taurus) runs through a marcescent fringe of *Quercus anatolica* O. Schwarz. The heights in central Anatolia reproduce the southern or northern transitional cliseries, on a smaller scale with formations of *Pinus pallasiana* (south) or *Pinus sylvestris* (north).

As far as the increasing cold permits, the eastwardly increasing altitude in Anatolia and the increasing humidity result in mosaics of marcescent formations, basically *Quercus brantii* Lindl., which give way further eastwards to high steppes about which little is yet known.

In the southern half of the Aegean side, with a typically Mediterranean climate and shielded from influences from the steppe, is the largest area of sclerophylls in Turkey, consisting chiefly of *Quercus calliprinos*, while the more humid northern half is host to marcescent formations of *Quercus cerris* L. and *Quercus frainetto* Ten., with massifs crowned by stands of *Pinus pallasiana*.

However, there are still very few studies available on diagnostic aspects of Turkish phytoclimates. Most of the authors who have studied Turkish phytoclimates have worked with the indices of Emberger, De Martonne and Thornwaite. The most important phytoclimatic studies are those of Tschermak (1949), Erinç (1950, 1969), Güman (1957), Akman (1962), Baldy (1960), Erinç (1969), Akman & Daget (1971), Charre (1972), Nahal (1972) and Akman (1982).

Some studies have recently been undertaken using the phytoclimatic systems of Allué-Andrade (1990-1997), for diagnosis and establishment of phytoclimatic homologues with Spain, for Turkish formations of *Cedrus libani* (García-López *et al.*, 1990, 1997) and *Pinus brutia* (García-López *et al.*, 1993). These include specific phytoclimatic positions like that of *Abies bornmuelleriana* (García-López, 1999a), a preliminary phytoclimatic classification of Turkey as a whole (García López, 1997), and a global phytoclimatology, addressing diagnosis, homologues, dynamics and vocation (García-López, 1999b).

The present study establishes the numeric taxonomy of mediterranean phytoclimates for the whole of Turkey, using the numeric diagnostic model of Allué-Andrade (1990-1997).

For the purposes of this study, a Mediterranean phytoclimate is defined as one having a hibernal or equinoctial rainfall regime (i.e., with maximum in winter and minimum in summer or with 2 equinoctial maxima and 2 summer and winter minima, the latter normally in the lee of large massifs), cool to subtropical temperatures (i.e., a minimum monthly mean temperature between 0 and 11°C) and semi-arid to arid humidity (from 2.5 to 10 months of aridity in the sense of Gaussen), preferentially coinciding with sclerophyll vegetable strategies. Most of the genuine Mediterranean phytoclimates are however hibernal, cool and semi-arid.

The study also deals tangentially with phytoclimates that are not genuinely Mediterranean but whose phytological content exhibits a strong Mediterranean tendency, such as nemoro-Mediterranean and boreo-Mediterranean phytoclimates.

MATERIAL AND METHODS

The basic meteorological data used were taken from the compilation of the Turkish Meteorological Service published in 1974 (D.M.I.G.M., 1974), which comprises 375 meteorological stations with data from 1929 to 1970. These stations cover the entire country more or less homogeneously and constitute the entire official meteorological network (Figure 1). This compilation was chosen rather than other more modern ones because it contains compendia from before the 1970s, during which decade the western Mediterranean appears to have undergone some thermoxeric climatic changes.

The principal global geobotanic studies on which this work is based are essentially those of Dönmez (1969) for eastern Thrace, Akman *et al.* (1978) for southern Anatolia, Quézel & Pamukcuoglu (1970) for the mountain areas of north-west Anatolia, Quézel (1973) for the upper ranges of the Taurus mountains, Quézel & Pamukcuoglu (1973) for the tree formations in the Taurus massif, Quézel *et al.* (1980) for northern Anatolia, and the work of Atalay (1994) for the country as a whole. In addition, valuable information was gained from the study of Turkish forests by Mayer & Aksoy (1986) and the notes appended to the vegetation maps of Quézel & Barbero (1985) and Noirfalise (1987). The information on the eastern and south-eastern regions of Turkey came from a variety of fragmentary secondary sources which are not cited here but can be found in the references chapter.

There is still very little cartographic data, and what there is does not always suit our purposes. The 1:2,500,000 forestry map of Gokmen (1962) was inadequate because he presented maps of forest vegetation of the time without serial phytological interpretation and hence contained little geobotanic synthesis. The first set of synthetic maps attributing final serial phytologies were those of Quézel & Barbero (1985); these were set in a broader area focussing on the eastern Mediterranean, on a scale of 1:2,500,000, but they did not include Turkish regions east of Erzincan. The cartography that was finally taken as basis was Noirfalise (1987). This includes a compilation of existing maps and therefore takes into account all those of Quézel & Barbero (1985), plus the eastern parts of the country not mapped by the latters.

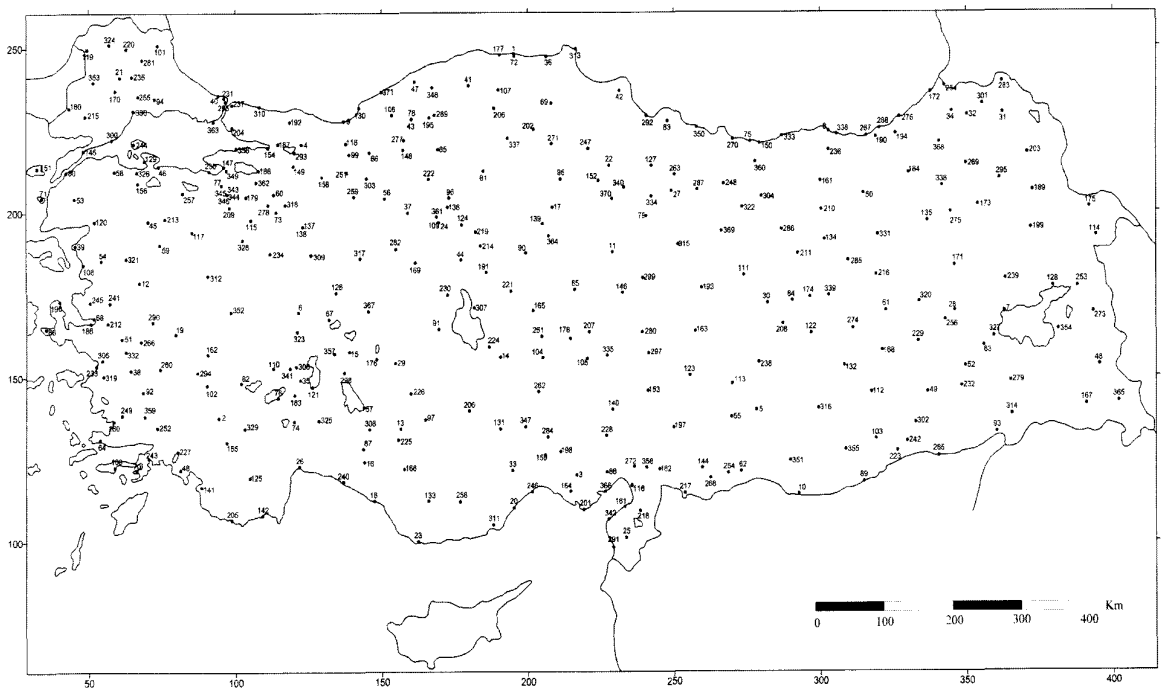

Figure 1. Location of the meteorological stations in Turkey used in this work

The shortcomings of the existing phytological data meant that these had to be partially checked by field surveys. The laboratory work and written data were verified and supplemented by 4 journeys to Turkey. There, with the assistance of Forestry Service personnel where possible, 8000 km of road and forest track were covered by vehicle and the principal formations of interest were visited on foot. Routes were planned so as to cover the maximum possible number of localities with meteorological stations.

Phytoclimatic methods

The numeric phytoclimatic diagnosis models of Allué-Andrade (1990-1997) were used. A summary of these models follows of certain aspects which are particularly helpful for a clear understanding of the study, leaving aside formal and more or less mathematical aspects which are less helpful in this way.

The concept underlying the system is phytoclimatology as a discipline whose purpose is to relate the limited variety of meteorological courses of a place (climate) to the phytological aspects that these elicit (phytologies). This approach is chiefly motivated by the fact that phytologically causal climatic information is not available, since neither the conventional meteorological data nor a Euclidean treatment of these is sufficient. However, correlation offers a possible alternative; in other words, although the causal data are not available, the data that are available may correlate with these to some extent, and hence their effects may also correlate. These correlations will emerge in a given minimum number of years, which in any case will be equal to or greater than the time required for typological stabilisation of mean and extreme values.

A n-dimensional factorial space can be devised whose axes are the n phytoclimatic factors F_i chosen as presumably more closely related than others to the direct causal data that are lacking.

In this space we can establish a number m of more or less mutually exclusive ambits (A_j) which are limited by the extreme values of the factors, each ambit corresponding to the m different vegetable types or strategies (phytologies) that are possible within the applicable scope of the model – for example, sicci-desert, durilignous, duriaestilignous, aestilignous, aciculilignous, frigori-desert etc.).

Points in this climatic factorial space can be structured with respect to each ambit by attribution of certain standardised geometric discriminating magnitudes (scalars) which express the degree to which these points fit the ambit. These scalars simultaneously evaluate two aspects of this structuring of factorial space: its position (or proximity to the ambits) and the characterising power of its climatic values with respect to all the ambits. The scalar is not therefore a classic measure of distance in multi-dimensional space but a dual measure of proximity/potentiality with respect to all the strategies of each station, and hence between them.

Thus, any of these precincts or ambits organises the points in the factorial space into different zones of fitness. For instance, "*Genuine*" (G) refers to points inside an ambit, "*Analogous*" (A) to points outside but proximate to the ambit, and "*Disparate*" (D) to points outside and distant from the ambit.

The quotient of the scalar of any situation with respect to a given type of vegetable life and the maximum possible scalar with respect to this type (standard scalar) not only provides an objective idea of the efficiency of the situation but also permits comparison of the efficiencies of any other situations with respect to that type.

All the standard scalars of a point with respect to the various phytoclimatic ambits together constitute the "*phytoclimatic coordinates*" of that point. The standard scalars estimate, point by point, its per cent "*distance*" from the phytological optimum of each type of life. By comparing all these distances with one another, it produces a nuanced and highly synthetic comparative (polythetic) vocational diagnosis. For example, to say that a climatic situation is proper to *Quercus pubescens* – i.e., aestidurilignous – is a loose, monethetic statement. It may be sufficient, but if we also say that it is proximate to climactic *Pinus sylvestris* – i.e., aciculilignous – and distant from *Quercus ilex* – i.e., durilignous – and we further quantify these "*phytological distances*" by means of scalars, then we increase the probabilities of qualitative accuracy by the relative corroboration of the positions, and we increase the probabilities of precision by qualification of the diagnosis thanks to the elements of analagousness and disparity.

These final diagnoses can therefore help overcome a number of initial difficulties : unlike classical climatic treatments, the proposed scalar space, which replaces the classic factorial space, is Euclidean and hence offers a specifically phytological rather than parametric scale of measurement, which would otherwise be unattainable.

As a direct application of the comparative polythetic character of the proposed phytoclimatic model and an alternative means of synthetic expression of the phytoclimate rather than expressing all its "*phytoclimatic coordinates*", we can calculate a "*phytoclimatic tern*" which expresses the most important aspects of the set of coordinates in abbreviated form. The terns used for abbreviated phytoclimatic diagnosis have the form (G; A1; A2; A3; D1; D2), where G is the number of the genuine phytoclimatic subtype, A1, A2 and A3 are analogous subtypes in descending order of (scalar) proximity and D1 and D2 are the numbers of the most proximate disparate phytoclimatic subtypes (larger scalars). The numbers of the subtypes are shown in table 1.

In the case of Turkey the basic phytological attributes adopted were the broad physiognomic types of Brockmann-Jerosch & Rübel (1912) and the macrotypes of Walter & Lieth (1960) because they are simple while retaining strong transcendent significance. The available typological units were organised in such a way as to attain the maximum possible ecological significance in terms of broad physiognomic strategies of vegetable life.

Details of these Mediterranean phytoclimatic significances are given in table 1. Also included are the broad physiognomic types of Brockmann-Jerosch & Rübel, the phytoclimatic types of Walter & Lieth, and the phytoclimatic subtypes proposed by us for each category (name, phytoclimatic and typological symbol and indicative floristic synthesis).

The factors used are shown in table 2. These were calculated from the Walter-Lieth climodiagrams using the relevant module of the "Climoal" computer programme developed by Manrique *et al.* (1995).

VEGETATION		PHYTOCLIMATIC SUBTYPE			FLORA	
PHYSIOGNOMY	**TYPE**	**NAME**	**SYMBOL**	**No.**	**SYMBOL**	**INDICATIVE SYNTHESIS**
DURILIGNEOUS	MEDITERRANEAN Sclerophyll broadleaf IV	XERO-MEDITERRANEAN	IV(III)	1	M1	Steppoid degradation with *Pistacia atlantica* and *Amygdalus orientalis* in the Mesopotamian zone
		THERMO-MEDITERRANEAN	IV[2]	4	M3	*Oleo-Ceratonion* in the Aegean and Mediterranean littoral
		EURI-MEDITERRANEAN	IV[3]	3	M2	Steppoid degradation with *Pistacia atlantica* and *Amygdalus orientalis*, upper Mesopotamia
		EU-MEDITERRANEAN	IV[4]	5	M4	Holm-oak stands : *Quercus ilex* and *Quercus calliprinos*
		SUBSTEPPE-MEDITERRANEAN	IV(VII)	2	M5	Steppoid degradation with *Pyrus eleagnifolia* and *Quercus anatolica*, central Anatolia
AESTILIGNEOUS	NEMOROID Cold-deciduous broadleaf VI	NEMORO-MEDITERRANEAN	VI(IV)[1]	6	NM1	*Quercus frainetto* oak woods in the north-east
		NEMORO-MEDITERRANEAN	VI(IV)[2]	7	NM2	Formations of *Ostrya carpinifolia* and *Carpinus orientalis*, Taurus
		ATTENUATED NEMORO-MEDITERRANEAN	VI(IV)[3]	8	NM3	Mixed stands of *Quercus dschorochensis* with *Carpinus orientalis* and *Carpinus betulus* sub-Pontic
		NEMORO-LAUROID	VI(V)	12	NL	Mixed stands of *Quercus iberica* with *Castanea sativa* and *Fagus orientalis*, Black Sea littoral
		NEMORAL	VI	13	N	Beech woods of *Fagus orientalis*, with *Picea orientalis* and *Pinus sylvestris*, Black Sea
		NEMORO-STEPPE	VI(VII)[1]	9	NE1	Treed steppe with *Q. brantii* in eastern Anatolia
		NEMORO-STEPPOID	VI(VII)[2]	10	NE2	Treed steppe with *Q. anatolica* Anatolian perimeter
		NEMOROID	VI(VII)[3]	11	NE3	Pre-steppe mixed oak and beech woods, sub-Pontic
ACICULILIGNEOUS	BOREALOID Needle leaf VIII	BOREO-MEDITERRANEAN	VIII(IV)[1]	15	BM1	Pine woods of *Pinus pallasiana*
		BOREO-MEDITERRANEAN	VIII(IV)[2]	14	BM2	Cedar-fir woods of *Cedrus libani* and *Abies cilicica*, Taurus
		BOREO-STEPPE	VIII(VII)[1]	18	BE1	Pre-steppe savin, *Juniperus excelsa*
		ATTENUATED BOREO-STEPPE	VIII(VII)[2]	17	BE2	Clear pre-steppe pine woods of *Pinus sylvestris*
		BOREO-STEPPOID	VIII(VII)[3]	16	BE3	Pine woods of *Pinus sylvestris*, sub-Pontic
		BOREALOID	VIII	19	B	Woods of *Picea orientalis* and *Pinus sylvestris*, Black Sea
FRIGORI-DESERT	STEPPE Sub-arboreous VII	ORO-STEPPE	VII[1]	23	E1	Sub-alpine steppe, eastern Anatolia
		SUPRA-STEPPE	VII[2]	22	E2	Mountain steppe with *Artemisia*, eastern Anatolia
		INFRA-STEPPE	VII[3]	21	E4	Lower steppes with *Astragalus*
		MESO-STEPPE	VII[4]	20	E3	Tall graminacious steppe in the north-east
	ARCTICOID Alpinoid X(IX)	ALPINE	X(IX)[1]	25	A1	Meadows of *Alchemilla* and *Campanula*
		ALPINOID	X(IX)[2]	24	A2	Meadows of *Trifolio-Polygonion*, Taurus and Kurdistan

Table 1. Phytoclimatic meanings in Turkey

ABBREVIATION	FACTOR	UNIT
K	Intensity of aridity (As/Ah, where Ah is the humid area of the climodiagram (Pi curve above the Ti curve, i.e., 2Ti<Pi) and As is the dry area of the climodiagram (Pi curve below the Ti curve, i.e. 2Ti>Pi)) (ALLUE-ANDRADE,1990)	
A	Duration of aridity, in the sense of GAUSSEN (No. of months in which curve Ti is situated above the Pi curve, i.e., when 2Ti>Pi.)	months
P	Total annual precipitation	mm.
PE	Minimum summer precipitation (June, July, August or September)	mm.
TMF	Lowest monthly mean temperature	°C
T	Annual mean temperature	°C
TMC	Highest monthly mean temperature	°C
TMMF	Average of the minimum temperatures in the month with the lowest mean temperature	°C
TMMC	Average of the maximum temperatures in the month with the highest mean temperature	°C
HS	Freezing certain (No. of months in which TMMF <=0)	months
HP	Freezing probable (No. of months in which F<=0 and TMMF >0	months
OSC	Thermal oscillation (TMC-TMF)	°C

Table 2. Phytoclimatic factors used

N°	Subtype	K	A	P	PE	T	TMF	TMC	TMMF	TMMC	HS	OSC	HP
3	IV^3	0.998	6.13	1289	3	19.2	7.0	33.4	3.7	41.2	3	31.4	7
		0.202	3.53	345	0	10.1	0.0	25.1	-3.6	32.0	0	25.0	2
1	IV(III)	1.678	6.82	426	1	18.1	6.6	32.3	3.2	41.1	0	26.3	7
		1.001	5.34	328	0	16.9	4.3	29.7	0.8	36.1	0	25.0	5
4	IV^2	0.929	6.69	1380	25	20.2	12.7	30.2	9.9	36.3	1	21.0	6
		0.087	2.67	441	0	13.9	9.0	23.9	4.0	28.9	0	13.2	0
5	IV^4	1.057	6.81	1516	17	18.9	8.9	30.5	6.1	36.9	1	24.9	9
		0.200	2.56	334	0	8.1	3.0	19.5	-0.7	24.9	0	15.9	2
2	IV(VII)	0.999	6.18	1350	27	14.5	2.9	27.1	-0.2	34.4	5	24.9	8
		0.200	2.51	233	0	8.5	0.0	17.0	-4.8	23.0	1	16.0	2
6	VI(IV)^1	0.199	4.79	799	33	14.9	7.1	25.1	4.0	31.3	4	23.5	8
		0.032	2.50	401	0	8.2	0.0	17.2	-4.4	22.9	0	14.7	4
7	VI(IV)^2	0.199	4.50	1507	25	17.3	8.9	27.9	5.7	34.0	4	24.4	7
		0.028	2.50	800	0	9.3	0.0	18.4	-3.7	25.9	0	16.1	0
10	VIII(IV)^2	0.340	4.78	1489	12	12.6	-0.1	25.6	-3.1	32.0	6	24.9	7
		0.065	2.50	800	0	5.8	-4.9	17.7	-9.0	23.6	2	18.4	3
9	VIII(IV)^1	0.380	4.50	798	21	10.1	-3.1	21.9	-6.9	29.3	6	24.9	7
		0.068	2.50	500	0	5.7	-5.0	16.0	-11.4	23.0	3	19.4	3
8	VI(IV)^3	0.213	2.49	1218	42	16.3	8.4	24.7	5.1	30.8	3	21.8	9
		0.001	1.00	430	0	7.3	2.0	16.0	-1.7	20.8	0	12.3	4

Table 3. Phytoclimatic ambits in Turkey

RESULTS

Phytoclimatic ambits

Ambits of existence of factorial values were calculated for each phytoclimatic subtype. The upper and lower limits of the ambits were calculated simultaneously with the specific and real data from the 375 meteorological stations considered and with estimated data from the 115,138 interpolated points by "kriging" from the digitisation of isolines of monthly temperature and precipitation (García-López, 1999b). Table 3 shows the results of the calculation of phytoclimatic ambits. Tangential relationships between ambits are highlighted by thicker lines.

Qualitative phytoclimatic key

Where it is not necessary to determine all the values of phytological attributes but only the category of genuineness, calculation can be dispensed with and a simple qualitative key will suffice. The tangential relationships established for the phytoclimatic ambits served to devise a simple qualitative yes/no key for separation of phytoclimatic subtypes using a small number of factors (TMC, OSC, TMF, A, HS, K and PE).(Table 4). Figure 2 shows the geographic distribution of all the mediterranean phytoclimates in Turkey, and figure 3 indicates their detailed distribution by subtypes

Terns of phytoclimatic coordinates

The multifactorial phytoclimatic model served to calculate the terns of phytoclimatic diagnosis (G; A1; A2; A3; D1; D2) of the Turkish stations used, where G is the number of the genuine phytoclimatic subtype, A1, A2 and A3 are the analogous subtypes in descending order of proximity (scalars) and D1 and D2 are the numbers of the closest disparate subtypes (larger scalars), following the methodology of Allué-Andrade (1990). The subtype numbers are those given in table 1. These were calculated using the relevant module of the "Climotur" computer programme developed by Manrique (1998). The results are shown in annex 1.

Annex 1 groups phytoclimatic diagnoses by strictly homologous sets. There are several possible levels of homologousness between any two stations depending on the degree of similarity between their phytoclimatic coordinates. Obviously, the maximum level of homologousness is where the values of the two phytoclimatic coordinates coincide completely.

However, at a more practical level, the terns (G;A1;A2;A3;D1;D2) for abbreviated determination can be used on their own to define strict homologousness where the subtypes in the five given categories (G, A1, A2, A3, D1 and D2) coincide. It is also possible to define less strict levels of homologousness by ignoring the disparate subtypes and their order or some other such criterion.

This definition of phytoclimatically homogeneous areas can be extremely useful for defining regions of origin of genetic material and for defining protocols for the importation and exportation of vegetable material.

DISCUSSION

Mediterranean phytoclimates or phytoclimates tending towards Mediterranean are to be found in eastern Thrace, except for some parts in north-eastern Thrace, and in the Aegean and Mediterranean littoral of Anatolia (Figures 1 & 2). Moving inland, the transition from steppe or nemoro-steppe areas produces highly original Mediterranean phytoclimates.

One such case is the substeppe-Mediterranean phytoclimate IV(VII), which is found in large areas of the western-central Anatolian plateau and extends in a SW-NE direction as far as the mouths of the rivers Kizilirmak and Yesilirmak on the Black Sea. This last is due to an altitudinal breach in the coastal ranges and a consequent partial reduction of their shield effect, as a result of which steppe conditions occur in the lee of the highest mountains. This phytoclimate lacks the large temperature fluctuations typical of steppe and nemoro-steppe subtypes in eastern Anatolia, but there is a degree of proximity to these in that mean winter temperatures are low although not sub-zero. This is a highly original phytoclimate on a world scale, whose closest homologues are perhaps to be found in areas of northern Oregon in the USA leeward of the Cascade Mountains (García-López, 1999b).

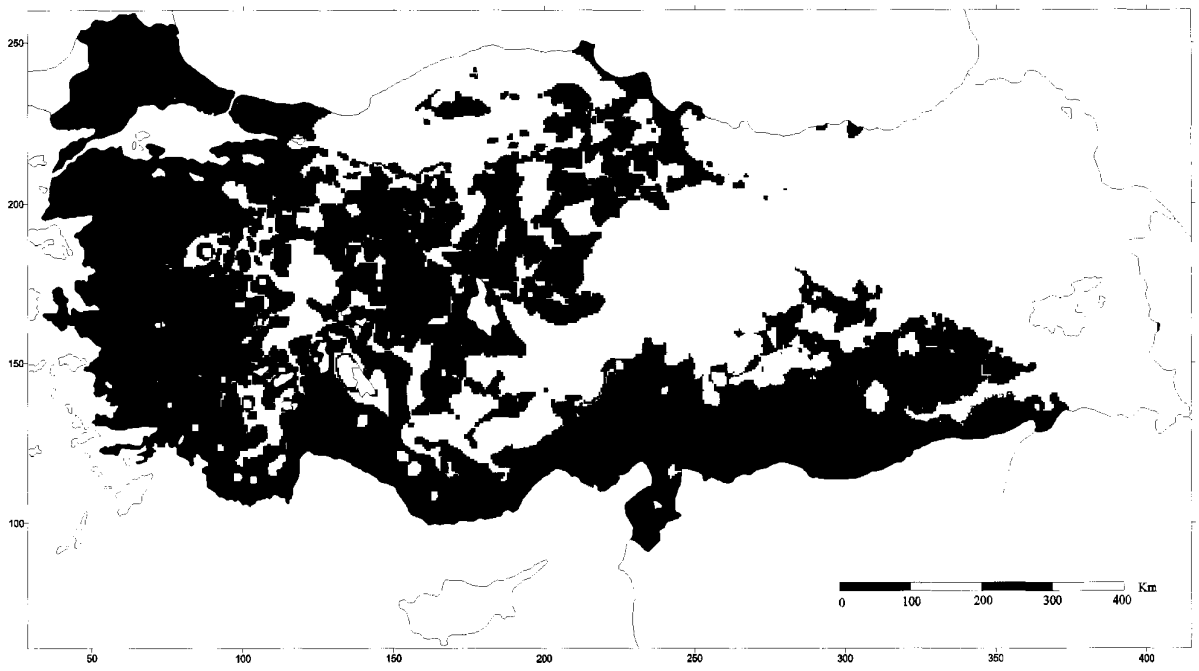

Figure 2. Mediterranean phytoclimates and phytoclimates of Mediterranean tendency in Turkey

QUALITATIVE PHYTOCLIMATIC KEY								No.	SUBTYPE
TMC<13 Arcticoid	A ≥ 1.5 Aesti-xeric							24	X(IX)[2]
	A < 1.5 Aesti-axeric							25	X(IX)[1]
TMC ≥ 13 Non Arcticoid	A ≥ 2.5 Thermo-xeric	OSC ≥ 25 Euritherm (highly continental)	TMF<0 Cold	TMF<-16				23	VII[1]
				TMF ≥ -16	TMF<-7			22	VII[2]
					TMF ≥ -7			9	VI(VII)[1]
			TMF ≥ 0 Cool	K<1				3	IV[3]
				K ≥ 1				1	IV(III)
		OSC<25 Stenotherm (scarcely continental)	TMF ≥ 0 Nor cold	TMF ≥ 9 Subtropical				4	IV[2]
				TMF<9 Cool	K ≥ 0,200 Drier	TMF•3		5	IV[4]
						TMF<3		2	IV(VII)
					K<0,200 Less dry	P<800		6	VI(IV)[1]
						P≥800		7	VI(IV)[2]
			TMF<0 Cold	TMF ≥ -5	P ≥ 800			14	VIII(IV)[3]
					P<800	TMF ≥-3		10	VI(VII)[2]
						TMF< -3	P<500	21	VII[3]
							P ≥500	15	VIII(IV)[4]
				TMF<-5				18	VIII(VII)[1]
	A<2.5 Thermo-xeric	HS ≥ 5 Borealoid	A<1 Genuine	P ≥ 700 Pontic (maritime)				19	VIII
				P<700 NE Sub-pontic (continental)				17	VIII(VII)[2]
			A ≥ 1 Transitional		TMF ≥-7			16	VIII(VII)[3]
					TMF<-7			20	VII[4]
		HS<5 Non Borealoid	A<1 Genuine (Pontic)		TMF ≥ 3 Littoral			12	VI(V)
					TMF<3 Sub-littoral			13	VI
			A ≥ 1 Transitional (Sub-pontic)		TMF ≥ 2			8	VI(IV)[3]
					TMF<2			11	VI(VII)[3]

Table 4. Qualitative phytoclimatic key for Turkey

SURFACE AREAS OCCUPIED BY TURKISH PHYTOCLIMATIC SUBTYPES							
VEGETATION		PHYTOCLIMATIC SUBTYPE		AREAS			
PHYSIOGNOMY	TYPE	NAME	SYMBOL	%	Km²	%	Km²
DURILIGNOUS	MEDITERRANEAN IV	XERO-MEDITERRANEAN	IV(III)	0,73	5,687	37.50	292,125
		THERMO-MEDITERRANEAN	IV²	3.10	24,149		
		EURI-MEDITERRANEAN	IV³	5.47	42,611		
		EU-MEDITERRANEAN	IV⁴	11.74	91,455		
		SUBSTEPPE-MEDITERRANEAN	IV(VII)	16.46	128,223		
AESTILIGNOUS	NEMOROID VI	NEMORO-MEDITERRANEAN	VI(IV)¹	5.75	44,792	34.23	266,651
		NEMORO-MEDITERRANEAN	VI(IV)²	1.17	9,114		
		ATTENUATED NEMORO-MEDITERRANEAN	VI(IV)³	2.09	16,281		
		NEMORO-LAUROID	VI(V)	2.19	17,060		
		NEMORAL	VI	2.34	18,229		
		NEMORO-STEPPE	VI(VII)¹	5.97	46,506		
		NEMORO-STEPPOID	VI(VII)²	11.64	90,676		
		NEMOROID	VI(VII)³	3.08	23,993		
ACICULILIGNOUS	BOREALOID VIII	BOREO-MEDITERRANEAN	VIII(IV)¹	2.14	16,671	8.56	66,683
		BOREO-MEDITERRANEAN	VIII(IV)²	2.04	15,892		
		BOREO-STEPPE	VIII(VII)¹	1.72	13,399		
		ATTENUATED BOREO-STEPPE	VIII(VII)²	1.36	10,594		
		BOREO-STEPPE	VIII(VII)³	0.66	5,141		
		BOREALOID	VIII	0.64	4,986		
FRIGORIDESERT	STEPPE VII	ORO-STEPPE	VII¹	0.28	2,181	14.32	111,552
		SUPRA-STEPPE	VII²	5.65	44,013		
		INFRA-STEPPE	VII³	6.61	51,492		
		MESO-STEPPE	VII⁴	1.78	13,866		
	ARCTICOID X(IX)	ALPINE	X(IX)¹	2.41	18,775	5.39	41,989
		ALPINOID	X(IX)²	2.98	23,214		

Table 5. Areas occupied by Turkish phytoclimates

The second instance of penetration of Mediterranean phytoclimates in the continental interior is east of the Gulf of Iskenderun as far as 42° E, close to the Iraqui border. Phytoclimate IV³ is strongly transitional towards the more northerly nemoro-steppe phytoclimates of *Quercus brantii*; southwards, increasing xerothermicity produces a transition towards Syrian semi-desert types by way of phytoclimate IV(III). Both Mediterranean phytoclimates present clear features of transition towards other more definitely steppe types. In common with the latter they exhibit very pronounced continental temperature fluctuation, but mean monthly temperatures are always above zero. These are without doubt the most original of the Turkish phytoclimates on a world scale.

The dry boreo-Mediterranean phytoclimates VIII(IV)¹, largely characterised by *Pinus pallasiana*, are located in the high Mediterranean and Aegean massifs, with a fringe on the leeward side of these forming a discontinuous band around the central Anatolian plateau, except at the eastern end, which is open to steppe influences. Moist boreo-Mediterranean phytoclimates VIII(IV)² are found mainly windward of the Taurus mountains, which attract the moist winds from the Mediterranean. The main final species are *Cedrus libani*, *Abies cilicica* or a mixture of the two.

The less xerothermic nemoro-Mediterranean phytoclimates VI(IV)³ are located preferentially in northern sub-Pontic regions, while the more xerothermic types occur in north-west Anatolia and Thrace. This applies to type VI(IV)¹, largely typified by *Quercus frainetto*, and in some areas leeward of the Taurus mountains, for example VI(IV)². In this last case the high aridity, which is in principle not favourable to marcescent formations, can generate such vegetation locally – although never in abundance – as a consequence of azonalities produced by phreatic compensation in thalwegs or the feet of rocky precipices.

The intra-Pontic Mediterranean enclaves occurring in the shelter of massifs are particularly interesting. These include the middle valley of the river Kelkit (Erbaa, Niksar, Resadiye etc.) where there are eu-Mediterranean phytoclimates IV⁴, nemoro-Mediterranean phytoclimates on the Black Sea littoral,

for instance between Sinop and Samsun, and the Trabzon area.

Table 5 includes the surface areas of each of the phytoclimatic subtypes identified in Turkey. Indeed, approximately half of the territory corresponds to Mediterranean phytoclimates in the broad sense (50.68%). 37.5% corresponds to typically Mediterranean climates with minimum rainfall in summer, more than 2.5 months of aridity and mean monthly temperatures above zero. The rest comprises phytoclimates which are not strictly Mediterranean but exhibit a pronounced Mediterranean influence, such as nemoro-Mediterranean (9%) and boreo-Mediterranean (4.18%).

As much as 44% of the total area of strict Mediterranean phytoclimates (128,223 km^2 out of 292,125 km^2) is substeppe-Mediterranean type IV(VII). This is in fact the largest of all single Turkish subtypes, accounting for 16% of the country.

CONCLUSION

This study presents a number of new contributions to the field of Turkish Mediterranean phytoclimates. As far as methodology is concerned, the Allué-Andrade models make it possible to go beyond the strictly qualitative characterization of the various different Turkish phytoclimatic subtypes undertaken by Tschermak (1949), Erinç (1950, 1969), Güman (1957), Akman (1962, 1982), Baldy (1969), Erinç (1969), Akman & Daget (1971), Charre (1972) or Nahal (1972), and to quantify them on a numeric basis.

The use of estimated factorial data for 115,138 points interpolated from digitized temperature isolines and monthly precipitations constitutes a decisive step in obviating the chronic shortage of meteorological stations in Turkey, which is possibly the most serious limiting factor on any phytoclimatic study to date.

For numeric quantification, it is necessary not only to establish phytoclimatic ambits for each subtype, but also to use a comparative diagnosis in a scalar phytoclimatic space instead of a classic diagnosis of a factorial space like the one used hitherto in such studies (Emberger space or others). In this way it is possible to define nuanced diagnostic terns, which contribute decisively to the detailed characterization of these phytoclimates and the transitions among them.

From a practical point of view, the efficiency of the defined subtypes is more than acceptable in terms of their ability to predict phytologies in zonal conditions: Over 80% of the stations diagnosed as IV^1 (Mediterranean) correspond to Mi (sclerophyll) phytologies. Over 75% of the stations diagnosed as $VI(IV)^1$ (nemoro-Mediterranean) correspond to NMi (marcescent) phytologies; and over 80% of those diagnosed as IV(VII) (substeppe-Mediterranean) correspond to the difficult Central Anatolian phytological complex NE2+E4+M5.

The combination of numeric quantification of Turkish phytoclimates with interpolation as a means of extending the diagnosis to all of Turkey defines criteria for the comparison of diagnostic terns, thus opening up important avenues for future research in the field of phytoclimatic homologation among Mediterranean countries. The ultimate goal of all this is the interchange of vegetable material, techniques and knowledge, a field in which Spain and Turkey have been advancing in recent years (García-López, 2000a & 2000b).

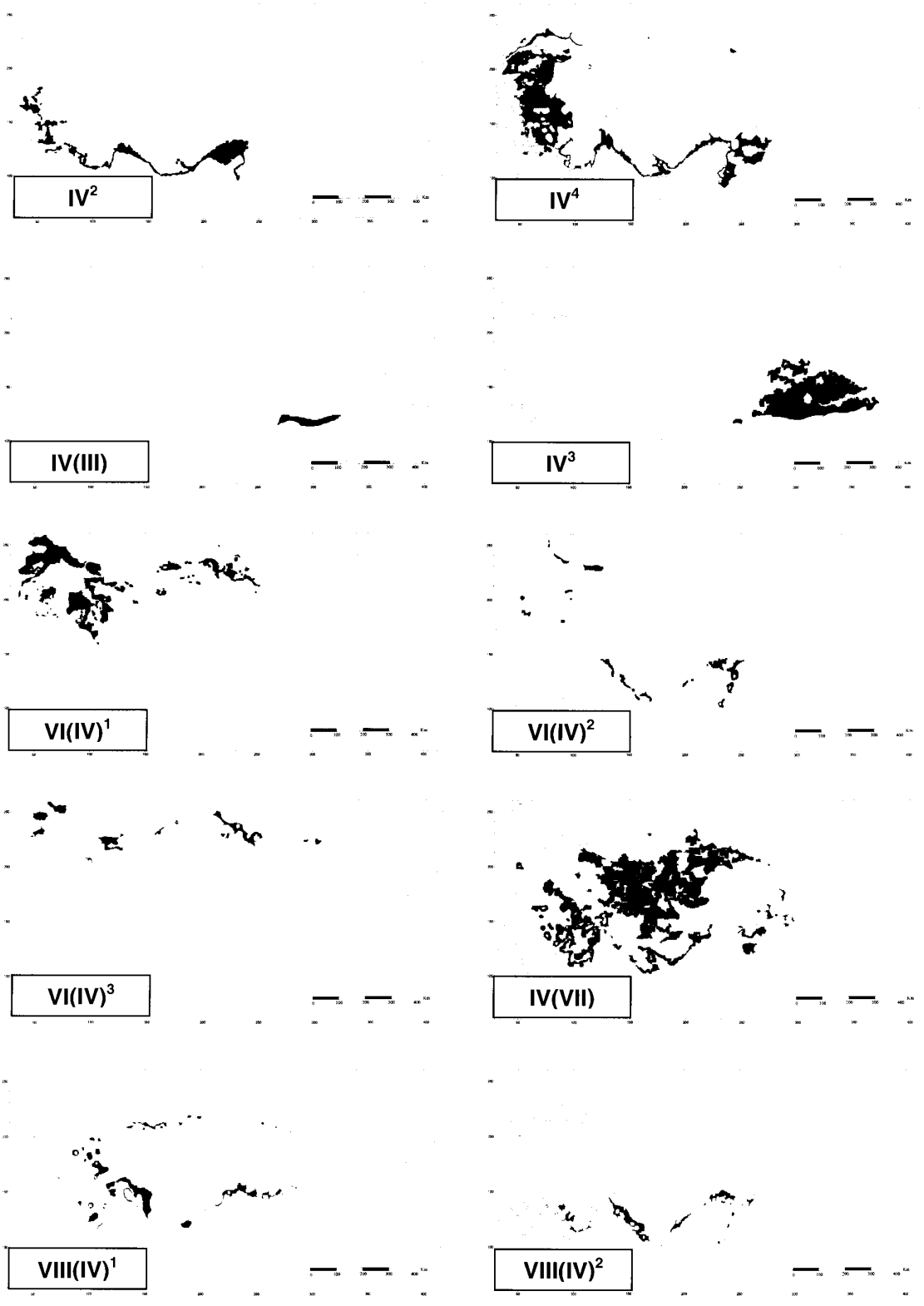

Figure 3. Geographic distribution of mediterranean phytoclimates and phytoclimates of mediterranean tendency in Turkey (IV^{2}: Thermomediterranean; IV^{4}: Eu-mediterraean; IV(III): Xero-mediterranean; IV^{3}: Euri-mediterranean; $VI(IV)^{1}$: Nemoro-mediterranean; IV(VII): Subesteppe-mediterranean; $VIII(IV)^{1}$: Boreo-mediterranean.

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ANNEX I. Values of phytoclimatic factors of stations and phytoclimatic diagnosis organised in strictly homologous groups.

STATION	N°	K	A	P	PE	HS	TMF	T	TMC	TMMF	F	TMMC	C	HP	OSC	PHYTOCLIMATE
BIRECIK	62	1,182	6,63	368	0,5	0	5,3	17,8	31	1,5	-10,3	39,5	45,2	6	25,7	(1; -, -, -; 3, 5)
AKCAKALE	10	1,678	6,82	331,1	0	0	6	18,1	31,3	2,2	-8	39,3	45,2	7	25,3	(1; -, -, -; 5, 4)
ACIPAYAN	2	0,361	4,76	532,8	2,6	2	2,2	12,7	23,8	-1,7	-16,6	31,5	37,5	5	21,6	(2; -, -, -; 3, 5)
ATABEY	35	0,305	4,5	563,3	3,4	2	2	12,5	23,5	-0,8	-12,5	29,4	35,4	5	21,5	(2; -, -, -; 3, 5)
BURDUR	76	0,491	4,43	436,8	5,9	2	2,5	13,2	24,3	-0,8	-16,7	31,9	39,6	5	21,8	(2; -, -, -; 3, 5)
ELMALI	125	0,39	4,86	542,4	4	2	2,5	13,1	24,2	-1,7	-16,5	31	40	5	21,7	(2; -, -, -; 3, 5)
SEREFLIKOCHISAR	307	0,708	5,24	348,7	2,7	2	2	12,9	23,9	-0,5	-13,2	29,6	36,4	6	21,9	(2; -, -, -; 3, 5)
BEYPAZARI	56	0,624	5,28	390,1	7,7	2	1,8	13,2	24,2	-1	-13	30,5	37,8	5	22,4	(2; -, -, -; 5, 3)
DINAR	110	0,345	3,97	486,6	7,8	2	2,7	12,8	23,4	-1,1	-16,6	30,6	37	5	20,7	(2; -, -, -; 5, 3)
GOKHOYUK	152	0,73	5,11	366,9	6,2	2	2,8	13,6	23,7	-2,4	-23,4	31,1	44,2	5	20,9	(2; -, -, -; 5, 3)
USAK	352	0,288	4,16	540,6	8,4	2	2	12,3	23,6	-1,6	-24	30,6	39,8	7	21,6	(2; -, -, -; 5, 7)
BOYABAT	69	0,445	4,31	388,7	16,9	2	2,4	13,4	23,4	-1,1	-10,5	30,5	41	5	21	(2; -, -, -; 5, 9)
NALLIHAN	259	0,439	4,73	428,5	9	2	2,1	12,5	23,4	-0,8	-16	30,7	38	5	21,3	(2; -, -, -; 5, 9)
OSMANCIK	271	0,496	4,05	416,2	11,9	2	2,4	13,6	24,3	-0,8	-12,4	31	40,4	6	21,9	(2; -, -, -; 5, 9)
ARDANUC	32	0,241	3,27	446,3	27,3	3	1,9	13	23,3	-2	-19,5	30,1	41	4	21,4	(2; -, -, -; 6, 7)
GOLHISAR	155	0,246	4,06	634,7	2,5	2	2,4	12,6	23,4	-1,4	-14,2	30,6	36,5	5	21	(2; -, -, -; 6, 7)
ILGIN	176	0,281	3,31	451,2	8,2	3	1,6	11,4	21,4	-2	-22	28,4	34,6	4	19,8	(2; -, -, -; 6, 7)
TAVSANLI	328	0,259	3,89	487,1	5	2	1,1	11,4	20,9	-2,7	-19,7	29,3	36,5	7	19,8	(2; -, -, -; 6, 7)
TOSYA	337	0,248	3,96	462,9	16,5	2	0,8	11,7	21,9	-1,7	-13,5	28	38	5	21,1	(2; -, -, -; 6, 7)
YALVAK	357	0,247	3,61	523	6,6	2	0,6	11,5	22,8	-2,3	-21	28,9	34,6	5	22,2	(2; -, -, -; 6, 9)
CAMLIBEL	79	0,282	3,65	385,2	4,1	4	1	9,2	18,1	-2,2	-25,8	25,4	35,5	5	17,1	(2; -, -, -; 6,10)
AYAS	37	0,298	4,21	454,8	5,3	2	1	11,7	22,2	-1,8	-17,5	29	37	5	21,2	(2; -, -, -; 9, 3)
BOLVADIN	67	0,376	3,74	388,9	4,8	3	1,6	11,3	21,6	-1,8	-17,6	28,6	35	4	20	(2; -, -, -; 9, 3)
CICEKDAGI	90	0,739	5,2	322,1	3,9	3	1,3	12,2	23,6	-3,3	-26,5	31	41,3	5	22,3	(2; -, -, -; 9, 3)
EMIRDAG	126	0,449	4,52	396,6	5,8	2	1,4	12,2	22,6	-2,1	-15,5	30,5	38,5	5	21,2	(2; -, -, -; 9, 3)
INCESU	178	0,529	4,01	369,7	4	3	1,1	11,8	22,6	-2,5	-18,5	29,5	37	4	21,5	(2; -, -, -; 9, 3)
KESKIN	214	0,414	4,55	383,4	6,5	3	1,1	11	21,8	-1,8	-17	27,6	34,5	4	20,7	(2; -, -, -; 9, 3)
KIRIKKALE	219	0,812	5,25	328,6	6,1	2	1,2	12,6	23,9	-2,4	-21,1	30,1	39	5	22,7	(2; -, -, -; 9, 3)
KULU	230	0,454	4,56	361,1	6	4	1,4	10,8	21,6	-1,4	-13,3	29,8	37,1	4	20,2	(2; -, -, -; 9, 3)
POLATLI	282	0,629	4,78	346,7	3,8	2	0,9	11,9	22,8	-2	-15,4	29,8	36,8	5	21,9	(2; -, -, -; 9, 3)
YENIMAHALLE	361	0,443	4,35	418	7,1	2	1,3	12,2	22,9	-1,8	-17	30,4	38	5	21,6	(2; -, -, -; 9, 5)
YUNAK	367	0,326	3,89	451,8	6	2	1	11,3	22	-1,5	-16,4	27,8	34,5	5	21	(2; -, -, -; 9, 5)
ZILE	370	0,338	4,05	456,1	7,5	2	1,2	11,8	21,6	-2,6	-17,6	28,6	41,3	6	20,4	(2; -, -, -; 9, 5)
SEBEN	303	0,304	4,15	471,2	10,1	3	1,4	11,6	21,5	-1,4	-19,2	29,9	37,3	4	20,1	(2; -, -, -; 9, 7)
AKOREN	13	0,393	4,18	448,2	1	3	0,9	11,6	22,8	-3	-23	30	37	5	21,9	(2; -, -, -; 9,10)
AKSARAY	14	0,61	4,51	356,6	2,8	2	0,8	11,8	22,7	-3,3	-21,9	30,2	37,4	6	21,9	(2; -, -, -; 9,10)
ALTINOVA	29	0,598	4,22	349,8	2,4	4	1	11,9	22,7	-3,5	-21,5	29,7	39	3	21,7	(2; -, -, -; 9,10)
KOCAS	224	0,832	4,96	318,8	1,7	4	0,7	12,2	23,6	-4,6	-27	30,8	39	5	22,9	(2; -, -, -; 9,10)
MERZIFON	247	0,444	4,03	378,7	10,6	3	1,3	11,7	21,4	-2,2	-20,5	28,4	41,9	6	20,1	(2; -, -, -; 9,10)
SUHSERI	322	0,312	3,93	419,9	5	3	1,2	11,1	20,7	-1,8	-13,2	27,2	36	4	19,5	(2; -, -, -; 9,10)
TEFENNI	329	0,309	4,39	507,4	4,6	3	0,8	11,6	22,7	-3,7	-19,2	30,2	36	5	21,9	(2; -, -, -; 9,10)
ALACA	17	0,426	3,91	379	4,4	5	0,6	10,8	20,8	-3,9	-23,6	27,4	37,5	3	20,2	(2; -, -, -;10, 9)
BEYSEHIR	57	0,338	4,38	477,4	3,8	4	0,5	11,3	22,1	-3,6	-22,9	29,2	36,6	5	21,6	(2; -, -, -;10, 9)
EREGLI (KONYA)	131	0,694	4,87	298,8	4,3	3	1,1	11,1	21,2	-3,6	-22,4	29,9	37	6	20,1	(2; -, -, -;10, 9)
SIRNAK	314	0,305	4,52	857,2	1,4	2	2,6	13,8	26,9	-0,5	-14,5	32,2	37,9	4	24,3	(2; 3, -, -; 5, 7)
GAZIANTEP	144	0,482	5,16	558,8	1,7	2	2,6	14,5	27,1	-1	-17,5	34,4	42,8	5	24,5	(2; 3, -, -; 5, 9)
POZANTI	284	0,247	3,76	703	5	1	2,8	13,6	25,2	-0,2	-12,9	31,8	38	6	22,4	(2; 5, -, -; 7, 6)
BILECIK	60	0,34	3,89	436,2	10,4	1	2,5	12,3	21,7	-0,4	-16	28	40,6	6	19,2	(2; 5, -, -; 9, 7)
TOKAT	334	0,343	3,78	455,3	10,7	1	2,7	12,7	22	-0,9	-19,3	29,4	40	6	19,3	(2; 5, -, -; 9, 7)

STATION	N°	K	A	P	PE	HS	TMF	T	TMC	TMMF	F	TMMC	C	HP	OSC	PHYTOCLIMATE
SAFRANBOLU	289	0,361	3,71	431	15,4	1	2,9	12,9	22,8	-0,2	-12,4	30,9	42	5	19,9	(2; 5, -, -; 9, 8)
INEGOL	179	0,21	3,56	543	11	2	2,5	12,7	22,1	-1,8	-22,7	29,2	40	5	19,6	(2; 6, -, -; 7, 5)
ISPARTA	183	0,208	3,72	619,4	10,3	2	1,8	12,2	23,2	-1,6	-17,8	30,4	37,5	5	21,4	(2; 6, -, -; 7, 5)
DURSUNBEY	117	0,212	3,67	617,3	4,4	1	2,5	12,5	21,6	-0,5	-15,4	29,5	37,7	5	19,1	(2; 6, 5, -; 7, 8)
SULOGLU	324	0,215	3,97	529,9	13,5	1	1,8	12,7	22,8	-1,6	-13,2	29,9	37,5	5	21	(2; 6, 5, -; 7, 9)
SEYDISEHIR	308	0,213	4,2	771,5	3	3	0,9	11,6	22,5	-2,2	-18,6	29,8	35,9	5	21,6	(2; 6, 7, -;14, 9)
BALA	44	0,517	4,49	404,4	1,3	2	0,5	12,5	24,4	-2,1	-14	30,4	38	4	23,9	(2; 9, 3, -;10, 5)
ANKARA	24	0,539	4,58	367	8,5	4	0,3	11,8	23,3	-3,5	-24,9	30,3	40	5	23	(2;10, -, -; 9, 3)
CIHANBEYLI	91	0,733	4,81	292,9	3	3	0,4	10,9	22,4	-3,2	-21,6	29,1	37,4	5	22	(2;10, -, -; 9, 3)
ESKISEHIR TOP.SU	138	0,414	4,17	377,8	4,7	4	0,1	10,9	21,4	-4,1	-22,2	29,1	39,7	5	21,3	(2;10, -, -; 9, 3)
KIRSEHIR	221	0,511	4,36	378,6	4,1	4	0,1	11,4	22,9	-4,2	-28	29,4	39,4	5	22,8	(2;10, -, -; 9, 3)
KONUKLAR	225	0,427	3,54	373,5	2,7	4	0,1	10,9	21,9	-4,8	-24,2	29,6	37,5	5	21,8	(2;10, -, -; 9, 3)
NEVSEHIR	261	0,424	4,23	388,6	1,4	2	0,3	10,9	21,1	-3	-23,6	27,7	37,6	7	20,8	(2;10, -, -; 9, 3)
SEYITGAZI	309	0,401	4,35	364,8	5	3	0,4	10,6	20,5	-2,6	-16,4	28	35,5	4	20,1	(2;10, -, -; 9, 3)
SIVRIHISAR	317	0,421	4,36	393,2	3,8	2	0,3	11,4	22,1	-2,7	-18	28,7	38,5	5	21,8	(2;10, -, -; 9, 3)
SUHUT	323	0,811	4,99	301,3	0,6	4	0,2	11,4	21,6	-3,6	-21,4	27,4	35,6	4	21,4	(2;10, -, -; 9, 3)
AFYON	6	0,256	3,51	455,4	8,4	4	0,3	11,2	22,1	-3,8	-27,2	29,7	37,8	5	21,8	(2;10, -, -; 9, 6)
CANKIRI	81	0,43	4,31	397,2	12,4	4	0,2	11,5	23,3	-3,5	-25	30,5	41,8	4	23,1	(2;10, -, -; 9,14)
KAMAN	191	0,35	4,24	455,3	4,4	2	0	10,9	21,2	-2,6	-14,5	27,1	35,6	4	21,2	(2;10, -, -; 9,14)
SARKI KARAAGAC	298	0,328	3,97	445,1	5,5	3	0,1	11,1	22,2	-4	-18,9	29,3	38,8	4	22,1	(2;10, -, -; 9,14)
MARDIN	242	0,432	4,94	713,2	0,4	0	2,7	15,8	29,6	0,2	-13,9	34,3	42	7	26,9	(3; -, -, -; 5, 2)
SAVUR	302	0,619	4,79	507,5	0,8	0	3	15,8	29,8	0,1	-12,7	36,1	42	6	26,8	(3; -, -, -; 5, 2)
CIZRE	93	0,575	5,33	712,2	0	0	6,4	19,1	33,4	2,9	-8,4	41,2	46,4	5	27	(3; -, -, -; 5, 4)
NUSAYBIN	265	0,985	5,81	461,8	0	0	6,6	19,2	32,7	3,7	-6	40,3	45,8	4	26,1	(3; -, -, -; 5, 4)
BATMAN	49	0,529	4,51	552,2	0,4	1	2,8	15,8	30,2	-1,2	-19,4	39	44,1	6	27,4	(3; -, -, -; 5, 9)
ERGANI	132	0,381	4,61	767,5	0,6	2	2,1	15,3	29,6	-0,4	-13,2	35,1	41,6	4	27,5	(3; -, -, -; 5, 9)
SIIRT	373	0,361	4,39	756,1	0,4	1	2,5	15,9	30,4	-0,9	-19,3	36,7	42,7	5	27,9	(3; -, -, -; 5, 9)
SIVEREK	316	0,582	5,08	545,7	0,6	1	2,9	16,3	30,4	-0,2	-14,3	36,6	42,4	5	27,5	(3; -, -, -; 5, 9)
KEBAN	208	0,529	4,36	493,7	2	2	1,6	14,7	28,6	-1,6	-17,2	35,7	41,4	5	27	(3; -, -, -; 9, 2)
DIYARBAKIR	112	0,649	5,01	495,8	0,6	3	1,8	15,9	31	-2,4	-24,2	38,2	46,2	4	29,2	(3; -, -, -; 9, 5)
HANI	168	0,286	4,15	1101,3	0	2	1,6	15,5	29,2	-1,1	-13,5	35	40	2	27,6	(3; -, -, -; 9, 5)
KURTALAN	232	0,413	4,76	680,2	0,1	2	1,5	15,7	31	-3,2	-18,5	38,5	43,5	5	29,5	(3; -, -, -; 9, 5)
CEMISKEZEK	84	0,326	4,3	664,6	1,5	3	0,9	13,7	26,7	-1,9	-12,3	34,2	39	4	25,8	(3; 2, 9, -; 7,10)
KIZILTEPE	223	0,888	5,53	467,3	0,4	0	5,7	18,2	31,8	2,5	-8,5	38,6	44	5	26,1	(3; 5, -, -; 1, 4)
NIZIP	264	0,844	6,13	464	0,3	0	5,2	17,4	30,2	2,9	-9	37,2	42,6	6	25	(3; 5, -, -; 1, 4)
URFA	351	0,876	5,99	473	0,4	0	5,1	18,1	31,7	1,4	-12,4	38,5	46,5	6	26,6	(3; 5, -, -; 1, 4)
OGUZELI	268	0,707	5,92	465,2	0,8	0	4,1	15,8	30	0,3	-12	36,6	41,8	7	25,9	(3; 5, -, -; 2, 1)
OSMANIYE	272	0,331	4,31	852,5	1,1	0	3,3	15,7	29,6	0,2	-13,4	35,4	41	6	26,3	(3; 5, -, -; 2, 7)
SIRVAN	374	0,331	4,31	852,5	1,1	0	3,3	15,7	29,6	0,2	13,4	35,4	41	6	26,3	(3; 5, -, -; 2, 7)
BESNI	55	0,423	5,06	784,5	1	0	2,5	15,4	28,3	0,5	-10	34	39,5	5	25,8	(3; 5, -, -; 2, 9)
VIRANSEHIR	355	0,642	5,41	566,3	0	0	5,6	17,8	30,9	2,5	-9,2	37,9	42,9	5	25,3	(3; 5, -, -; 4, 1)
BAYKAN	52	0,309	4,15	1053,3	0,5	0	3,5	16,2	30,2	0,6	-14,5	37,8	42,6	5	26,7	(3; 5, -, -; 9, 2)
ADIYAMAN	5	0,44	4,89	835,5	1	0	4,3	17	30,6	1,2	-9,4	37	42,6	6	26,3	(3; 5, -, -; 9, 4)
DERIK	103	0,436	4,77	774,2	0	0	4,4	16,9	30,4	1,5	-10,5	37	43,5	5	26	(3; 5, -, -; 9, 4)
PALU	274	0,383	4,33	585,6	2,6	2	0,4	13,9	27,4	-3,6	-21	35,2	40,7	5	27	(3; 9, -, -; 2, 5)
KULP	229	0,275	4	1159,7	0	2	1,2	15,1	29,7	-1,6	-13	36,9	43,9	4	28,5	(3; 9, -, -; 5, 2)
ALATA (ERDEMLI)	20	0,51	5,69	730,9	0,1	0	10,2	18,5	27,6	6,4	-3	31,8	38,8	3	17,4	(4; -, -, -; 5, 3)
ANAMUR	23	0,472	5,6	1032,5	0,4	0	11,7	19,5	28,4	8,4	-4,7	33,8	44,2	2	16,7	(4; -, -, -; 5, 3)
BODRUM	64	0,595	5,82	772,9	0,2	0	11,3	19	28	7,8	-4,1	33,8	43,6	5	16,7	(4; -, -, -; 5, 3)
BOZBURUN	70	0,502	5,38	929,5	0	0	11,4	19,1	27,5	8	-4,7	32,3	39,2	2	16,1	(4; -, -, -; 5, 3)
FETHIYE	141	0,444	5,45	993,4	1,8	0	10,6	18,8	27,9	6,3	-5,8	34,9	43,7	5	17,3	(4; -, -, -; 5, 3)
FINIKE	142	0,474	5,42	986,3	0,7	0	11,3	18,6	27,2	7,2	-1,6	33	40,2	2	15,9	(4; -, -, -; 5, 3)

STATION	N°	K	A	P	PE	HS	TMF	T	TMC	TMMF	F	TMMC	C	HP	OSC	PHYTOCLIMATE
GULLUK	160	0,586	5,73	706,2	0,4	0	10,5	18,1	26,5	7,1	-2,5	32,4	42	2	16	(4; -, -, -; 5, 3)
KAS	205	0,536	5,52	906,5	0	0	12,6	20	28,3	9,7	1,2	32,2	37,9	0	15,7	(4; -, -, -; 5, 3)
SILIKKE	311	0,672	6,23	636,4	1	0	10,3	19,1	28,1	6,8	-6,3	33,4	43	4	17,8	(4; -, -, -; 5, 3)
ALANYA	18	0,388	4,96	1102,6	0,6	0	11,6	18,8	27,1	7,7	-2,9	31,8	41,9	3	15,5	(4; -, -, -; 5, 7)
DALAMAN	98	0,354	4,71	1107,7	0,3	0	10,3	18,1	26,8	6,3	-3,4	33,6	44	4	16,5	(4; -, -, -; 5, 7)
DATCA	100	0,527	5,22	836,4	0	0	12,2	19,3	27,1	9,9	0,2	31,3	39,9	0	14,9	(4; -, -, -; 5, 7)
DORTYOL	116	0,087	2,67	1021,8	25,1	0	10,4	19,3	28,1	6,8	-6,3	32,2	43	5	17,7	(4; -, -, -; 5, 7)
ISKENDERUN	181	0,324	4,03	785,3	4	0	11,9	20,2	28,6	8,4	-3,2	31,8	43,2	2	16,7	(4; -, -, -; 5, 7)
MANAVGAT	240	0,348	4,84	1288,2	0,5	0	10,5	18,2	27,6	6,8	-2,1	32,4	42,8	2	17,1	(4; -, -, -; 5, 7)
MARMARIS	243	0,35	4,47	1257,2	1	0	10,6	18,6	27,7	6,3	-4	35,3	47	5	17,1	(4; -, -, -; 5, 7)
ULUCINAR	342	0,449	4,55	703,9	1,5	0	11,5	19,6	28	8,3	-3	32,6	39	2	16,5	(4; -, -, -; 5, 7)
YUMURTALIK	366	0,339	4,07	835,2	0,5	0	10,4	18,8	27,4	6,1	-3,1	30,8	37,8	3	17	(4; -, -, -; 5, 7)
ADANA	3	0,484	4,86	647	4,3	0	9,3	18,7	28,1	4,8	-8,4	34,8	45,6	5	18,8	(4; 5, -, -; 3, 7)
ANTALYA	26	0,423	5,16	1068,3	1,8	0	10,1	18,7	28,2	6,3	-4,6	33,5	44,6	5	18,1	(4; 5, -, -; 3, 7)
CESME	86	0,597	6,43	640,5	0	0	9,2	17,1	25,2	5,9	-3,4	29,7	37,1	3	16	(4; 5, -, -; 3, 7)
HACI-ALI	164	0,396	4,72	774,2	4	0	9	18,3	27,2	4	-10,2	33	40,8	5	18,2	(4; 5, -, -; 3, 7)
KARATAS	201	0,504	6,15	787	0,4	0	9,6	18,9	28	5,3	-6,8	31,3	39	4	18,4	(4; 5, -, -; 3, 7)
MERSIN	246	0,602	5,94	617,4	5	0	9,5	18,5	27,9	5,5	-6,6	30,9	40	5	18,4	(4; 5, -, -; 3, 7)
KOYCEGIZ	227	0,353	4,58	1151,2	3	0	9,5	18,3	27,8	5,4	-7	34,3	43	4	18,3	(4; 5, -, -; 7, 3)
KOZAN	228	0,215	3,65	855,1	9,9	0	9,9	19,3	29,1	6,8	-3	36,3	43,5	3	19,2	(4; 5, -, -; 7, 3)
SAMANDAG	291	0,256	3,92	1008,4	3,8	0	9,1	18,7	27,2	6,1	-2	30,8	39,8	2	18,1	(4; 5, -, -; 7, 3)
AMASYA	22	0,583	4,63	411,5	7,2	0	3,2	13,9	23,9	0,1	-11,8	30,7	43,2	7	20,7	(5; -, -, -; 2, 3)
CARDAK	82	0,503	4,2	443,8	2,3	0	3,2	13,5	24,3	0,2	-16,5	31,4	38,5	7	21,1	(5; -, -, -; 2, 3)
KARGI	202	1,057	5,03	334,7	7,8	0	3	14,2	24,6	0,3	-13,7	31,7	40,8	7	21,6	(5; -, -, -; 2, 3)
KEPSUT	213	0,283	4,24	624,6	6	1	3,8	14,4	24,5	-0,3	-18,6	31,3	43,2	6	20,7	(5; -, -, -; 2, 7)
YENISEHIR	362	0,298	4,04	482,6	13,1	1	3,6	13,6	23,3	-0,7	-29,4	31,2	43	6	19,7	(5; -, -, -; 2, 7)
KARABUK	195	0,382	4,33	461,2	13,6	0	3,6	13,9	24	0,3	-11,4	31,8	44,1	7	20,4	(5; -, -, -; 2, 9)
ERMENEK	133	0,316	4,49	564,6	3	0	3	11,6	23,8	1,4	-2,9	30,1	37	5	20,8	(5; -, -, -; 3, 2)
SARKOY	300	0,377	5,11	540,9	3,6	0	4,7	14,7	24	1,9	-10,2	28	35,3	6	19,3	(5; -, -, -; 3, 2)
AKHISAR	12	0,45	4,99	609,4	3,6	0	6,2	16,1	26,7	1,8	-13,6	33,8	44,6	7	20,5	(5; -, -, -; 3, 4)
ALASEHIR	19	0,616	5,11	513,6	3,4	0	6,5	16,9	27,6	3,3	-7,5	34,4	42	6	21,1	(5; -, -, -; 3, 4)
BERGAMA	54	0,34	4,65	755,2	6,9	0	6,1	16,1	26,1	2,6	-11,4	32,8	41,5	6	20	(5; -, -, -; 3, 4)
DENIZLI	102	0,457	4,81	546,8	4,1	0	5,7	15,8	26,6	2	-11,6	33,9	41,2	6	20,9	(5; -, -, -; 3, 4)
ISLAHIYE	182	0,4	4,9	850,7	2,4	0	5,2	16,8	27,8	2,2	-11,8	34,3	43,2	6	22,6	(5; -, -, -; 3, 4)
KAHRAMAN MARAS	197	0,457	4,95	722,8	0,8	0	5,1	16,7	28,2	1,2	-9	35,9	42,6	7	23,1	(5; -, -, -; 3, 4)
KILIS	217	0,616	5,62	542,8	0,9	0	5,4	16,9	28	1,6	-12	36,9	43	6	22,6	(5; -, -, -; 3, 4)
KIRIKHAN	218	0,749	6,18	576,2	0	0	7,8	18,9	29,7	4,1	-7	36,1	42	5	21,9	(5; -, -, -; 3, 4)
MANISA	241	0,37	4,56	746,8	2,8	0	6,8	16,8	27,6	3	-17,5	34,6	44,5	7	20,8	(5; -, -, -; 3, 4)
MUT	258	0,977	6,81	421,3	2,4	0	6,3	17,3	29,2	2,4	-10,1	36,2	43	6	22,9	(5; -, -, -; 3, 4)
NAZILLI	260	0,517	5,25	611	2,6	0	7,6	17,6	28,6	3,6	-15,1	36,3	42,8	7	21	(5; -, -, -; 3, 4)
ODEMIS	266	0,409	4,75	698,3	2,7	0	7,2	17	28	2,7	-13,6	35,2	43,2	7	20,8	(5; -, -, -; 3, 4)
SARAYKOY	294	0,853	6,16	442,2	3,7	0	6,6	17,2	28,4	2,7	-9,3	35,3	41,9	7	21,8	(5; -, -, -; 3, 4)
SOMA	321	0,349	4,84	687,1	6	0	6	15,7	25,6	2,8	-11	32,3	40,4	6	19,6	(5; -, -, -; 3, 4)
TAHIROVA-GONEN	326	0,346	4,12	563,6	1,6	0	5,4	14,8	24,2	2,4	-10,5	29,2	39	6	18,8	(5; -, -, -; 3, 4)
AYDIN	38	0,466	4,93	677,6	2,2	0	8,1	17,7	28,2	4,3	-11	35,8	43	6	20,1	(5; -, -, -; 4, 3)
AYVALIK	39	0,536	5,73	640,6	2,8	0	8	16,9	26,2	4,8	-7,6	31,2	37,8	4	18,2	(5; -, -, -; 4, 3)
BORNOVA	68	0,408	4,63	700,2	1,6	0	8,2	17,3	27,5	4,5	-8,4	33,8	42,4	6	19,3	(5; -, -, -; 4, 3)
DIKILI	108	0,473	5,33	667,9	2,2	0	7,9	16,5	25,7	4,5	-7,8	30,8	41,8	5	17,8	(5; -, -, -; 4, 3)
EDREMIT	120	0,374	4,9	738,6	3,9	0	6,9	16,4	26,4	3,5	-7,6	32,1	40,5	6	19,5	(5; -, -, -; 4, 3)
ERBAA	127	0,482	4,51	430,5	9,3	0	5,4	14,6	23,8	1,7	-14,6	31,8	43,2	7	18,4	(5; -, -, -; 4, 3)
ERDEK	129	0,402	4,39	542	8	0	5,4	15,5	24,6	2,9	-7	28,5	37,7	4	19,2	(5; -, -, -; 4, 3)

STATION	N°	K	A	P	PE	HS	TMF	T	TMC	TMMF	F	TMMC	C	HP	OSC	PHYTOCLIMATE
MENEMEN	245	0,48	4,9	606,4	0,9	0	7,4	16,9	26,7	4,2	-7,6	33	39,6	6	19,3	(5; -, -, -; 4, 3)
NIKSAR	263	0,416	4,23	475,4	10,8	0	5,3	14,7	23,7	0,4	-13	30,4	41,5	5	18,4	(5; -, -, -; 4, 3)
RESADIYE	287	0,37	3,91	481,6	6,2	0	5,7	13,9	23,5	1,2	-12	30,9	41,4	7	17,8	(5; -, -, -; 4, 3)
SALIHLI	290	0,631	5,37	492,1	4,3	0	7	16,7	26,8	3,4	-10,2	33,9	40,6	6	19,8	(5; -, -, -; 4, 3)
SELCUK	305	0,386	5,3	780	0	0	7,6	16,4	25,9	2,7	-9	33	40	7	18,3	(5; -, -, -; 4, 3)
TIRE	332	0,396	4,84	842,7	3,5	0	7,5	17,2	27,2	3,8	-11	34,8	42,7	5	19,7	(5; -, -, -; 4, 3)
YATAGAN	359	0,407	4,88	673,3	3,9	0	6,8	16,3	26,5	3,1	-6,3	34	40,1	5	19,7	(5; -, -, -; 4, 3)
BOZCAADA	71	0,302	4,33	681,4	4,7	0	7,5	15,7	23,4	5	-5,4	26,8	35,5	3	15,9	(5; -, -, -; 4, 7)
IZNIK	188	0,319	4,03	528,1	13,3	0	6,9	15,4	24,3	4,4	-6,6	30,8	42,4	5	17,4	(5; -, -, -; 4, 7)
EGRIDIR	121	0,275	4,52	673,6	4,5	0	3,4	13,5	24,1	1,4	-9,7	28,2	34,5	6	20,7	(5; -, -, -; 6, 7)
BALIKESIR	45	0,31	4,51	609,4	7,7	0	4,9	14,6	24,6	1,6	-21,8	31	43,7	7	19,7	(5; -, -, -; 7, 3)
CANAKKALE	80	0,309	4,75	629,1	7,4	0	6	14,9	24,7	2,9	-11,5	30,4	38,7	6	18,7	(5; -, -, -; 7, 4)
KEMALPASA	212	0,292	4,49	1061,9	3,9	0	7,3	16,2	26	4,4	-5	33,8	39,5	3	18,7	(5; -, -, -; 7, 4)
BAYRAMIC	53	0,291	4,83	655,1	5,2	0	5	14,5	24,2	1,7	-13,5	31	39,8	7	19,2	(5; -, -, -; 7, 6)
BIGADIC	59	0,3	4,55	650,9	3,8	0	5,4	14,8	24,4	2	-19	31	40,2	7	19	(5; -, -, -; 7, 6)
GOKCEADA	151	0,259	4,71	758,5	6,1	0	6,6	15,2	24	3,9	-9,5	28,9	38	5	17,4	(5; -, -, -; 7, 6)
MUDANYA	250	0,26	4,51	629,1	12,1	0	6,2	15,3	23,9	3,7	-6,8	27,5	41,3	4	17,7	(5; -, -, -; 7, 6)
GUNEY	162	0,335	4,5	569,4	6,8	1	3	13,7	24	-0,3	-15,4	30,2	36,9	5	21	(5; 2, -, -; 3, 9)
BAYINDIR	51	0,515	5,12	647	1,2	0	8,5	17,9	27,8	4,4	-8,5	34,3	41,4	5	19,3	(5; 4, -, -; 3, 7)
CEYHAN	88	0,375	4,48	671,9	5	0	8,6	18,3	28	3	-11,3	35,9	45,1	5	19,4	(5; 4, -, -; 3, 7)
CINE	92	0,543	5,45	634,6	4,8	0	8,5	18,1	28,8	4,5	-6	36,3	43,3	6	20,3	(5; 4, -, -; 3, 7)
IZMIR	186	0,508	5,35	700,1	1	0	8,6	17,6	27,6	5,6	-8,2	32,8	42,7	5	19	(5; 4, -, -; 3, 7)
KARABURUN	196	0,42	4,74	782,8	0,1	0	8,4	17,1	26,3	5,8	0	33,8	40	3	17,9	(5; 4, -, -; 3, 7)
KUSADASI	233	0,476	5,2	659,5	0,6	0	8,8	16,7	25,2	5,1	-7,1	30,3	41,5	6	16,4	(5; 4, -, -; 3, 7)
MILAS	249	0,471	5,1	760,9	0,6	0	8,7	17,9	28,2	5,1	-4,2	35,6	44,8	5	19,5	(5; 4, -, -; 3, 7)
KARAISALI	198	0,241	4,2	930	11,9	0	8,8	18,3	27,3	6,1	-3,3	33,6	39,1	3	18,5	(5; 4, -, -; 7, 3)
SOKE	319	0,359	4,55	1001,7	1	0	8,9	17,6	26,8	5,9	-4,6	31,6	40,2	3	17,9	(5; 4, -, -; 7, 3)
TEKIRDAG	330	0,225	3,94	590,6	9,2	0	4,3	13,8	23,5	1,5	-13,5	28,1	37,6	7	19,2	(5; 6, -, -; 7, 2)
IPSALA	180	0,207	3,75	627,2	8,7	1	3,5	14	24,2	-0,5	-16,7	30,8	38,2	6	20,7	(5; 6, 2, -; 7, 3)
BANDIRMA	46	0,218	4,1	702,1	9,3	0	5,4	14,4	23,8	2,2	-14,6	28,4	41,3	6	18,4	(5; 6, 7, -; 4, 3)
GELIBOLU	145	0,22	4,23	696,6	11,3	0	5,4	14,8	24,1	2,6	-8,4	27,9	36	6	18,7	(5; 6, 7, -; 4, 3)
KARTAL	204	0,214	4,02	680,2	17	0	6,5	15	24,2	3,8	-9	29,3	40	5	17,7	(5; 6, 7, -; 4, 8)
MUGLA	252	0,227	4,07	1221	7,1	0	5,4	15	26	1,8	-12,6	33	41,2	6	20,6	(5; 7, -, -; 3, 4)
ANTAKYA	25	0,216	3,7	1173,2	2,5	0	8,1	18,2	27,6	4,8	-14,6	31,8	43,9	5	19,5	(5; 7, -, -; 4, 3)
BUCAK	74	0,21	3,73	744	13	1	3,5	14,1	25,3	-0,7	-13,2	32,1	37,5	6	21,8	(5; 7, 6, 2; 8, 9)
HAYRABOLU	170	0,177	3,41	618,8	8	1	0,9	13,4	23,4	-2,1	-14,4	31	39,2	5	22,5	(6; 2, -, -; 7, 5)
KIRKLARELI	220	0,17	3,2	575,7	21,2	1	1,7	13,2	23,6	-1,4	-13,7	30,3	39,7	5	21,9	(6; 2, -, -; 7, 5)
ALMUS	27	0,174	3	541,1	7,8	3	2,1	11,2	19,9	-1,7	-19	26,3	37,1	6	17,8	(6; 2, -, -; 7, 8)
EDIRNE	119	0,143	2,98	599,3	22	2	1,9	13,5	24,6	-1,4	-22,2	31,3	41,5	5	22,7	(6; 2, -, -; 7, 8)
LULEBURGAZ	235	0,145	2,86	614,5	16,5	2	2,9	13,1	23,4	-0,7	-24,2	30,5	42,8	6	20,5	(6; 2, -, -; 7, 8)
GOYNUK	158	0,11	2,84	609	11,9	2	2	10,8	19,8	-2,2	-17,6	26,7	36,5	5	17,8	(6; 2, -, -; 7,11)
CORLU	94	0,185	3,39	568,5	15,4	1	2,8	12,7	22,4	-0,8	-16,9	28,4	39	6	19,6	(6; 2, 5, -; 7, 8)
SOGUT	318	0,136	3,07	622,9	11	1	2	12,2	21,5	-0,5	-16	28,6	39	5	19,5	(6; 2, 5, -; 7, 8)
UZUNCOPRU	353	0,171	3,46	677,3	16	1	0,9	13,6	24,4	-1	-16	30,8	39	5	23,5	(6; 2, 7, -; 5, 9)
SENIRKENT	306	0,179	3,68	733,3	7,9	2	1,6	12,3	23,5	-1,2	-14	29,1	35	4	21,9	(6; 2, 7, -; 9, 5)
DOMANIC	115	0,113	3,15	702,6	11,6	2	1,1	10,9	20,2	-2,4	-16,5	27,2	36,5	5	19,1	(6; 2, 7, -;11, 8)
AKSEHIR	15	0,147	3,07	679,7	9,4	2	1,2	12,1	22,7	-2,9	-26,7	29,8	40,5	5	21,5	(6; 2, 7, -;11,14)
ULUBORLU	341	0,14	3,29	739,4	9,8	1	2,3	12,2	22,9	-0,6	-10,8	29,6	35	6	20,6	(6; 2, 7, 5; 8,11)
PINARHISAR	281	0,124	2,7	630	15,5	1	2,6	13,2	22,9	-1,7	-18	29,3	38	5	20,3	(6; 2, 8, 5; 7, 9)
KUTAHYA	234	0,157	3,4	564,6	11,8	4	0,3	10,6	20,4	-3,6	-28,1	28	36,8	6	20,1	(6; 2,10, -; 7,14)
MUDURNU	251	0,143	3,57	559	12,1	4	0,4	10,1	19,3	-3,6	-19,8	27,4	36	4	18,9	(6; 2,10, -; 7,14)
BOZUYUK	73	0,171	3,48	549,8	12,5	3	0,2	10,8	20,4	-3,8	-25,7	27,8	39,5	6	20,2	(6; 2,10, -;14, 7)

STATION	N°	K	A	P	PE	HS	TMF	T	TMC	TMMF	F	TMMC	C	HP	OSC	PHYTOCLIMATE
FLORYA	143	0,188	4,08	649	18,4	0	5,1	13,9	23,3	2,5	-12,6	28,8	38,6	6	18,2	(6; 5, -, -; 7, 4)
GEYVE	149	0,154	3,31	632,1	17,2	0	4,1	14,1	23,2	0,9	-14,9	28,8	42,1	7	19,1	(6; 5, -, -; 7, 8)
KESAN	215	0,199	3,22	648,8	15	0	4	14,5	24,8	1,8	-12	31	37,4	6	20,8	(6; 5, -, -; 7, 8)
ALPULLU	21	0,192	3,27	601,3	16,4	1	3,4	13,8	24,1	0	-20,4	30,5	42,9	7	20,7	(6; 5, 2, -; 7, 8)
MURATLI (TEKIRDAG)	255	0,142	2,89	726,2	16,1	1	3	13,6	23,2	-0,1	-13,9	30,2	37,6	5	20,2	(6; 7, 2, 5; 8,11)
GEMLIK	147	0,181	3,55	691,5	9,4	0	6,9	14,9	23,6	3,7	-9	30,1	40,6	6	16,7	(6; 7, 5, -; 4, 8)
GONEN	156	0,196	4,06	706,2	13	0	5	14,5	23,8	1,5	-9	29,4	39,2	7	18,8	(6; 7, 5, -; 4, 8)
MUSTAFAKEMALPASA	257	0,184	3,5	683,7	10,6	0	4,8	14,6	23,3	1,4	-21	29,6	41,7	6	18,5	(6; 7, 5, -; 8, 2)
BIGA	58	0,182	3,77	765,7	10,2	0	4,9	14,2	23,5	2	-11,4	29,2	39,8	6	18,6	(6; 7, 5, -; 8, 4)
BURSA	77	0,142	3,35	712,8	17	0	5,2	14,4	24,2	1,7	-25,7	30,6	42,6	7	19	(6; 7, 5, -; 8, 4)
GOLCUK	154	0,142	2,92	663,7	22,3	0	6,3	14,3	23,8	2,9	-8,8	30,1	37,5	6	17,5	(6; 7, 5, -; 8, 4)
KUMKOY	231	0,115	3,34	717,2	19,8	0	5,8	13,9	23,1	2,8	-11,7	26,7	39,1	6	17,3	(6; 7, 5, -; 8, 4)
SARIYER	296	0,11	3,53	752,5	23,6	0	5,4	13,8	22,8	2,8	-11	26,3	39,6	6	17,4	(6; 7, 5, -; 8, 4)
SILE	310	0,092	2,97	747	22,7	0	5,4	13,6	22,7	2,7	-11,1	26,1	39,5	6	17,3	(6; 7, 5, -; 8, 4)
UMURBEY	349	0,162	3,52	689	15,1	0	5,2	14,5	23,5	2,4	-10,5	28,4	39,5	6	18,3	(6; 7, 5, -; 8, 4)
YALOVA	356	0,102	2,94	759,6	22,1	0	6,1	14,3	22,9	2,7	-9,7	27,3	40,2	6	16,8	(6; 7, 5, -; 8, 4)
YESILKOY	363	0,125	3,92	691,4	18,2	0	5,3	13,7	23,2	2	-8,6	28,9	35,4	6	17,9	(6; 7, 5, -; 8, 4)
AKCAABAT	8	0,06	2,66	687,4	30,9	0	7,1	14,6	22,7	3,9	-3,6	26,3	35,1	5	15,6	(6; 8, 7, -; 5, 4)
BAFRA	42	0,072	2,65	725,9	25	0	6,2	14,1	22,6	3,4	-7,9	26,1	37,2	5	16,4	(6; 8, 7, -; 5, 4)
SINOP	313	0,067	2,56	679,6	27,7	0	6,7	14,1	22,8	4	-8,4	25,7	34,5	6	16,1	(6; 8, 7, -; 5, 4)
BOLU	66	0,097	2,52	533,6	18,4	4	0,1	10,2	19,7	-4,4	-34	27,9	39,4	6	19,6	(6;11,10, 2; 7,14)
YARPUZ	358	0,143	3,45	1087,8	1,5	2	2,7	12,4	21,9	-0,9	-15	27,8	33,5	3	19,2	(7; 2, -, -; 5, 8)
CEVIZLI	87	0,148	3,5	1367,4	4,6	2	1,6	11,8	22,8	-2,9	-16	29,8	36,6	5	21,2	(7; 2, -, -;14, 9)
SUTCULER	325	0,149	3,26	895,5	8,4	1	2,2	12,5	24,3	-1	-8,5	30	36	4	22,1	(7; 2, 5, -; 6, 8)
GULEK	159	0,168	3,55	981,9	5,2	0	3,5	13,8	23,6	0,3	-7,6	30,5	36,3	6	20,1	(7; 5, -, -; 6, 2)
FEKE	140	0,19	3,81	946,5	9,7	0	5	15,6	26,5	1,5	-10,6	34	41	5	21,5	(7; 5, -, -; 6, 3)
AKSEKI	16	0,159	3,58	1350,6	5,3	1	3,1	13,5	24,4	-0,1	-12	29,9	36	5	21,3	(7; 5, 2, -; 3, 8)
MARMARA ADASI	244	0,195	4,03	835,1	8	0	6,2	15,5	24,3	3,5	-7,5	28,2	36,7	4	18,1	(7; 5, 6, -; 4, 8)
SIMAV	312	0,152	3,69	845,8	9,6	2	2,3	12	21,8	-1,5	-19	29,7	37,8	6	19,5	(7; 6, 2, -; 5, 8)
MAHMUTSEVKETPAS	237	0,104	3,6	817,8	20	0	3,9	13,2	21,6	0,7	-17,7	27,7	38,8	6	17,7	(7; 6, 5, -; 8, 2)
ARSLANKOY	33	0,088	3,19	814,3	10	3	0	10,4	21,1	-3,3	-13,2	26,7	33,1	5	21,1	(7; 6,14, 2;11, 9)
KELES	209	0,081	2,77	834,5	10,7	4	0,1	9,9	19	-3,4	-19	26,7	34,7	5	18,9	(7; 6,14,11; 8, 9)
IZMIT	187	0,04	1,72	767,9	26,1	0	5,4	14,5	23,5	2,5	-18	29,8	42,9	6	18,1	(8; -, -, -; 5, 6)
KANDIRA	192	0,023	2,24	1153,4	38,7	0	8	16,3	24,3	1,2	-15,6	29,2	39,8	6	16,3	(8; -, -, -; 7, 4)
TRABZON	338	0,014	1,49	822,7	36,8	0	7,3	14,6	23,1	4,4	-7,4	26,2	38,2	6	15,8	(8; -, -, -;12, 4)
MACKA	236	0,012	1,25	731,7	34,7	0	4,8	12,6	19,9	0,9	-11	24,5	39,5	6	15,1	(8; -, -, -;12,13)
ARTVIN	34	0,06	2,48	644,9	27,8	0	3,4	12,7	21,1	0,5	-16,1	26,6	43	7	17,7	(8; 6, -, -; 7, 5)
SAMSUN	292	0,052	2,43	735	31,4	0	6,9	14,4	23,2	3,7	-9,8	26,8	39	6	16,3	(8; 6, 7, -; 5, 4)
BAHCEKOY ORMAN	40	0,037	2,48	1074,4	28,7	0	4,5	12,9	21,8	1,5	-15,8	27,1	39,7	6	17,3	(8; 7, -, -; 5, 6)
DUZCE	118	0,003	1,09	845	41,3	1	3,2	13,3	22,4	-0,4	-20,5	29	42	5	19,2	(8;12,13,11; 2, 5)
BITLIS	63	0,16	3,66	975,6	2,8	4	-2,4	9,5	23,2	-6,5	-19	30,5	36,8	4	25,6	(14; 9, -, -;10, 7)
PULUMUR	285	0,131	3,44	792,2	4	5	-3,8	8,3	20,7	-8,9	-23,5	28,8	39,5	5	24,5	(15;14, 9,18;22,10)

N°: reference of the meteorological station; **K**: Intensity of aridity; **A**: Duration of aridity, in months; **P**: total annual precipitations in mm; **PE**: Minimum summer precipitation (June, July, August or September) in mm; **HS**: Freezing certain (No. of months in which TMMF <=0); **TMF**: Lowest monthly mean temperature, in °C; **T**: Annual mean temperature, in °C; **TMC**: Highest monthly mean temperature, in °C; **TMMF**: Average of the minimum temperatures in the month with the lowest mean temperature, in °C; **F**: absolute minimum temperature, in °C; **TMMC**: Average of the maximum temperatures in the month with the highest mean temperature, in °C; **C**: absolute maximum temperature, in °C; **HP**: Freezing probable (No. of months in which F<=0 and TMMF >0; **OSC**: Thermal oscillation (TMC-TMF), in °C.

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Proposta per una parametrizzazione dei fattori stazionali nell'indice di Mitrakos

Proposal for a site conditions parametrization with the Mitrakos' Index

Riccardo GUARINO

Dipartimento di Botanica dell'Università, Via A. Longo 19, I-95125 Catania, Italia.

RIASSUNTO

Viene parametrizzata l'influenza dell'inclinazione ed esposizione dei versanti, dell'altitudine e della distanza dal mare sullo stress invernale ed estivo subito dai vegetali in area mediterranea. Per ciascuno di questi fattori stazionali viene riportato un esempio dei cambiamenti della vegetazione al loro variare e viene proposta una formula per determinare un valore mensile da sommare o da sottrarre ai valori di "drought stress" e di "cold stress", determinati mediante l'indice di Mitrakos, in modo da ottenere una valutazione dello stress più aderente alle condizioni reali. I valori dell'indice ottenuto in tal modo, potranno essere utilizzati in ambito sinecologico e fitosociologico per esprimere in maniera sintetico-correlativa la valenza ecologica delle comunità vegetali in funzione dei principali fattori stazionali.

Parole chiave : indice di Mitrakos, stress stagionali, fattori stazionali, Regione Mediterranea

ABSTRACT

The influence of slope gradient and exposure, of altitude and of distance from the sea on the winter and summer stresses sustained by the Mediterranean vegetation have been parametrized. An example of vegetation changes driven by the variation of any of such environmental factors is reported, and a mathematical formula is proposed to determine a monthly value to add to or subtract from the drought stress and cold stress values, estimated by the Mitrakos' index, in order to better approximate real conditions. Values obtained in such way can be used in synecology and phytosociology to express in a synthetic-correlative way the ecological valence of plant communities with respect to the main physiognomical features of their growing sites.

Key-words: Mitrakos' index, seasonal stresses, site conditions, Mediterranean area

RESUME

Les influences de l'exposition et de l'inclinaison des versants, de l'altitude et de la distance à la mer sur le stress hivernal et estival subi par les végétaux ont été paramétrisées pour le bioclimat de la région méditerranéenne. Pour chacun de ces facteurs est proposé un exemple des changements de végétation et une formule pour calculer une valeur mensuelle qui peut être sommée ou soustraite aux valeurs de "drought stress" et de "cold stress", déterminées avec l'indice de Mitrakos ; ceci dans le but d'obtenir une évaluation du stress plus proche des conditions réelles. Les valeurs de l'indice obtenues pourront être utilisées dans le cadre d'études synécologiques et phytosociologiques, afin d'exprimer de façon synthétique la valence écologique des communautées végétales en fonction des principaux facteurs stationnels.

Mots clés : indice de Mitrakos, stress saisonniers, facteurs stationnels, région méditerranéenne

ABRIDGED ENGLISH VERSION

According to the Mitrakos' theory, the Mediterranean vegetation suffers during the year two distinct critical periods : a winter one, called by the author "cold stress" (C.S.) and a summer one, due to the deficit of rainfalls, called "drought stress" (D.S.). Both stresses are monthly estimated by the following formulas: C.S. = 8(10 - t) and D.S. = 2(50 - p), where t is the mean minimum temperature and p the average rainfall of each month. The author artificially limits the range of D.S. and C.S. values between 0 and 100.

Mitrakos' index does not consider climatic factors on the whole, but only their critical values, expressing the intensity of such phases. So it is not fit to distinguish isoclimatic areas potentially inhabited by the same vegetation series, but it well describes the climatic mildness, that means the different way of expression of climatic factors in areas belonging to the same bioclimatic unit. This is the main difference between Mitrakos' index and the other most used bioclimatic indices.

An attempt to improve the potentialities of Mitrakos' index and to achieve a valuation of stresses closer to reality is here proposed, by introducing in the formulas variables strictly related to the site conditions, which are often responsible of particular microclimatic situations. This is possible without modifying the original index, since Mitrakos' formulas fit the linear combination of variables. This means also that it will be possible to exclude each time variables resulting negligible, or to add new significative ones in the formulas without any influence on the other variables. In the present paper, formulas expressing the influence of slope gradient and exposure, of altitude and distance from the sea on C.S. and D.S. are proposed, but some other environmental factors could be parametrized and introduced as well, by following the instructions and suggestions reported. The only important thing is that the weight of each parameter should be fixed *una tantum*.

By following the present proposal and by the application of the index to a statistically significant number of cases, it will be possible, for example, to find out a numerical interval expressing in a synthetic-correlative way the ecological valence of a plant community with respect to the site conditions.

The sloping degree influences the soil thickness and the angle of incidence of sunbeams on the soil surface. This may increase the D.S. suffered by the Mediterranean vegetation. The curve of the drought increment due to the sloping degree (figure 4, curve 1) is given by the following expression:

$$I = \frac{10^4}{10^3 + 1{,}18^{(90-\alpha i)}}$$

where is the sloping angle in decimal degrees. "I" varies between 0 and 10 according to the variation of , and its value should be summed to the monthly value of D.S. calculated according to the Mitrakos' formula.

The exposure, together with latitude, influences the insolation time of a slope during the year. This may increase the D.S. suffered by the Mediterranean vegetation. The curve of the drought increment due to the sloping degree (figure 5, curve 1) is given by the following expression:

$$E = 5(1 - \cos \rho) + 1{,}05^{-\left(\frac{\zeta - 270}{10}\right)^2}$$

where ζ is the exposure angle expressed in decimal degrees. "E" varies between 0 and 10 according to the variation of ζ, and its value should be summed to the monthly value of D.S. calculated according to the Mitrakos' formula. When a site is flat and there are no orographic obstacles reducing the insolation time, "E" will be considered equal to 10. Whenever orographic obstacles will reduce the potential insolation time (I_{pot}) of a site, it can be directly measured the real insolation time (I_{eff}) in any day of the year. Then, given the latitude and exposure, it is possible to calculate I_{pot} (in appendix 2 it is shown how to do) and compare the two values according to the proportion :

$$I_{pot} : n = I_{eff} : n_1 \quad \longrightarrow \quad n_1 = \frac{n \cdot I_{eff}}{I_{pot}}$$

where n is the "E" value without obstacles and n_1 is the effective value of "E".

Exposure and sloping degree influence the C.S. as well, since from the angle of incidence of solar radiation depends the quantity of heat per surface unit reaching the earth, according to the expression $Q_1 = Q$ sen (figure 8). For example, when = 30°, the quantity of heat per surface unit is halved. From a microclimatic standpoint, it is evident the advantage of having quite a number of hours with solar rays incidence close to 90°, during the coldest periods. Moreover, in the Mediterranean area south-facing slopes are usually sheltered from colder winds.

The trend of the C.S. reduction due to the mentioned factors (figure 10) is given by the following expression:

$$I \cap E = \frac{8(1 - \cos \rho)^4}{\left[6 + 1{,}12^{(\gamma - \alpha i)}\right]\left[1 + 1{,}12^{(\alpha i - \gamma_1)}\right]}$$

where is the angle of exposure and the sloping angle, both expressed in decimal degrees, γ is the slope angle for which, given the latitude of a site, incident rays are perpendicular on January 11 and and γ_1 is the slope angle *increased of 10 units* for which, at the same latitude, incident rays are perpendicular on December 21. "IE" varies between 0 and 15.5 and its value should be subtracted from the monthly value of C.S. calculated according to the Mitrakos' formula.

Summer high temperatures determine the hydric saturation of a thick stratum of air onto the sea surface. On sunny days, saturated air masses are pushed inland by the sea breeze during the afternoon, reducing the evapotranspiration of plants along the coast and causing an abundant dew condensation during the night. The entity of this phenomenon depends on the altitude and distance from

the sea of a given site. Moreover, the altitude at which the condensation effect is maximum (Q_m) is influenced by latitude, according to the expression : $Q_m = 40(60\ \varphi)$, where φ is the latitude of a given site. The trend of the D.S. reduction, due to these factors, is given by the following expression:

$$Q \cap D = \frac{63 \cdot \left[1 + 1{,}07^{-\left(\frac{h - Q_m}{20}\right)^2}\right]}{8 + 1{,}05^{d}}$$

where d is the distance from the sea in km, h is the altitude in meters and Q_m is the above mentioned altitude (figure 11). "QD" varies between 0 and 14 and its value should be subtracted from the monthly value of D.S. calculated according to the Mitrakos' formula. Of course, the parameter "QD" will be considered only where no orographic obstacles are interposed between the sea and the studied site.

A general rule is here presented: scales of D.S. and C.S., as proposed by Mitrakos, are limited between 0 and 100 for practical reasons. Nonetheless, the monthly evaluation of stresses brings often to values <0 or >100. Stress components determined by site conditions, estimated as here proposed, should be added or subtracted to/from Mitrakos' values before any rounding. When values are still <0 or >100, rounding as proposed by Mitrakos can be done.

INTRODUZIONE

Nel 1980 Mitrakos evidenziò che nell'area mediterranea la vegetazione è sottoposta, nell'arco dell'anno, a due periodi critici ben distinti : uno, invernale, dovuto al freddo, ed uno, estivo, dovuto alla siccità. I due fattori di stress, chiamati "cold stress" (C.S.) e "drought stress" (D.S.) sono valutati mensilmente grazie alle formule : C.S. = 8(10 - t) e D.S. = 2(50 - p), ove t rappresenta la media delle temperature minime giornaliere verificatesi nel corso del mese e p le precipitazioni mensili espresse in mm.

C.S. e D.S. possono essere rappresentati sinotticamente mediante un istogramma o espressi sinteticamente mediante le somme annuali (Y.C.S. e Y.D.S.) o stagionali dei valori mensili. Tra queste ultime, particolarmente significative sono la somma invernale del C.S. (W.C.S.) e quella estiva del D.S. (S.D.S.), che mettono in risalto la marcata stagionalità dell'influenza dei fattori di stress nella regione mediterranea (Mitrakos, 1980a).

Mitrakos si servì dell'indice in campo corologico ed ecofisiologico, interpretando la distribuzione in Grecia di alcune sclerofille sempreverdi e studiando la temperatura di germinazione dei loro semi e la resistenza delle loro gemme al freddo ed alla siccità (Mitrakos, 1980a, b ; 1981). Attraverso questi studi l'autore ha formulato l'ipotesi che le specie sempreverdi sclerofille, comunemente considerate l'espressione più tipica del clima mediterraneo, siano in realtà espressione relitta di un'epoca con inverno più mite di quello attuale. In seguito diversi autori si sono occupati dell'indice, sperimentandone l'applicabilità, da solo o con altri indici, per distinguere a livello regionale aree fitoclimaticamente omogenee (Pierangeli,1988 ; Schirone, 1988 ; Blasi, 1994) oppure avvalendosene in ricerche fitosociologiche (Blasi *et al.*, 1998 ; Caneva *et al.* 1997 ; Scoppola & Pelosi, 1995 ; Stanisci, 1994), ecofisiologiche (Gratani, 1994 ; Gratani & Crescente, 1997) ed in indagini fenologiche (Schirone, *l.c.*). In questa sede si propone l'utilizzo dell'indice di Mitrakos per valutare, previa introduzione di alcuni parametri di semplice determinazione, l'influenza del microclima nel determinare il passaggio da un'associazione vegetale ad un'altra, qualora tale passaggio sia determinato principalmente da variazioni dei fattori stazionali e non da fattori di altro tipo ; siano essi accidentali, quali incendi, o persistenti, quali l'azione umana di sfruttamento delle risorse.

PECULIARITÀ DELL'INDICE DI MITRAKOS E CONSIDERAZIONI APPLICATIVE

Un indice bioclimatico deve consentire di rimarcare univocamente le differenze vegetazionali che si riscontrano in un territorio e la sua formula deve inoltre prendere in considerazione fattori i cui dati siano di facile reperibilità, in modo da essere agevolmente applicabile. Quest'ultimo requisito fa sì che nella totalità degli indici bioclimatici più usati figurino solamente variabili termometriche e pluviometriche : le sole di cui attualmente si abbia una campionatura statisticamente significativa. Malgrado questo limite, è indubbio che comprendendo in un'unica formula valori medi annuali di piovosità e temperatura si ottenga una potenzialità analitica inferiore a quella ottenibile separando le due variabili in due espressioni diverse, ed ancor più bassa rispetto ad una formula che prenda in considerazione di volta in volta le variazioni mensili dei due fattori invece delle loro medie annuali.

Per evidenziare questa considerazione è stato selezionato un gruppo di località italiane (Figura 1 ; Appendice 1) il cui clima soddisfacesse i caratteri

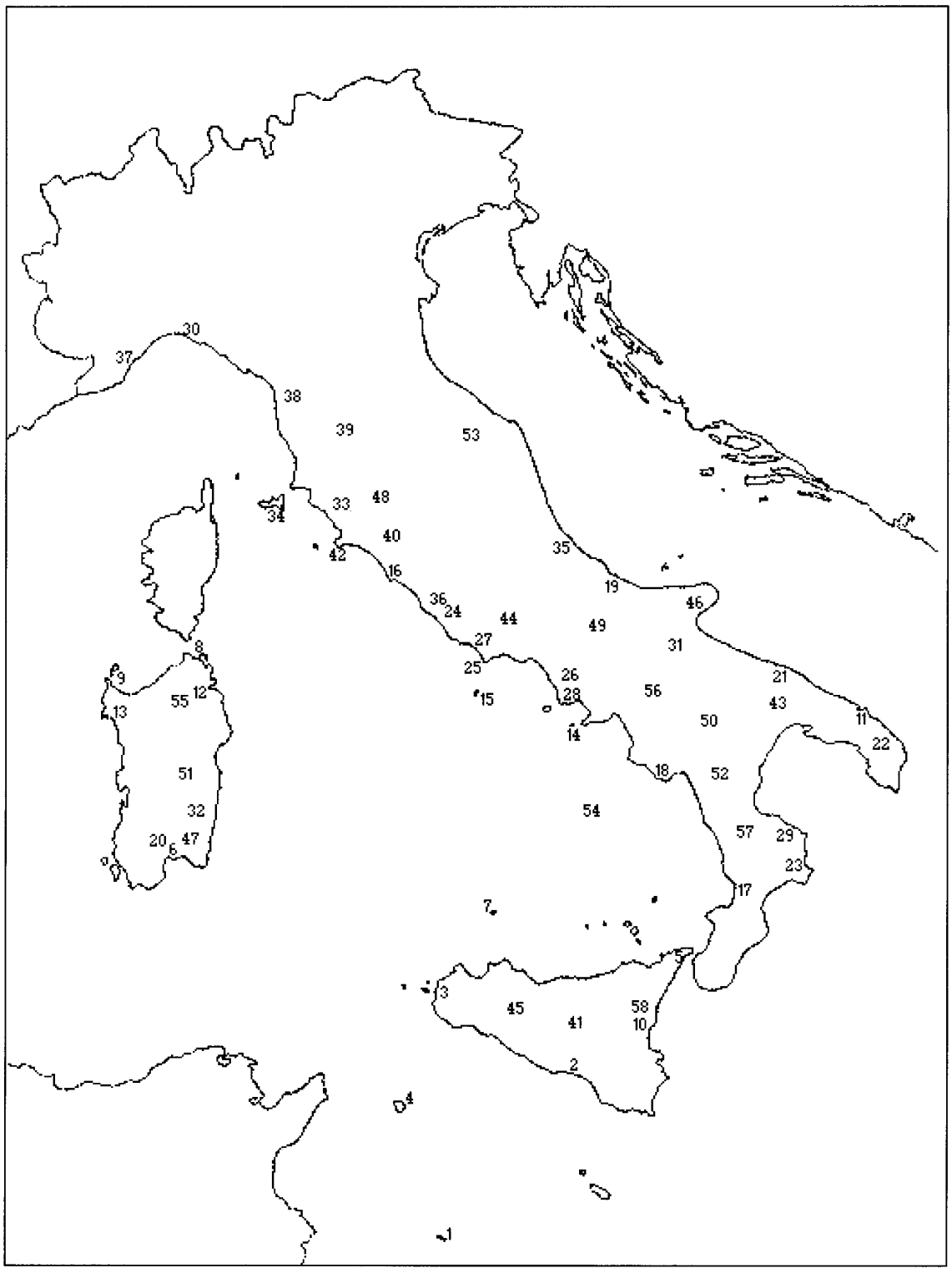

Figura 1. Localizzazione delle stazioni meteorologiche considerate.
Localisation of the considered weather stations.

generali del clima mediterraneo enumerati da Daget (Daget, 1977 ; 1980), comprendendo alcune situazioni limite significative. Tutti i dati climatici utilizzati nel presente lavoro, relativi al trentennio 1961-'90, sono stati forniti dall'Istituto Tecnico di Assistenza al Volo dell'Aeronautica Militare, con l'eccezione di quelli relativi alla stazione di Floresta, del Servizio Idrografico del Ministero dei Lavori Pubblici, e di quelli di Vallicciola, Serpeddì ed Etna (loc. Casa Cantoniera), presi da Pignatti *et al.* (1980). Per ciascuna di queste sono stati determinati Y.D.S., S.D.S., Y.C.S. e W.C.S. dopo averle ordinate secondo le suddivisioni bioclimatiche proposte da Rivas-Martínez per la regione mediterranea (Rivas-Martínez, 1981 ; Rivas-Martínez *et al.*, 1991 ; Rivas-Martínez, 1997 ; Rivas-Martínez & Loidi Arregui, 1999). Rivas-Martínez distingue le aree isobioclimatiche grazie alla combinazione di due valori numerici (uno dato dall'indice di termicità e l'altro dalle precipitazioni annuali in mm) esprimenti rispettivamente l'ombrotipo eed il termotipo di un territorio. Nella Appendice 1 le stazioni campione sono ordinate per termotipo e, nell'ambito dello stesso termotipo, per aridità decrescente.

La scelta di affidarsi alle categorie bioclimatiche di Rivas-Martínez è motivata dal fatto che tale metodo di suddivisione è il più analitico tra quelli finora proposti per la regione mediterranea, è approssimativamente concorde con le distinzioni individuate precedentemente da altri autori, e, soprattutto, conta innumerevoli applicazioni su molti territori Mediterranei (Biondi & Baldoni, 1995 ; Blasi *et al.*, 1988 ; Blasi, 1994 ; Brullo *et al.*, 1996 ; Peinado Lorca & Rivas-Martínez, 1987 ; Rivas-Martínez , 1996 ; Biondi & Baldoni, 1995 ; Blasi *et al.*, 1988 ; Blasi, 1994 ; Brullo *et al.*, 1996).

Poiché sia i tipi climatici di Rivas-Martínez sia Y.D.S., S.D.S., Y.C.S. e W.C.S. vengono determinati considerando separatamente dati termometrici e pluviometrici, ci si dovrebbe aspettare dal loro confronto un andamento omogeneamente comparabile : all'aumentare dell'indice di termicità di Rivas-Martínez, Y.C.S. e W.C.S. dovrebbero diminuire linearmente, così come coll'aumento delle precipitazioni dovrebbero diminuire Y.D.S. e S.D.S.. Ciò si verifica solo in parte : i valori di D.S. e C.S. tendono a decrescere, ma con un ampio intervallo di fluttuazione (si notino ad esempio in Appendice 1 i valori del C.S. di Catania Fontanarossa, di Cagliari o di Alghero, paragonabili non tanto a quelli delle stazioni di tipo termomediterraneo quanto piuttosto a quelli delle stazioni di tipo mesomediterraneo ; oppure i valori dell'isola di Asinara, inferiori a quelli di Trapani, malgrado quest'ultima stazione abbia termicità superiore). I valori di D.S. risultano mediamente più aderenti all'andamento reale delle precipitazioni, tuttavia anche tra questi si osservano notevoli oscillazioni (per esempio Vallicciola, Calopezzati e la località Casa Cantoniera, sull'Etna, di ombrotipo rispettivamente umido superiore, umido inferiore e subumido superiore, presentano D.S. maggiore di quello di Bari, di tipo secco superiore).

Il motivo degli ampi scostamenti dell'indice di Mitrakos dall'andamento dei valori su cui si basano le delimitazioni di Rivas-Martínez è insito nelle caratteristiche dei due indici : mentre il secondo prende in considerazione precipitazioni e temperature nella loro totalità, il primo le considera solamente quando i loro valori scendono al di sotto di una certa soglia. Le caratteristiche del secondo sono adatte per individuare le aree isoclimatiche presentanti le stesse potenzialità per la vegetazione climax ; il primo meglio si presta ad evidenziare la mitezza del clima, ovvero il diverso modo di manifestarsi dei fattori climatici nell'ambito di territori appartenenti alla stessa categoria bioclimatica ed a rimarcare la stagionalità e l'intensità dell'azione limitante esercitata dai fattori sullo sviluppo della vegetazione mediterranea.

Per evidenziare queste differenze sono state confrontate tra loro le caratteristiche climatiche delle stazioni campione con il metodo più analitico possibile : la costruzione di un dendrogramma (Figura 2) mediante l'elaborazione di una tabella riportante per ciascuna stazione : la media delle temperature massime giornaliere della prima, seconda e terza decade di ogni mese ; la media delle temperature minime giornaliere della prima, seconda e terza decade di ogni mese ; la media dell'umidità relativa mese per mese ; la media mensile delle precipitazioni ; il numero medio di giorni al mese con precipitazione superiore o uguale ad 1 mm ; il numero medio di giorni al mese con precipitazione superiore o uguale ad 10 mm.

Lasciando invariata la gerarchizzazione, sono state ruotate le ramificazioni del dendrogramma lungo i loro assi cercando di ordinare i cluster in modo da lasciare a sinistra le stazioni più calde ed aride e a

destra quelle più fredde ed umide, allo scopo di renderne più agevole la lettura. In Figura 2 sono evidenti i diversi rapporti di similitudine messi in risalto dai due metodi di classificazione bioclimatica : grossolanamente si può dire che le distinzioni di Rivas-Martínez ricalchino le distinzioni della parte distale del grafico, mentre l'indice di Mitrakos agisce nella parte prossimale. Si considerino ad esempio le stazioni di Trapani, Pantelleria (termomediterraneo inferiore secco superiore), Ustica ed Asinara (termomediterraneo superiore secco superiore) : tra tutte le stazioni appartenenti al loro stesso tipo bioclimatico, esse presentano valori di C.S. e D.S. stettamente affini e ciò è evidenziato dalla loro posizione nel dendrogramma. Proseguendo verso destra troviamo Cagliari, Decimomannu e Guardiavecchia : questo raggruppamento si distingue dal precedente per avere dei valori di C.S. decisamente maggiori. Si noti inoltre l'affinità climatica tra Enna ed il Monte Argentario (mesomediterraneo superiore secco inferiore), sottolineata da valori di C.S. e D.S. assai simili, la maggiore affinità tra Radicofani e Campobasso rispetto a Potenza (tutte supramediterraneo inferiore subumido inferiore, ma l'ultima con D.S e C.S. sensibilmente diversi dalle altre due), la grande differenza tra Circeo - Pratica di Mare da un lato e Grazzanise - Latina dall'altro (tutte mesomediterraneo inferiore subumido superiore), dovuta da un regime delle precipitazioni completamente diverso, e così via. In base a quanto osservato si desume che l'indice di Mitrakos si presta a fornire importanti indicazioni sull'escursione termica, sul regime delle precipitazioni (si noti in Appendice1 l'aumento di D.S. al diminuire della percentuale di precipitazione estiva), sull'intensità e durata del freddo patito dalle piante (si noti in Appendice 1 la corrispondenza tra C.S., numero di giorni e media delle ore/giorno con temperatura inferiore allo 0) : in sostanza esso fornisce una misura sintetica della mitezza del clima, ma non è adatto a definire sinteticamente le grandi variazioni ecologico-ambientali all'origine dei diversi tipi climatici riconosciuti da Rivas-Martínez né, a maggior ragione, le differenze alla base delle distinzioni, ancor più ampie, fatte dagli autori precedenti (quali Emberger, 1930, 1942 ; Le Houérou, 1959 ; Debrach, 1981). A questo punto si possono fare alcune considerazioni :

1. L'indice di Mitrakos è adatto ad essere utilizzato, come ha fatto il suo ideatore, per indagini autoecologiche, in cui i limiti bioclimatici relativi alla distribuzione, alla fioritura, all'habitus vegetativo di una data specie si possono esprimere tramite un intervallo di valori di D.S. e C.S. tollerati dalla specie stessa. L'indice è parimenti utilizzabile, come ha fatto Blasi (1994), a completamento delle informazioni ottenute mediante la correlazione di una data serie vegetazionale ad un tipo climatico individuato con l'ausilio di un indice adatto ad essere impiegato in indagini territoriali su vasta scala, quale quello, appunto, di Rivas-Martínez.

2. Non sembra corretto il suo impiego per ricercare delimitazioni confrontabili con quelle di altri indici bioclimatici, in quanto l'indice di Mitrakos non prende in esame i fattori climatici nella loro totalità, ma solo le loro fasi critiche, esprimendone l'intensità. Le delimitazioni ottenibili con il solo utilizzo dell'indice di Mitrakos non esprimono quindi l'equità climatica quanto piuttosto l'equità della mitezza del clima. Con ciò si spiegano i valori a volte concordanti e a volte discordanti ottenuti da Schirone (1988) nel paragonare l'indice di Mitrakos a quelli di Le Houerou o di Emberger ed in questa sede nel paragonarlo a quelli di Rivas-Martínez : solamente quando si limita l'indagine a territorî poco estesi e/o presentanti deboli diversità climatiche o, al contrario, quando si prendono in esame siti con grandi diversità climatiche (ad es. stazioni litoranee e stazioni di montagna interna) tutti gli indici sono in accordo.

3. Non è sempre verificata l'ipotesi di Pierangeli (1988) che identifica nel rapporto W.C.S./S.D.S. >1 il limite tra tipi climatici eumediterranei ed oromediterranei, nonché il limite superiore per l'affermazione delle sclerofille mediterranee : tale disequazione è infatti verificata, ad esempio, per le stazioni di Latina, Napoli Capodichino, Genova, Roma ed Albenga (Appendice 1).

4. Generalmente negli studi fitosociologici, data l'ampiezza di scala su cui operano gli indici bioclimatici, si correlano ad essi intere serie dinamiche. L'indice di Mitrakos invece è potenzialmente correlabile a ciascuna delle associazioni che compongono le macroserie per esprimere, previe opportune integrazioni, le condizioni di stress imposte alla vegetazione dalle caratteristiche stazionali.

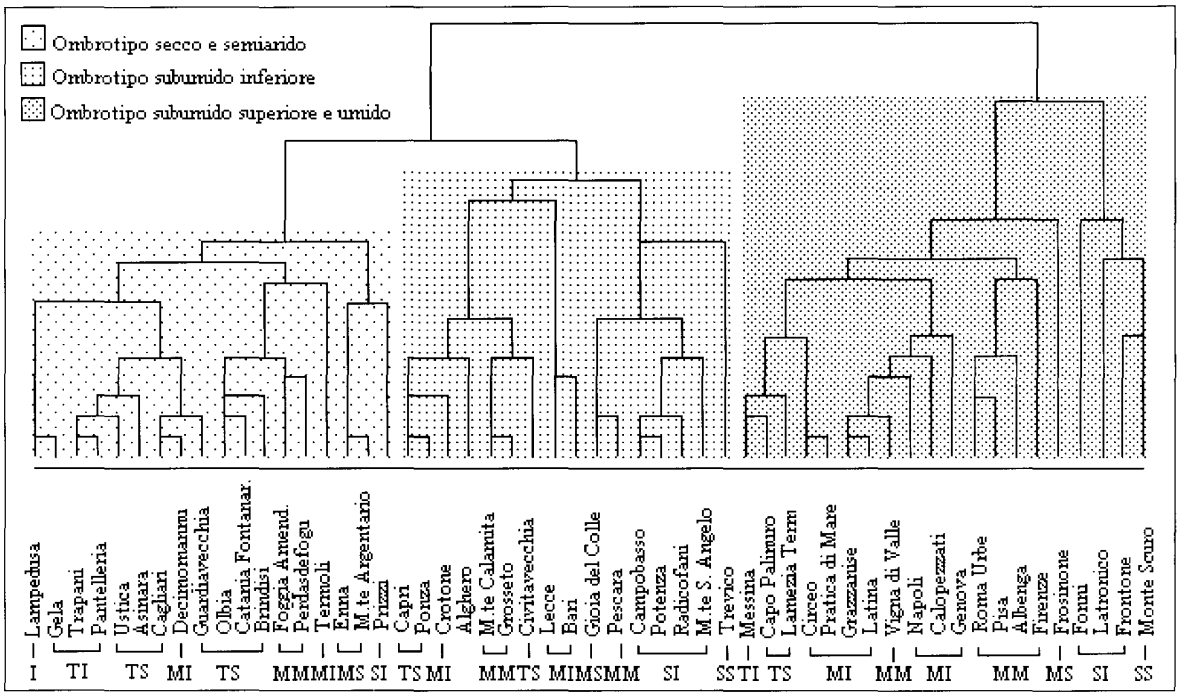

Figura 2. Dendrogramma delle stazioni considerate. L'ombrotipo di Alghero e Bari è secco superiore, ma le loro precipitazioni sono assai prossime alla soglia dell'ombrotipo subumido inferiore (600 mm), in cui si trovano inquadrate. Per lo stesso motivo Capo Palinuro e Lamezia Terme, di ombrotipo subumido inferiore, si trovano inquadrate tra le stazioni di ombrotipo subumido superiore. In basso vengono indicate le iniziali dei rispettivi termotipi (Tab.1). Le stazioni di Floresta, Vallicciola, Serpeddì ed Etna sono state escluse dall'elaborazione per insufficienza di dati.
Dendrogram of the considered weather stations. The ombrotype of Alghero and Bari is upper dry, but values of their annual rainfall are very close to the lower subhumid threshold (600 mm), where they result included. For the same reason, Capo Palinuro and Lamezia Terme (ombrotype: lower subhumid) are included among the stations having an upper subhumid ombrotype. Initials of the correspondent thermotypes are reported below. Weather stations of Floresta, Vallicciola, Serpeddì and Etna have been excluded from the cluster analysis for insufficient data.

Attraverso l'applicazione dell'indice su un congruo numero di stazioni primarie ove sia presente una data fitocenosi, si potrebbe determinare un intervallo numerico che contribuisca ad una migliore definizione della valenza ecologica della fitocenosi in esame, analogamente a quanto fatto da Mitrakos per alcune specie. Un tale impiego impone tuttavia delle integrazioni che consentano all'indice di Mitrakos di prendere in considerazione i fattori microclimatici responsabili del passaggio da una fitocenosi all'altra. E' necessario cioè potenziare l'analiticità dell'indice mediante l'introduzione di variabili strettamente legate alle caratteristiche stazionali.

CONSIDERAZIONI METODOLOGICHE E PARAMETRIZZAZIONE DEI FATTORI STAZIONALI

È possibile introdurre nella formula dell'indice di Mitrakos alcune variabili legate ai fattori stazionali senza complicare la formula originaria dell'indice, grazie alla sua caratteristica di prestarsi alla combinazione lineare delle variabili : come i valori stagionali ed annuali di stress vengono determinati sommando i singoli valori mensili, così è possibile sommare o sottrarre a ciascuno di questi ultimi uno o più valori derivati da formule diverse esprimenti

l'influenza di ciascun fattore sulla vegetazione. Il principale vantaggio offerto dalla combinazione lineare è la possibilità di escludere dalla formula le variabili che di volta in volta risulteranno trascurabili o di aggiungerne altre significative senza che ciò vada ad influire sull'espressione delle altre variabili. In questa sede verranno proposte formule esprimenti l'influsso dei più frequenti fattori stazionali : esposizione, inclinazione dei versanti, altitudine e distanza dal mare, ma, ad esempio, qualora si studiassero le forre tali fattori potranno essere trascurati per parametrizzare l'influenza su D.S. e C.S. dei gradienti termico ed igroscopico ; su un vulcano si potrà stabilire una costante che esprima l'incremento di D.S. dovuto alla bassissima capacità di ritenzione idrica delle sabbie vulcaniche e così via. L'importante è che per ciascun fattore venga stabilito *una tantum* il peso che esso dovrà assumere nelle formule di Mitrakos.

Prima di passare all'esposizione dei risultati, è opportuno esporre i criterî determinanti la scelta e la parametrizzazione dei fattori da far comparire nelle formule:

1. Dato che l'omogeneità nella copertura vegetale è un buon indicatore spaziale dell'omogeneità stazionale, in primo luogo vanno individuati, in un gruppo di stazioni caratterizzate da serie di vegetazione analoga, i fattori ecologici più importanti nel determinare le condizioni ambientali responsabili dell'omogeneità vegetazionale. Non è il caso di appesantire eccessivamente la formula per eccesso di minuzia nelle osservazioni ambientali, sia per praticità, sia perché, dato che l'indicizzazione di qualsiasi variabile comporta un proprio margine di errore, l'errore risultante dalla combinazione lineare delle variabili potrebbe non essere più accettabile. E' importante soprattutto che l'effetto di ciascun fattore ambientale considerato non sia assimilabile o in parte sovrapponibile a quello di un'altro che si voglia includere nella formula. Questo controllo di indipendenza può essere fatto su base logica o su base numerica mediante una matrice di contingenza 2x2.

2. È fondamentale che le variabili che si vogliono considerare siano agevolmente quantificabili in modo attendibile, poiché l'utilità di un indice sta nella possibilità di confrontare empiricamente il maggior numero possibile di situazioni reali. Senza dubbio sarebbe più aderente alle condizioni reali di stress introdurre nelle formule di Mitrakos variabili derivate, anziché dall'esposizione, acclività o distanza dal mare di una stazione, da un campionamento statistico effettuato nell'arco di trent'anni sull'effettiva insolazione mensile e sull'evapotraspirazione reale nella stazione medesima, ma in tal modo non sarebbe salvaguardata quell'immediatezza di applicazione dovuta alla facile reperibilità dei dati richiesti.

3. Per determinare l'espressione matematica dei fattori da prendere in considerazione, è opportuno cercare di individuare l'andamento grafico dell'incidenza del fattore sullo stress subito dalle piante. Tale andamento dovrà essere ricavato da osservazioni fatte su un numero sufficiente di ecotopi analoghi. Ad esempio, per determinare l'andamento dello stress dovuto all'inclinazione dei versanti sono state compiute osservazioni su un geosigmeto sviluppantesi a quote comprese tra 10 e 400 m s.l.m. e situato nell'immediato entroterra della piana di Paestum (Salerno), in esposizioni comprese tra NW e SW. La matrice del substrato è ovunque calcarea ed il suolo dei versanti, ad un superficiale esame fisionomico, si presenta bruno, mediamente aggregato, con scheletro scarso o nullo in superficie laddove raggiunge o supera lo spessore di 1 m.. Localmente, nelle zone scoscese lo strato superficiale si presenta fortemente eroso, con frequenti affioramenti di rocce calcaree compatte. In basso prevalgono i suoli alluvionali, notevolmente profondi e ricchi di componente argillosa, fino a presentare talvolta caratteri vertici. La Figura 3 è una rappresentazione cronosequenziale (molto approssimativa) delle differenze vegetazionali osservabili in funzione della pendenza nell'area considerata : in primo piano è rappresentato il diverso utilizzo colturale : sui suoli alluvionali, e fino a pendenze di 25°-30° prevalgono le colture irrigue (1) (soprattutto medicai, granoturco, pomodori, ortaggi). Tra i 30° e i 45° si osservano soprattutto oliveti e vigneti (2), con una predominanza dei vigneti su terreni più scoscesi e sassosi. Oltre tali pendenze si trovano sporadiche coltivazioni di fichi (3). Non sono considerate le associazioni infestanti in quanto non determinate direttamente dalla pendenza ma soprattutto dalla diversa lavorazione del suolo. In secondo piano sono rappresentati i tipi di vegetazione erbacea perenne che si instaurano a pochi anni dall'abbandono delle colture : le comunità della zona alluvionale, sono costituite da un contingente dominante degli *Arrhenatheretalia*, compenetrato ad elementi sinantropici degli *Artemisietea* e *Stellarietea*

mediae (4). Ove il suolo presenta caratteri vertici vi è ancora una forte presenza di specie degli *Arrhenatheretalia*, ma risulta dominante il contingente floristico degli *Agropyretea intermedii-repentis* (5). Nel complesso comunque risulta evidente la relativa mesofilia di tali associazioni prative. La vegetazione erbacea degli oliveti, per pendenze comprese tra 30° e 40° presenta un aumento progressivo delle specie dei *Thero-Brachypodietea* (= *Lygeo-Stipetea, sin. synt.*), che diventano dominanti su inclinazioni superiori a 40° (6). Pendenze superiori a 60° presentano una cotica erbosa discontinua, inframmezzata ad affioramenti rocciosi sempre più cospicui. Qui alle specie dei *Thero-Brachypodietea* si uniscono numerose camefite eliofile amanti dei suoli scheletrici, quali *Teucrium flavum, Thymus spinulosus, Onosma echioides, Lobularia maritima, Thymus longicaulis, Micromeria graeca, Sedum rupestre, Sedum album, Sedum hispanicum* ed il complesso forma una sinusia con pratelli terofitici degli *Stipo-Trachynietalia distachyae* (7). Analogamente, i pendii scoscesi esposti a sud, sono dominati da *Hyparrhenia hirta* in sinusia con le comunità terofitiche suddette (8). Simili popolamenti si rinvengono, ad esempio, sotto l'abitato di Altavilla Silentina e denotano condizioni ambientali decisamente termoxeriche. Tralasciando la vegetazione arbustiva, sullo sfondo è rappresentata l'ipotetica vegetazione naturale potenziale : *Lauro-fraxinetum oxycarpae* su suoli alluvionali con falda superficiale e *Carpino-Quercetum cerridis* su suoli con caratteri vertici, entrambi dei *Querco-Fagetea* e con mantello dei *Rhamno-Prunetea* (9) ; *Oleo-Quercetum virgilianae* su versanti con inclinazioni inferiori a 45° e *Viburno-Quercetum ilicis* su pendenze superiori, entrambi dei *Quercetea ilicis* e con mantello dei *Pistacio rhamnetalia alaterni* 10. Sebbene il bosco planiziale sia pressoché scomparso dal territorio indagato, ne restano alcuni lembi significativi nella riserva di Persano (Pedrotti & Gafta, 1996), oltre a numerosi toponimi significativi, siti nei comuni di Altavilla Silentina e di Albanella, alcuni facenti riferimento a *Quercus robur*, (contrade Quercioni, Cerzavecchia, Cerzagrossa), altri riferentisi a *Q. cerris* (contrade Cerrina, Due Cerri). Da questo esempio risulta chiaro che la componente di stress dovuta all'inclinazione del versante si mantiene quasi nulla per valori compresi tra 0° e 30° ; quindi aumenta

Figura 3. Rappresentazione del geosigmeto-esempio. Representation of the *Geosygmetum*-example

progressivamente fino a raggiungere il massimo per inclinazioni superiori a 70°. Il progressivo aumento dello stress è testimoniato da cambiamenti macroscopici nella vegetazione. Ad ogni fitocenosi individuata è possibile assegnare una coppia di valori, di cui il primo è dato dall'inclinazione del versante, il secondo viene desunto da una scala numerica arbitraria esprimente la variazione di D.S. e C.S. in funzione dell'inclinazione del versante. Riportando su un piano cartesiano ciascuna coppia di valori, si ottiene una rappresentazione bidimensionale costituita da un insieme di punti la cui curva di regressione, se sono stati scelti correttamente gli ecotopi campione, è assimilabile ad una funzione matematica o ad una combinazione di più funzioni. Per quanto riguarda il nostro esempio, la funzione esprimente l'incremento di D.S. dovuto alla pendenza ha l'andamento della curva 1, rappresentata in Figura 4.

4. Determinata la formula generica della funzione esprimente l'andamento della curva che interessa è necessario individuare, nel fascio di curve descritto dalla funzione, quella che le farà assumere il giusto peso nella formula di Mitrakos. La scelta delle costanti arbitrarie rappresenta la fase più delicata della procedura. In tale fase, alla competenza ed all'esperienza del ricercatore si affianca l'analisi statistica con le metodologie di confronto incrociato e lo studio dei casi limite. Il valore delle costanti arbitrarie, come già detto, deve essere stabilito *una tantum*, ed esclusivamente per far assumere a ciascun parametro che si vuole introdurre nelle formule di Mitrakos l'opportuno ordine di grandezza. Se non si dispone di un numero di osservazioni sufficiente a determinare i valori opportuni delle costanti arbitrarie, o, soprattutto, se non è stato possibile effettuare una verifica mediante lo studio dei casi limite, è preferibile indicare un intervallo numerico tra cui sono compresi i valori che presentare come esatti valori largamente approssimativi, rischiando che essi possano essere invalidati qualora successive applicazioni ne dimostrino la scorrettezza. Qualora ciò accadesse, tutte le applicazioni fatte fino a quel punto sarebbero invalidate di conseguenza.

RISULTATI

Seguendo la procedura esposta nel paragrafo precedente sono state parametrizzate l'influenza dell'inclinazione ed esposizione dei versanti, dell'altitudine e della distanza dal mare sullo stress termico ed idrico subito dalle fitocenosi. Per ciascuno di questi fattori stazionali viene proposta una formula per determinare il valore mensile da sommare o da sottrarre al D.S. ed al C.S. in modo da ottenere una quantificazione dello stress più aderente alle condizioni reali.

Influenza dell'inclinazione dei versanti sul D.S.

L'inclinazione dei versanti determina (unitamente ai caratteri intrinseci di struttura e tessitura) lo spessore medio del suolo e (unitamente alla latitudine) l'angolo di incidenza dei raggi solari sulla superficie del suolo nei diversi periodi dell'anno. Dell'incidenza dei raggi solari si parlerà dopo aver trattato l'esposizione dei versanti, in quanto i due aspetti sono strettamente correlati.

Lo spessore medio del suolo, superata la pendenza di 30°-35°, chiamata dai geomorfologi "angolo di riposo", decresce assai rapidamente (Baver, 1956) (Figura 4, curva 2). Ciò nel periodo estivo ha, unitamente all'esposizione ed alle caratteristiche intrinseche del suolo, importanti ripercussioni sul prosciugamento e sull'escursione termica giornaliera della rizosfera : a parità di condizioni i suoli più profondi si prosciugano meno rapidamente dei suoli sottili e poiché l'inerzia termica dell'acqua è maggiore di quella dei suoli (e quest'ultima è a sua volta superiore a quella delle rocce), ne consegue che minore è il contenuto idrico e lo spessore di un suolo, maggiore sarà la sua variazione termica nell'arco della giornata. Ciò ha ovvî effetti sullo stress idrico subito dalla vegetazione in area mediterranea, ove la scarsità di piogge estive mantiene i suoli ben al di sotto della soglia di saturazione idrica durante i tre mesi più caldi dell'anno (Turc, 1961).

Sulla base di osservazioni personali e delle informazioni reperite in letteratura (Boyko, 1947 ; Loissant P., 1983) è stato costruito l'andamento del fattore di stress idrico dovuto all'inclinazione dei versanti (Figura 4, curva 1).

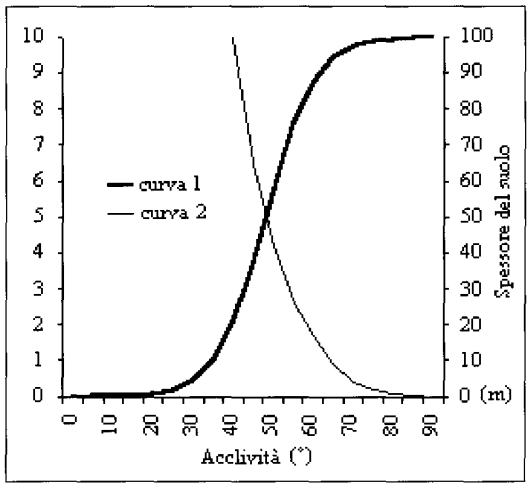

Figura 4. Curva dell'influenza dell'inclinazione dei versanti sul D.S. (curva 1). Ad essa è stata correlata la curva della variazione dello spessore del suolo in funzione dell'acclività nella piana di Paestum e zone limitrofe, desunta dai dati forniti da due ditte di trivellazione.
Curve of the influence of sloping degree on D.S. (curve 1). It has been related to the curve of the soil thickness in the surrounding of Paestum (Scele plain, Campania region), derived from measures kindly supplied by two drilling firms.

L'andamento della curva 1 è espresso dalla seguente formula :

$$I = 10^4 / (10^3 + 1{,}18^{(90-\alpha_t)})$$

in cui α_t rappresenta l'angolo di inclinazione del pendio espresso in gradi decimali. Il valore di I, che va sommato al valore mensile di D.S., varia tra 0 e 10 esclusivamente in funzione delle variazioni di α_t.

Influenza dell'esposizione sul D.S.

L'esposizione determina (unitamente alla latitudine) la durata dell'insolazione diretta di un pendio nei diversi periodi dell'anno. E' pertanto responsabile del surriscaldamento dell'aria e del suolo, che fa incrementare notevolmente, a livello microclimatico, la traspirazione (Wells, 1989). Data la scarsa nuvolosità che caratterizza nel periodo estivo il bacino mediterraneo, l'esposizione diviene un fattore stazionale di primaria importanza nell'incremento dello stress idrico.

Le prove della sensibilità della vegetazione all'esposizione sono così frequenti e note, non solo in area mediterranea, che risulta superfluo approfondire il discorso in questa sede : basti pensare che lo studio delle differenze nella copertura vegetale dei versanti delle vallate alpine con andamento Est-Ovest si annovera tra le prime applicazioni del metodo fitosociologico.

Seguendo la procedura esposta in precedenza, è stato preliminarmente determinato l'andamento grafico del fattore di stress idrico dovuto all'esposizione (Figura 5, curva 1). Lo scostamento della curva 1 rispetto all'andamento normale (Figura 5, curva 2) è dovuto al fatto che per esposizioni rivolte ad Ovest le ore di insolazione diretta coincidono con il periodo in cui l'umidità dell'aria raggiunge i valori minimi. Prova di ciò si può trovare anche al di fuori dei territorî mediterranei : si riporta, a titolo di esempio, il risultato di un'indagine sull'abbondanza delle specie più termoxerofile (quali *Satureja montana, Ononis pusilla, Argyrolobium zanonii, Heteropogon contortus, Artemisia alba, Centranthus ruber, Fumana procumbens, Galium lucidum, Euphorbia nicaeensis, Asperula cynanchica, Stachys recta*) tra quelle presenti nei brometi a cotica discontinua colonizzanti i pendii fortemente acclivi lungo le sponde del lago di Garda : si è notato che, nell'ambito della stessa associazione, l'indice di ricoprimento specifico di tali specie è sensibilmente più consistente sui pendii esposti a Ovest che sui pendii esposti ad Est (Figura 6). Si noti infine la corrispondenza tra l'andamento della curva 1 e quello

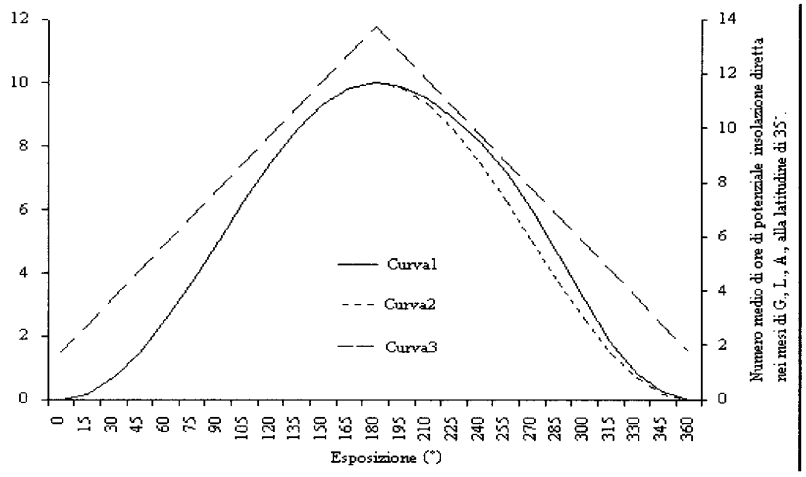

Figura 5. Curva dell'influenza dell'esposizione dei versanti sul D.S. (curva 1). Ulteriori spiegazioni nel testo.
Curve of the influence of slope exposure on D.S. (curve 1). Further explanations in the text.

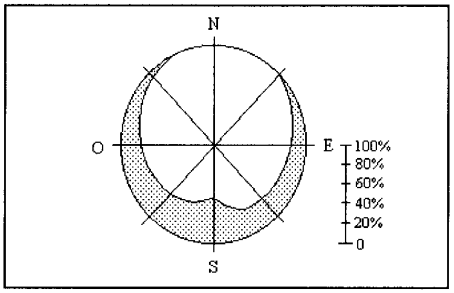

Figura 6. Percentuale di ricoprimento delle specie più termoxerofile sul totale delle superfici ricoperte dagli xerobrometi lungo le sponde del lago di Garda. Percentage of cover abundance of thermoxerophilous chamaephytes in areas (total) covered by *Xerobromion*-communities along the shores of Garda lake.

della cuspide (Figura 5, curva 3) rappresentante il numero medio di ore/giorno di potenziale insolazione diretta a seconda della diversa esposizione alla latitudine di 35°. Malgrado il numero medio di ore di sole/giorno varî a seconda della latitudine (Figura 7), non se ne tiene conto nella formula proposta, in quanto il minore numero di ore di sole che caratterizza la parte meridionale del bacino del Mediterraneo è ampiamente ricompensato dal maggiore angolo d'incidenza dei raggi solari, che determina maggiori temperature (Figura 8).

L'andamento della curva 1 è espresso dalla seguente formula :

$$E = 5(1-\cos \zeta) + 1{,}05^{-(\zeta-270/10)2}$$

ove ζ rappresenta l'angolo di esposizione del versante espresso in gradi decimali. Il valore di E, che va sommato al valore mensile di D.S., varia tra 0 e 10 esclusivamente in funzione delle variazioni di ζ. Se un sito è pianeggiante e non vi sono ostacoli orografici che riducano le ore d'insolazione, E assumerà comunque il suo massimo valore.

Qualora ostacoli orografici impediscano ad un sito di essere esposto alla totalità delle ore potenziali di insolazione previste dalla sua esposizione, si può misurare direttamente, in qualsiasi giorno soleggiato dell'anno, il numero effettivo di ore d'insolazione diretta di cui gode il sito (I_{eff}) e rapportare quindi tale valore a quello delle ore di sole di cui avrebbe goduto in quel giorno il sito, data la sua latitudine e la sua esposizione, in assenza dell'ostacolo orografico (I_{pot}).

Dalla seguente proporzione, in cui n rappresenta il valore di stress per la data esposizione in assenza di ostacoli orografici, si ricava infine n_1 che rappresenta il valore di stress per il sito in questione.

$$I_{pot} : n = I_{eff} : n_1 \quad \rightarrow \quad n_1 = n \cdot I_{eff}/I_{pot}$$

Per determinare I_{pot} è possibile seguire la semplice procedura algebrica riportata in appendice 2.

Influenza dell'inclinazione e dell'esposizione sul C.S.

Come già accennato, l'inclinazione di un versante ha influenza sull'angolo di incidenza dei raggi solari. Dall'angolo di incidenza dei raggi solari dipende il riscaldamento terrestre. La quantità di calore che arriva alla superficie superiore dell'atmosfera è espressa dalla formula $Q_1 = Q$ sen, ove Q rappresenta la costante solare, pari a 2 langley al minuto (1 langley = 0,9915 cal/cm^2) ed è l'angolo di incidenza. Per quantificare il calore che raggiunge la superficie terrestre sarebbe necessario tener conto anche della dispersione del calore nell'attraversamento dell'atmosfera, che è in media del 35% ; inoltre se l'angolo d'incidenza è piccolo, i raggi del sole devono compiere un percorso più lungo e di conseguenza la dispersione è maggiore (Bosellini, 1985). A parità di dispersione, comunque, la relazione trigonometrica espressa dalla formula anzidetta rimante valida.

Nei mesi invernali (Dic., Gen., Feb.), la declinazione solare (ε) varia tra 23°27' S (il 21 Dic.) e 5°33'25"S (il 29 Feb.). Corrispondentemente l'angolo massimo d'incidenza (α_i) dei raggi solari, alla latitudine di 35°N, [$\alpha_i = 90° - (35° + \varepsilon)$] varia tra 31,6° + μ (il 21 Dic.) e 49,4° + μ (il 29 Feb.), μ esprime la variazione dell'angolo d'incidenza dovuto all'indice di rifrazione dell'atmosfera; tuttavia, essendo tale variazione trascurabile per i nostri fini, la sua indicazione verrà d'ora in poi tralasciata. Di conseguenza nel periodo che va dall'1 Dic. all'11 Gen., un pendio esposto a S, situato a 35°N di latitudine ed avente inclinazione compresa tra 58,4° e 53° potenzialmente può ricevere per due volte i raggi del sole con incidenza perpendicolare quando il sole è allo zenith ; mentre nello stesso periodo, esposizioni comprese tra 346,9° N e 13,1°N non ricevono neppure un raggio di sole (esposizioni comprese tra 356° N e 4° N non prendono mai sole addirittura dal 12 Ott. al 29 Feb. !). Dall'11 Gen. al 29 Feb. un pendio esposto a S e con inclinazione compresa tra 52,8° e 40,6° potrà invece ricevere almeno una volta i raggi del sole con incidenza perpendicolare quando il sole è allo zenith.

È noto che nei mesi freddi i valori minimi delle temperature si raggiungono nelle giornate terse, quando, essendo ridotto l'effetto coibentante offerto dall'inerzia termica dell'acqua presente in atmosfera, sono più bruschi gli sbalzi termici. Se si considera che, in base alla formula $Q_1 = Q$ sen ι, per ι = 30° la quantità di calore per unità di superficie è ridotta della metà (Figura 8), appare evidente il vantaggio che offre, a livello microclimatico, poter beneficiare nel periodo più freddo dell'anno di un discreto numero di ore in cui l'incidenza dei raggi solari è prossima a 90° (Wells, 1989). A questo si aggiunge che i pendii esposti a mezzogiorno sono in genere riparati dalle correnti d'aria più fredde, che in area mediterranea spirano dai quadranti settentrionali.

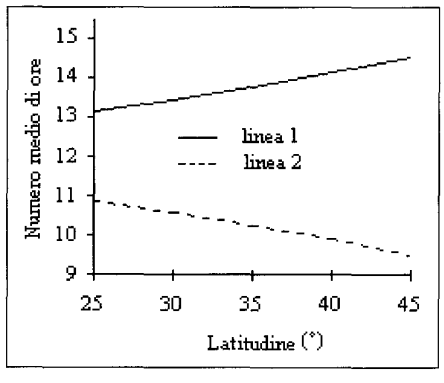

Figura 7. Numero medio giornaliero di ore di sole potenziali nei mesi di G., L., A. (linea 1) e di D., G., F. (linea 2) per latitudini comprese tra 25° e 45°.
Mean number of potential sunny hours per day on Jun., Jul., Aug. (line 1) and on Dec. Jan. Feb. (line 2) for latitudes between 25° and 45°.

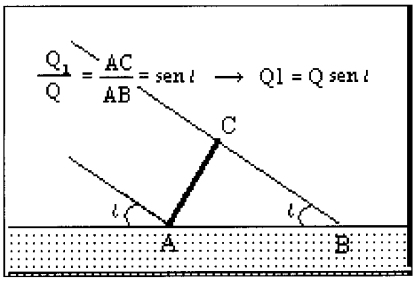

Figura 8. Rapporto tra quantità di calore (Q) per unità di superficie ed angolo d'incidenza (ι) dei raggi solari (da Bosellini (1985), modificato).
Ratio between quantity of heat (Q) per surface unit and angle of incidence (ι) of sunbeams (from Bosellini (1985), modified).

Ciò permette l'instaurazione a livello locale di un piccolo nucleo di alta pressione atmosferica che rimane stazionario fino a sera inoltrata, quando, cessato il rilascio del calore assorbito dal suolo durante il giorno, avviene il completo rimescolamento delle masse d'aria. Una dimostrazione di quanto esposto si può avere osservando i popolamenti di leccio lungo le sponde benacensi : la stragrande maggioranza di tali popolamenti si colloca in stazioni semirupestri su pendii con inclinazione compresa tra 60° e 75° (Figura 9). A ciò ha contribuito di certo un imponente disboscamento, perpetrato fino agli inizi del secolo attuale, per lasciar spazio alla coltivazione dell'ulivo (Bèguinot, 1924), ma è un dato sicuramente significativo che le uniche stazioni di leccio presenti su inclinazioni di 40° - 45°, come ad es. quella alle pendici del m.te Luppia, presso Garda, siano esposte a S e molto vicino al lago. Per i popolamenti esposti ad E, o ad O, quali quelli abbarbicati alle rocce tra Gargnano e Limone del Garda e quelli presso Malcesine, le pendenze risultano strettamente comprese tra i 60° ed i 75°. Ciò accade anche per le stazioni esposte a S nella bassa valle del Sarca, ove, allontanandocisi dal bacino benacense, è meno intensa l'influenza mitigatrice delle acque del lago. Considerando come latitudine media del lago di Garda quella di 45,6° N, i pendii che possono ricevere per due volte i raggi del sole con incidenza di 90° nel periodo 1 Dic. - 11 Gen. (quando il sole è allo zenith) sono proprio quelli con angolo d'inclinazione compreso tra 63,7° e 69,5°. Sulla base di questa e di altre osservazioni sull'ubicazione di popolamenti vegetali prossimi al loro limite distributivo, è stato definito l'andamento grafico dell'effetto mitigante che esposizione ed inclinazione hanno sul C.S. (Figura 10). Tale andamento è descritto dalla seguente formula :

$$I \cap E = 8(1-\cos \zeta)^4 / [(6 + 1{,}12^{(\gamma - \alpha_l)}).(1 + 1{,}12(\alpha_l - \gamma_l)]$$

in cui ζ rappresenta l'angolo di esposizione espresso in gradi decimali, α_l rappresenta l'angolo di inclinazione del pendio espresso in gradi decimali, γ rappresenta l'angolo d'inclinazione che porta ad essere perpendicolare l'incidenza dei raggi solari il giorno 11 Gen. (data la latitudine del sito) e γ_l rappresenta l'angolo d'inclinazione che porta ad essere perpendicolare l'incidenza dei raggi solari il giorno 21 Dic. (data la latitudine del sito) *aumentato di 10 unità*. Il valore di $I \cap E$, che va sottratto al valore mensile di C.S., varia tra 0 e 15,5 esclusivamente in funzione di ζ e di α_l.

Influenza della distanza dal mare e della quota sul D.S.

Le acque del Mediterraneo hanno influenza sia sul C.S. che sul D.S.. Dell'influenza mitigatrice sul C.S. è inutile parlare : essa è legata all'andamento delle temperature ed implicitamente determina, unita alla quota ed alla latitudine di un sito, il valore di C.S. calcolato mediante la formula di Mitrakos. Prenderemo in considerazione invece l'azione mitigatrice esercitata dalla vicinanza del mare sullo stress idrico subito dalla vegetazione durante i mesi più caldi dell'anno. Le alte temperature determinano un'imponente evaporazione della superficie marina, che satura di umidità uno strato d'aria piuttosto spesso a diretto contatto con la superficie marina (Colacino & Dell'Osso, 1977).

Tale massa d'aria viene giornalmente sospinta

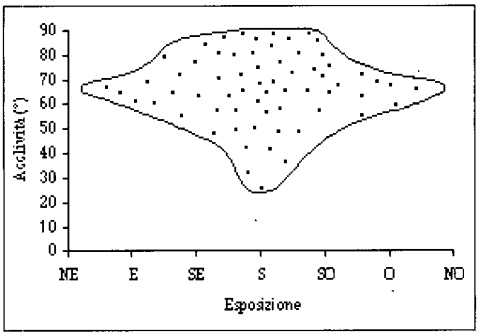

Figura 9. Relazione tra acclività ed esposizione dei popolamenti di leccio benacensi.
Relation between exposure and sloping gradient in holm-oak relict communities of Garda Lake.

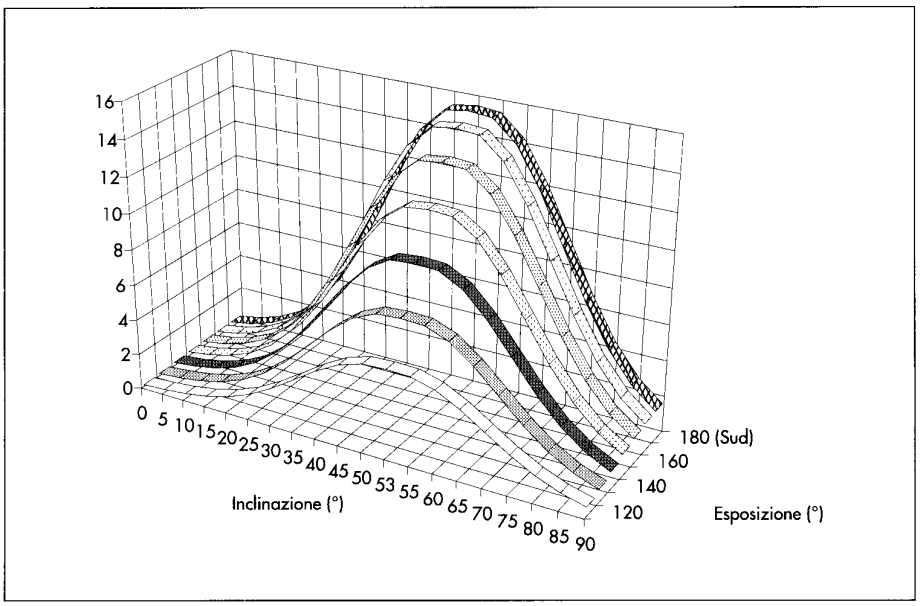

Figura 10. Andamento dell'influenza di esposizione ed inclinazione sul C.S. Per esigenze grafiche la superficie, in realtà continua, è stata frammentata nelle sue curve fondamentali.
Influence of exposure and sloping gradient on C.S. The continue surface has been represented with its fundamental curve, due to graphic exigences.

verso la terraferma dalla brezza marina, che spira verso terra dalle prime ore del pomeriggio fino al tramonto (Giacomelli, 1915 ; Pagliari, 1981). Questo fenomeno determina una vantaggiosa riduzione della traspirazione nelle ore pomeridiane ed è inoltre responsabile della condensazione di abbondante rugiada durante le ore notturne. Una specie legata a tale condensazione risulta essere per es. l'alloro, che essendo una specie evitante lo stress idrico per dispersione (Salleo & Lo Gullo,1988 ; Salleo, 1994) si avvantaggia notevolmente delle precipitazioni occulte : non è un caso che tale specie risulti spesso abbondante a monte delle valli costiere, ove le correnti di aria umida, incanalatesi al livello del mare, si espandono improvvisamente, cedendo di colpo la loro umidità, come avviene, ad esempio, lungo i fianchi dei monti alle spalle della Versilia.

In assenza di ostacoli orografici lungo la costa, la corrente di umidità sospinta dalla brezza si diffonde via via lungo un gradiente uniformemente decrescente

man mano che si procede verso l'interno ed il carico di umidità si esaurisce completamente a 70-80 Km dalla costa, vale a dire 20-30 Km oltre il limite strumentale medio della brezza.

In presenza di rilievi costieri, poiché salendo di quota la temperatura dell'aria diminuisce in media di 0,6° C ogni 100 m, il grosso dell'umidità si condensa bruscamente lungo una fascia situata a quota variabile in funzione della latitudine. Tale fascia, denominata in Italia secondo la definizione più attuale "fascia sannitica" (Pignatti, 1979), è indicata da un rapido cambiamento della vegetazione, che tende a privilegiare specie più marcatamente mesofile rispetto a quelle delle quote sottostanti. In Italia molti autori hanno scritto su tale fascia, tuttavia le loro definizioni non sono del tutto univoche nella determinazione dei limiti altitudinali, sia a causa di opinioni discordanti sul ruolo ecologico rivestito dalle diverse specie indicatrici, sia perché rare sono state le indagini estese a tutta la penisola. Per un ulteriore approfondimento sull'argomento si rimanda, oltre al lavoro di Pignatti (*l.c.*), ai lavori di Schmid (1963) Blasi (1994), Scoppola *et al.* (1993), Giacomini & Fenaroli (1958). Questi ultimi forniscono una sinossi delle posizioni di Giacobbe, Negri, Savi, e di altri autori dell'epoca.

Dalle indicazioni dei vari autori e da osservazioni personali, è stata estrapolata una funzione che permetta di determinare la quota ove l'effetto di condensazione è massimo (Q_m), evitando di cercare di delimitare inferiormente e superiormente la fascia ove si verifica il fenomeno, in quanto ciò è ulteriormente complicato da fattori orografici concomitanti e dall'intensità dei venti. Tale funzione è data da : $Q_m = 40(60 - \varphi)$, ove φ rappresenta la latitudine a cui si trova il sito considerato. In base a tale funzione, la quota media di condensazione in area mediterranea (25° N $\leq \varphi \leq$ 45° N, secondo Daget, 1977) risulta essere compresa tra 600 e 1400 m di quota. Un esempio ove tale fascia è ben individuabile si può trovare sui colli Albani, presso Roma : fino ad una quota di 450 - 500 m, in un paesaggio dominato da vigneti ed olivi, si rinvengono rare formazioni naturali interpretabili come residui impoveriti dell'*Orno-Quercetum ilicis* ; salendo di quota la vegetazione naturale è rappresentata dallo *Hieracio-Quercetum petreae* (l'antico *nemus Dianae* che diede il nome all'abitato di Nemi), oggi in gran parte sostituito da castagneti. Continuando a salire, proprio sulla sommità del M.te Cavo (956 m), ricompaiono formazioni di leccio in stazioni semirupestri. Senza dubbio la ricomparsa del leccio in tale situazione è dovuta soprattutto all'inclinazione ed esposizione del versante, ma è soprattutto significativa la quota inferiore d'arresto dell'*Orno-Quercetum ilicis*. Casi analoghi sono frequentissimi su tutti i rilievi prospicienti il mare (esempi analoghi sono osservabili ad esempio sul versante meridionale delle Alpi Liguri o sui M.ti Alburni).

Sulla base di quanto esposto è stata elaborata una funzione che esprime il valore da sottrarre al D.S. in base alla quota (Q) ed alla distanza dal mare (D) di un dato sito :

$$Q \cap D = 63.[1 + 1{,}07\text{-}(h\text{-}Qm/20)2] / (8 + 1{,}05^{d})$$

in cui d rappresenta la distanza dal mare in linea d'aria espressa in Km, h rappresenta la quota espressa in metri e Q_m è l'altitudine media di condensazione ricavata, data la latitudine, applicando la formula indicata in precedenza. La funzione $Q \cap D$, il cui valore è compreso tra 0 e 14, ha l'andamento grafico rappresentato nella Figura 11. Ovviamente, tale funzione verrà presa in considerazione solamente qualora tra l'area di studio ed il mare non siano frapposti ostacoli orografici.

In conclusione si espone una regola di carattere generale : le scale di D.S. e di C.S., così come proposte da Mitrakos, sono limitate tra 0 e 100 per motivi di praticità, tuttavia il calcolo mensile dei valori di stress conduce spesso alla determinazione di valori negativi o superiori a 100. Le componenti di stress determinate dai valori stazionali, valutate mediante le formule proposte in questa sede, vanno sommate o sottratte ai valori di Mitrakos prima di effettuare qualsiasi arrotondamento. Se, dopo tale operazione, si avranno ancora valori negativi o superiori a 100 si potrà effettuare l'arrotondamento proposto da Mitrakos.

CONCLUSIONI

Considerando il ruolo rivestito dai fattori stazionali nel mitigare od accentuare i due stress climatici subiti dalla vegetazione mediterranea, si è cercato di armonizzare alla variazione di tali fattori una

oscillazione dei valori di D.S. e C.S., per renderli più aderenti alle condizioni reali.

Ciò è stato fatto senza variare l'impostazione data da Mitrakos alle scale di stress e, soprattutto, senza proporne di nuove. Varie e discordanti sono le idee riguardo all'utilità degli indici bioclimatici e bioecologici nell'epoca dell'elaborazione elettronica, ma tutti si trovano d'accordo sull'opportunità di selezionare, tra i numerosi indici proposti, uno o pochi indici funzionali, da proporre come scale di riferimento per il maggior numero possibile di utilizzatori, perché "l'ecologia è la scienza delle relazioni, e non delle leggi assolute" (Borhidi, ex verbis). E' pertanto necessario che ciascuno possa prendere confidenza con le scale numeriche in uso, in modo da formarsi una propria idea empirica da associare a ciascun valore della scala (come si fa, per esempio, con le scale termometriche) altrimenti accade che l'indicazione numerica (o grafica) fornita venga trascurata per correre a vedere i dati termometrici, pluviometrici, la descrizione orografica, senza riconoscere al valore dell'indice quel ruolo sintetico-correlativo che dovrebbe avere.

Si spera che la possibilità di valutare C.S. e D.S. tenendo conto dei fattori stazionali possa essere d'aiuto per quantificare in maniera speditiva quei fenomeni di compensazione che fanno sì, ad es. che gli iparrenieti, presenti sotto l'abitato di Altavilla Silentina solo su pendenze superiori a 60°, in Sicilia occupino molto spesso stazioni pianeggianti, perché il D.S., che lì era incrementato dalla pendenza, qui è determinato da una maggiore scarsità di precipitazioni ed alle maggiori temperature estive. Se attraverso l'applicazione su territori diversi si giungerà a determinare l'intervallo di valori di stress tollerati da una data associazione vegetale, si farà assumere ad essa un significato non solo qualitativo, ma anche quantitativo come bioindicatore (Biondi, 1993). Di tale assunzione ci si potrà avvalere per indagini predittive sul dinamismo di un determinato sito o per interpretare quelle situazioni vegetazionali caotiche ed eterogenee che si rinvengono, ad esempio, sul versante meridionale delle Alpi Liguri e Marittime, ove esiste un'ampia "fascia di compenetrazione" ecologicamente alla portata sia di specie stenomediterranee che di specie alpine, che spesso convivono nella stessa cenosi (Martini, 1982 ; 1983).

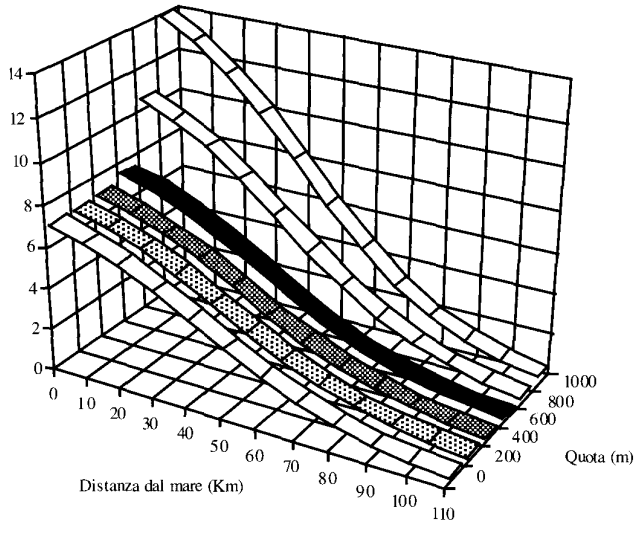

Figura 11. Andamento dell'influenza di quota e distanza dal mare sul D.S. Per esigenze grafiche, la superficie continua è stata frammentata nelle sue curve fondamentali.
Influence of exposure and sloping gradient on D.S. The continue surface has been represented with its fundamental curve, due to graphic exigences.

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APPENDICE 1 : dati relativi alle stazioni considerate. Nelle colonne relative a latitudine e longitudine delle stazioni di rilevamento, ove il dato non era reperibile, sono state riportate, rispettivamente, regione e provincia di appartenenza.

Num	Stazione	Q.A.	Lat.	Long.	T.M.	ma.	mi.	G.< 0	h.< 0	MA.	MI.	G.> 25	h. > 25
1	Lampedusa	15	35°30' N	12°36' E	19,2	15,3	11,8	*13,6	*1.1	28,5	24,3	*9,5	*0,43
2	Gela	33	37°05' N	14°03' E	17,3	14,6	8,6	*58	*5,3	26,8	21,3	*4,9	*0,2
3	Trapani Birgi	9	37°55' N	12°29' E	17,6	15	8,1	*63,6	*5,9	30,1	20,2	*32,1	*1,46
4	Pantelleria	198	36°49' N	11°58' E	18	13,7	9,4	*49,8	*4,8	28,4	21,6	*20,6	*1,23
5	Messina	54	38°12' N	15°33 E	18,3	14,5	9,8	*40,9	*3,2	29,9	23,5	*33,4	*1,73
6	Cagliari Elmas	2	39°15' N	09°32' E	16,5	14,2	5,7	*78,8	*9,9	29,8	19,1	*30,8	*1,3
7	I. Ustica	243	38°42' N	13°10' E	16,9	12,7	8,6	0,2	0	27,8	21,8	66	7,2
8	Guardiavecchia	170	41°13' N	09°24' E	16	12,9	8	\\\\	\\\\	26,7	20,2	53,2	4,9
9	I. Asinara	\\\\	Sardegna	Sassari	16,2	13	8,5	*54,4	*5,17	25,8	20,8	42,5	3,7
10	Catania Fontanarossa	17	38°28' N	15°03' E	17,3	15,8	5,3	*81,8	*9,2	32	19,2	*55,1	*2,66
11	Brindisi	10	40°39' N	17 57' E	16,5	12,7	6,3	1,5	0,03	28,6	20,6	76,1	8,33
12	Olbia	16	40°54' N	09°31' E	16,2	14,6	5,2	*77,9	*10,5	30,8	18,5	82,8	9
13	Alghero	28	40°38' N	08°17' E	16	13,9	6,3	*72,9	*9,47	28,8	18	67,7	6,3
14	Capri Damekuta	161	40°33' N	14°12' E	16,6	12,6	7,4	0,9	0,1	28,8	20,4	74,8	8,23
15	Ponza	185	40°55' N	12°57' E	16,3	11,8	8,3	0,4	0,01	27,3	21,3	64,1	6,6
16	Civitavecchia	4	42°02' N	11°50' E	16,3	12,8	7,1	1	0,03	27	20,5	61,4	5,23
17	Lamezia Terme	15	38°54' N	16°15' E	16,1	13,8	5,9	4,5	0,13	29,3	18,2	76,9	7,17
18	Capo Palinuro	185	40°01' N	15°17' E	16,7	12,9	7,2	0,8	0,03	28,3	20,8	74	7,76
19	Termoli	44	42°00' N	15°00' E	15,7	10,5	5,6	2,5	0,2	26,8	21,2	56,5	6,2
20	Decimomannu	12	Sardegna	Cagliari	16,3	14	4,5	6,9	0,2	31,4	18,3	86,1	9,46
21	Bari Palese	44	41°08' N	16°47' E	15,7	12,1	5	3,1	0,17	28,4	19,1	71,5	6,87
22	Lecce	53	40°14' N	18°08' E	16,3	12,6	4,6	8,1	0,23	30,9	19	85	9,8
23	Crotone	158	39°20' N	17°05' E	16,2	12,6	5,7	2,3	0,06	30,5	19,5	83,6	9,66
24	Pratica di Mare	12	41°39' N	12°28' E	15	12,7	4	9,1	0,33	28	17,5	71,1	5,03
25	Circeo	\\\\	Lazio	Latina	15,6	13,1	5,1	5,3	0,2	28,1	18,4	72,3	5,9
26	Grazzanise	10	41°04' N	14°05' E	14,6	12,7	3,3	13,3	0,33	29,7	17,4	81,2	7
27	Latina	26	41°33' N	12°55' E	15,5	13,4	3,3	13,5	0,43	30,4	17,3	82,4	7,57
28	Napoli Capodichino	72	40°51' N	14°18' E	15,5	12,5	3,8	9,5	0,33	29,5	17,9	79	7,3
29	Calopezzati	220	Calabria	Cosenza	14,8	10,4	5,6	4,7	0,26	26,6	19,4	52,5	4,26
30	Genova Sestri	3	44°25' N	08°51' E	15,6	10,9	5	3,6	0,23	27,2	20,6	62,2	6,33
31	Foggia Amendola	60	41°33' N	15°43' E	15,4	11,6	2,9	16,1	0,66	31,6	17,9	85	9,5
32	Perdasdefogu	608	39°40' N	09°26' E	13,6	9,2	3,8	7,4	0,47	28,2	17	61,9	16
33	Grosseto	7	42°46' N	11°04' E	14,8	11,9	2,7	19,5	2,5	29,8	17,1	81,2	7,06
34	M.te Calamita (Elba)	397	42°44' N	10°44' E	14	9,2	4,9	7,3	0,6	26,4	18,6	50,2	3,8
35	Pescara	11	42°26' N	14°12' E	14,3	10,5	1,7	24,3	1,03	28,9	17,1	75,6	6,23
36	Roma Urbe	19	41°57' N	12°30' E	15,1	12,1	1,9	26,6	1,06	31,2	16,7	84,2	8,33
37	Albenga	9	Liguria	Savona	13,7	11,7	0,5	38,6	1,7	28,7	15,9	70,4	5,13
38	Pisa S. Giusto	7	43°41' N	10°24' E	14,3	10,9	2	27	1,4	29,1	16,6	74,8	6
39	Firenze Peretola	38	43°48' N	11°12' E	14,6	10,1	1,4	30,2	2,03	31,1	17,2	80,7	8,26
40	Vigna di Valle	266	42°05' N	12°13' E	14,5	9,8	3,6	7,3	0,46	29,2	18	73,3	6,9
41	Enna	###	37°33' N	14°17' E	12,9	6,5	2,9	12,7	1,3	25,6	18,2	44,7	3,77
42	M.te Argentario	631	42°23' N	11°10' E	12,9	7,7	3,5	9,5	0,8	25,4	18,3	38	3,2
43	Gioia del Colle	352	40°46' N	16°56' E	13,6	9,8	1,9	25,1	1,4	29,5	16	74,2	6,13
44	Frosinone	185	41°39' N	13°18' E	14,1	10,6	0,5	37,3	1,9	30,2	16	80,3	6,9
45	Prizzi	###	37°43' N	13°26' E	12,3	7	1,9	17,3	5,4	26,9	16,6	55,7	4,4
46	Monte S. Angelo	847	41°42' N	15°57' E	11,4	5,6	1,3	26	3,5	24	16,8	47,2	2,77
47	Serpeddì	###	Sardegna	Cagliari	10,8	5,6	1,5	\\\\	\\\\	24,1	15,3	\\\\	\\\\
48	Radicofani	828	42°54' N	11°46' E	10,9	5,4	0,8	31,5	4,33	24,7	16,3	33,7	2,47
49	Campobasso	807	41°34' N	14°39' E	12	6,4	1,1	30,5	3,57	26,1	16,8	48,1	3,83
50	Potenza	845	40°38' N	15°48' E	11,2	6,2	0,8	31,3	3,63	25	15,3	38,8	2,5
51	Fonni	992	40°07' N	09°15' E	11,5	6,6	1,5	26,2	2,5	25,8	16,4	44	3,77
52	Latronico	896	40°05' N	16°01' E	11,4	6	1,7	23	2,9	24,1	16,4	29,5	2,07
53	Frontone	574	43°31' N	12°44' E	12,5	6,1	1,4	27,5	3,73	26,8	17,7	51,2	4,7
54	Vallicciola	###	Sardegna	Sassari	10,3	6,4	0,9	\\\\	\\\\	23,8	13,9	\\\\	\\\\
55	Floresta	###	Sicilia	Messina	10,9	5	0,2	\\\\	\\\\	25,8	15,8	\\\\	\\\\
56	Trevico	###	41°03' N	15°14' E	9,04	3	-1	49,8	8	22,9	14	21	1,13
57	M.te Scuro Silano	###	39°20' N	16°24' E	7,3	2,3	-2,1	62,2	10,4	19,3	12,3	4	0,2
58	Etna (cantoniera)	###	Sicilia	Catania	7,4	2,2	-3,9	\\\\	\\\\	20,9	12,7	\\\\	\\\\

Stazione	Y.C.S.	W.C.S.	I.T.	Termotipo	U.R.	P.	P.e.	%	Y.D.S.	S.D.S.	Ombrotipo
Lampedusa	0	0	463	Inframedit.	78	324,5	6,1	1,9	610	287,8	Semiarido sup.
Gela	27,2	21,6	404	Termomedit. inf.	74	354,2	17,2	4,9	522,6	265,6	Secco inf.
Trapani Birgi	48	36,8	408	Termomedit. inf.	73	448,6	15,8	3,5	396,4	268,4	Secco sup.
Pantelleria	11,2	11,2	410	Termomedit. inf.	68	484,6	21,1	4,4	413,6	257,8	Secco sup.
Messina	1,2	1,2	428	Termomedit. inf.	64	831,5	57,2	6,9	221,8	185	Subumido sup.
Cagliari Elmas	124	90,4	364	Termomedit. sup.	66	426,4	20,9	4,9	395,2	258,2	Secco inf.
I. Ustica	24,8	20	382	Termomedit. sup.	74	448,6	23,1	5,1	417,4	253,8	Secco sup.
Guardiavecchia	52	42,4	369	Termomedit. sup.	\\\\	469,1	41,6	8,9	360	216,8	Secco sup.
I. Asinara	25,6	19,2	377	Termomedit. sup.	\\\\	480,6	16,5	3,4	396,6	267	Secco sup.
Catania Fontanar.	144,8	100,8	384	Termomedit. sup.	65	547,2	19,9	3,6	369	260,2	Secco sup.
Brindisi	92,8	76	355	Termomedit. sup.	71	574,3	55	9,6	271,4	190	Secco sup.
Olbia	162,4	102,4	360	Termomedit. sup.	60	582,4	52,9	9,1	243,2	194,2	Secco sup.
Alghero	114,4	80	362	Termomedit. sup.	68	590,1	29,9	5,1	323,6	240,2	Secco sup.
Capri Damekuta	74,4	57,6	366	Termomedit. sup.	\\\\	633,6	77,9	12	202,4	144,2	Subumido inf.
Ponza	36	28,8	364	Termomedit. sup.	74	657,3	48,7	7,4	284,4	202,6	Subumido inf.
Civitavecchia	71,2	59,2	362	Termomedit. sup.	73	662,8	53,8	8,1	208,8	192,4	Subumido inf.
Lamezia Terme	122,4	92	358	Termomedit. sup.	72	768,8	50,9	6,6	248,8	198	Subumido inf.
Capo Palinuro	62,4	50,4	368	Termomedit. sup.	73	798,8	58,6	7,3	202,4	182,8	Subumido inf.
Termoli	106,4	88,8	318	Mesomedit. inf.	75	385,4	81,3	21	369,2	125,8	Secco inf.
Decimomannu	182,4	117,6	348	Mesomedit. inf.	63	483,5	28,7	5,9	326	242,6	Secco sup.
Bari Palese	148	106,4	328	Mesomedit. inf.	65	586,1	98,2	17	135,4	103,6	Secco sup.
Lecce	164	116	335	Mesomedit. inf.	65	627,4	70,8	11	226,6	158,4	Subumido inf.
Crotone	130,4	92,8	345	Mesomedit. inf.	60	680,6	36,9	5,4	238	161,2	Subumido inf.
Pratica di Mare	196,8	128,8	317	Mesomedit. inf.	75	819,5	69,4	8,5	187,8	161,2	Subumido sup.
Circeo	136,8	101,6	338	Mesomedit. inf.	\\\\	831,5	73,9	8,9	184	152,2	Subumido sup.
Grazzanise	224,8	144,8	306	Mesomedit. inf.	71	897,8	93,9	10	102,8	90,4	Subumido sup.
Latina	224	145,6	322	Mesomedit. inf.	68	930,7	102	11	100	96,2	Subumido sup.
Napoli Capodic.	199,2	134,4	317	Mesomedit. inf.	70	1007	100	9,9	100,8	100	Umido inf.
Calopezzati	132,8	96,8	308	Mesomedit. inf.	75	1019	86,2	8,5	127,6	127,6	Umido inf.
Genova Sestri	128	105,6	314	Mesomedit. inf.	68	1072	161	15	46,4	46,4	Umido inf.
Foggia Amendola	249,6	158,4	299	Mesomedit. medio	63	494,7	88,8	18	234	122,4	Secco sup.
Perdasdefogu	232	140,8	265	Mesomedit. medio	\\\\	564	60,3	11	251,4	179,4	Secco sup.
Grosseto	256,8	162,4	294	Mesomedit. medio	66	661,2	84,7	13	151,6	130,6	Subumido inf.
M.te Calamita	164,8	113,6	286	Mesomedit. medio	71	661,6	73,8	11	171,4	152,4	Subumido inf.
Pescara	277,6	180	265	Mesomedit. medio	69	674,3	131	19	75,4	44,6	Subumido inf.
Roma Urbe	275,2	176,8	291	Mesomedit. medio	69	837,3	99,8	12	105,8	100,4	Subumido sup.
Albenga	298,4	214,4	258	Mesomedit. medio	78	878,2	103	12	94,4	94,4	Subumido sup.
Pisa S. Giusto	273,6	177,6	272	Mesomedit. medio	68	900	124	14	66	66	Subumido sup.
Firenze Peretola	282,4	187,2	261	Mesomedit. medio	66	910,7	176	19	20,8	20,8	Subumido sup.
Vigna di Valle	214,4	140	279	Mesomedit. medio	67	965,3	106	11	88,4	88,4	Subumido sup.
Enna	254,4	156,8	223	Mesomedit. sup.	\\\\	360,8	48,6	13	497,2	202,8	Secco inf.
M.te Argentario	225,6	145,6	241	Mesomedit. sup.	69	419,4	47,6	11	383,4	204,8	Secco inf.
Gioia del Colle	305,6	182,4	253	Mesomedit. sup.	61	636,6	109	17	107,8	81,8	Subumido inf.
Frosinone	337,6	208	252	Mesomedit. sup.	69	1299	156	12	20,2	20,2	Umido inf.
Prizzi	305,6	182,4	212	Supramedit. inf.	55	544,4	38,1	7	307,4	223,8	Secco sup.
Monte S. Angelo	321,6	196,8	182	Supramedit. inf.	62	613,3	128	21	85,6	43,2	Subumido inf.
Serpeddì	350,4	160,8	179	Supramedit. inf.	63	617,7	16,6	2,7	402,8	358,2	Subumido inf.
Radicofani	362,4	212	173	Supramedit. inf.	69	626,4	116	18	83,2	68,6	Subumido inf.
Campobasso	324	200	195	Supramedit. inf.	60	627,5	111	18	91	77,8	Subumido inf.
Potenza	364	208,8	183	Supramedit. inf.	64	650,6	107	16	104,2	85,6	Subumido inf.
Fonni	341,4	196	195	Supramedit. inf.	70	800,7	60,2	7,5	182	179,6	Subumido sup.
Latronico	315,2	189,6	191	Supramedit. inf.	66	976,8	111	11	79	79	Subumido sup.
Frontone	270,4	191,2	199	Supramedit. inf.	60	1158	246	21	0	0	Umido inf.
Vallicciola	401,6	210,4	176	Supramedit. inf.	\\\\	1412	64	4,5	172	172	Umido sup.
Floresta	416,3	227,2	162	Supramedit. medio	\\\\	1273	87,3	6,9	125,4	125,4	Umido inf.
Trevico	476	252	115	Supramedit. sup.	65	612,4	85,2	14	164,8	129,6	Subumido inf.
M.te Scuro Silano	562,4	277,6	75	Supramedit. sup.	74	810,5	92,8	11	115,4	114,4	Subumido sup.
Etna (cantoniera)	601,6	292,8	57	Oromedit.1nf.	\\\\	978	44,8	4,6	210,4	210,4	Subumido sup.

Abbreviazioni (abbreviations) :

Q.A.	=	Quota altimetrica (m). Altitude (m).
Lat.	=	Latitudine (Regione). Latitude (Region).
Long.	=	Longitudine (Provincia). Longitude (Province).
T.M.	=	Temperatura media annuale. Mean annual temperature.
mi.	=	Media delle temperature massime del mese più freddo. Average of max. temperature of the coldest month.
ma.	=	Media delle temperature minime del mese più freddo. Average of min. temperature of the coldest month.
G.< 0	=	Numero medio di giorni con temperatura minima 0°C nei mesi invernali (D., G., F.). Mean number of days with min. temperature 0°C in winter months (D., J., F.). (* $T_{min.}$ 10°C).
h.< 0	=	Numero medio di ore/giorno con temperatura minima 0°C nei mesi invernali. Mean number of hours per day with min. temperature 0°C in winter months. (* $T_{min.}$ 10°C).
MA.	=	Media delle temperature massime del mese più caldo. Average of max. temperature of the hottest month.
MI.	=	Media delle temperature minime del mese più caldo. Average of min. temperature of the hottest month.
G.> 25	=	Numero medio di giorni con temperatura massima 25°C nei mesi estivi (G., L., A.). Mean number of days with max. temperature 25°C in summer months (J., J., A.). (* $T_{min.}$ 30°C).
h.> 25	=	Numero medio di ore/giorno con temperatura massima 25°C nei mesi estivi. Mean number of hours per day with max. temperature 25°C in summer months. (* $T_{min.}$ 30°C).
Y.C.S.	=	Year cold stress (Mitrakos, 1980).
W.C.S.	=	Winter cold stress (Mitrakos, 1980).
I.T.	=	Indice di termicità. Thermicity index. (Rivas-Martínez *et al.*, 1991).
U.R.	=	Media dell'umidità relativa nei mesi di G.,L.,A. (%). Mean relative humidity in Jun., Jul., Aug. (%).
P.	=	Media delle precipitazioni annuali (mm). Average year rainfall (mm).
P.e.	=	Media delle precipitazioni nei mesi di G., L., A. (mm). Average rainfall in Jun., Jul., Aug. (mm).
%	=	Percentuale delle precipitazioni di G., L., A. sul totale delle precipitazioni. Percentage of Jun., Jul., Aug. rainfall on the year amount.
Y.D.S.	=	Year drought stress (Mitrakos, 1980).
S.D.S.	=	Summer drought stress (Mitrakos, 1980).
\\\\	=	Dato non disponibile. Unavailable datum.

APPENDICE 2 :

Per calcolare in modo rapido e con buona approssimazione1 il numero di ore potenziali d'insolazione diretta godute da un sito in un determinato giorno, data la sua latitudine e la sua esposizione, si può procedere come segue :

1. Si determina l'angolo di declinazione solare (cioè l'altezza del sole sull'equatore celeste) per quel dato giorno : tale angolo varia tra 23°27' (= 23,45°) N (solstizio estivo) e 23°27' S (solstizio invernale) ; sapendo inoltre che la declinazione solare aumenta o diminuisce di 0,257° al giorno, risulta di immediata determinazione il valore dell'angolo della declinazione solare di qualsiasi giorno.
2. Si stabilisce di quanti minuti il sole sorge prima o dopo le ore 6 e tramonta dopo o prima delle ore 18 alla latitudine φ e per il dato giorno dell'anno con declinazione solare . Tale tempo di anticipo o di ritardo (T) viene espresso dalla seguente relazione trigonometrica :

   $T = 4\arcsen(tg\varphi \cdot tg\varphi)$ (da Bosellini, 1985, modificato).

   T, espresso in minuti primi più una parte decimale va convertito nel suo equivalente in ore, minuti e secondi (dividendo tutto per 60 e moltiplicando la parte decimale per $3/5)^2$.

   Se si vuol conoscere il numero di ore di sole potenziali per un dato giorno alla data latitudine, basta sommare (in Primavera ed in Estate) o sottrarre (in Autunno ed in Inverno) due volte a 12 il tempo d'anticipo così determinato.
3. Per stabilire il numero di ore d'insolazione diretta potenziale per una data esposizione ζ ed un dato giorno basta sommare (in Primavera ed in Estate) o sottrarre (in Autunno ed in Inverno) T al numero di ore d'insolazione diretta potenziale (h) godute dall'esposizione ζ durante gli equinozî. Queste ultime si determinano mediante la proporzione $180 : 12 = \zeta : h$ per $0° \bullet \zeta \bullet 180°$ e mediante la proporzione $180 : 12 = (360 - \zeta) : h$ per $180° \bullet \zeta \bullet 360°$.

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1 Non tenendo conto cioè delle minime variazioni determinate dalla rifrazione atmosferica (che provoca un aumento del periodo d'insolazione di circa 3 min. alla latitudine di 40°) e dalla quota del sito.

2 E' importante assicurarsi che le frazioni di grado dei valori degli angoli φ ed ε utilizzati nella formula siano espresse in forma decimale e non sessagesimale (ovvero in primi e secondi), come di solito vengono espresse da G.P.S. e carte topografiche.

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Survey of the naturalised plants and vertebrates in peninsular Spain

Bilan des végétaux et vertébrés naturalisés dans la péninsule ibérique

Montserrat VILÀ [1*], Emili GARCÍA-BERTHOU [2], Daniel SOL [3] & Joan PINO [1]

[1]Centre de Recerca Ecològica i Aplicacions Forestals, Universitat Autònoma de Barcelona, 08193 Bellaterra, Barcelona, Spain.

[2]Departament de Ciències Ambientals, Universitat de Girona, E-17071 Girona, Spain.

[3]Departament de Biologia Animal-Vertebrats, Facultat de Biologia, Universitat de Barcelona, Av. Diagonal nº 645, 08028 Barcelona, Spain. Present adress: Department of Biology, McGill University, 1205 Av. Docteur Penfield, Montréal, Québec, H3A 1B1, Canada.

[*]Author for correspondence: Tel: 93-5811987, Fax : 93-5811312, e-mail: vila@cc.uab.es.

ABSTRACT

The introduction of naturalised species is threatening the biodiversity of "hot-spot" regions around the World. Spain is one of the European countries with the highest diversity of species. However, a synthesis of the identity of the naturalised biota has never been conducted. We present a bibliographic survey to analyse the number and biogeography of naturalised plants and vertebrates in peninsular Spain. We found 637 naturalised plants, 20 fish species, 3 amphibians, 8 reptiles, 9 birds, and 11 mammals. The largest fraction of plants are of American origin whereas the origin of vertebrates depends on their taxonomic group. Except for amphibians and mammals, most naturalised species are found in highly disturbed habitats. The invasiveness of these species and their impact on the native biota have not been quantified. However, some of these species are very invasive in other regions of the World, and thus the probable impacts on the biodiversity conservation of Spain should be urgently investigated.

Key-words: alien plants, biological invasions, Iberian Peninsula, patterns of invasion, species diversity.

RESUME

La naturalisation d'espèces étrangères constitue une menace mondiale pour la biodiversité des zones de « hotspots ». L'Espagne constitue l'un des pays européens possèdant la plus grande diversité spécifique. Cependant, il n'existe pas pour ce pays de synthèse relative aux espèces introduites et naturalisées. Ainsi, ce travail vise à dresser une synthèse bibliographique concernant le nombre et l'origine biogéographique des végétaux vasculaires et des vertébrés naturalisés présents dans la péninsule ibérique. Ce bilan a permis de dénombrer 637 végétaux vasculaires naturalisés, 20 poissons, 3 amphibiens, 8 reptiles, 9 oiseaux et 11 mammifères non indigènes. La plus grande proportion de ces végétaux xénophytes est d'origine américaine, tandis que l'origine biogéographique des vertébrés dépend du groupe taxonomique auquel ils appartiennent. Hormis les amphibiens et des mammifères, la plupart des espèces naturalisées se rencontrent dans des biotopes fortement perturbés. L'invasibilité de ces espèces et leur impact sur les communautés et écosystèmes indigènes n'ont pas été encore quantifiés. Cependant, certaines espèces présentes en Espagne s'avèrent très dynamiques et envahissantes dans d'autres régions du Monde, et leurs impacts probables sur la biodiversité espagnole méritent d'être examiné de façon urgente.

Mots-clés : végétaux exotiques, invasions biologiques, Péninsule ibérique, modalités d'invasion, diversité spécifique

INTRODUCTION

Species dispersal driven by man is currently one of the main causes of change in the biota composition around the World (Drake *et al.*, 1989). The introduction of naturalized species has increasingly attracted the attention of ecologists because of their impact on natural systems, which include loss of biodiversity (Lodge, 1993), changes in disturbance regime (D'Antonio & Vitousek, 1992), changes in the biogeochemical cycles (Vitousek, 1994) and homogenization or creation of new landscapes (Atkinson & Cameron, 1993). The interest in naturalized species also comes from the fact that they can help to elucidate the processes that shape community structure and determine its function.

Surveys of naturalized species distribution at the regional level are the starting point to establish patterns and correlates of naturalized species diversity at the global scale (Daehler, 1998; Pysek, 1998; Lonsdale, 1999), and can also help to establish hypotheses of the ecological factors that determine which species are more invasive and which communities are more easily invaded (Crawley, 1987; Mack, 1996). In the last decade a significant effort has been achieved to determine patterns of invasion by naturalized species at the regional scale (e.g. Groves & Di Castri, 1991; Rejmánek & Randall, 1994; Weber, 1997), but there is still a lack of quantitative information on the naturalized component for major regions of the world (Heywood, 1989; Lonsdale, 1999).

Spain is one of the countries with the highest biological diversity of Europe; with a high proportion of endemic plants (Gómez-Campo *et al.*, 1984; Médail & Quézel, 1997), amphibians and reptiles (Pleguezuelos & Martínez-Rica, 1997), and birds (Blondel, 1985). Plant diversity is associated with the biogeographic location of the Iberian Peninsula and the high habitat and pedological diversity (Médail & Quézel, 1997). Spanish amphibians are more diverse than reptiles due to a combination of historical and ecological factors (Vargas & Real, 1997). The percentage of European species that are native to Spain is high for mammals and birds because they have large distribution areas and a low proportion of endemics (Oosterbroek, 1994; Covas & Blondel, 1998). The aquatic fauna of Spain is globally poor compared to the rest of Europe (Banarescu, 1992). The relatively low richness of freshwater fish (Doadrio *et al.*, 1991; Elvira, 1998; Carmona *et al.*, 1999) is generally attributed to the isolation of the Iberian peninsula and the scarcity of fresh water habitats (Hernando & Soriguer, 1992).

The naturalized component of the flora and fauna has been partially analysed for several regions within Spain and in most cases for different taxonomic groups (see Methods), yet a synthesis of both the naturalized flora and vertebrate fauna has never been conducted. This paper describes the naturalized component (exotic established species) of the flora and vertebrate fauna of Spain to answer the following questions: (i) How many naturalized plant and vertebrate species are there in Spain? (ii) What is their origin? and (iii) In which communities are naturalized species located? We limited the study to plants and vertebrates because these are well known taxa and therefore reliable information was available from most of their species.

MATERIAL AND METHODS

A database was created with all plant and vertebrate naturalized species of Spain excluding the Balearic and Canary islands. The main floras and plant species lists surveyed were: Alcázar (1984), Arnold & Burton (1995), Bolós *et al.* (1993), Campos & Herrera (1997), Carretero (1989), Casasayas (1989), Castroviejo *et al.* (1986-1997), Conesa (1992), González (1988), Greuter *et al.* (1984), Masalles *et al.* (1996), Pino (1999), Recasens & Conesa (1990, 1995), Tutin *et al.* (1993) and Valdés *et al.* (1987). The data gathered for animals came from Andrada (1985), Elvira (1998), Gozálbes (1987), Hagemeijer & Blair (1997), Lever (1985), Lobón-Cerviá & Elvira (1989), Long (1981), Llorente *et al.* (1995), MacDonald & Barrett (1993), Pleguezuelos & Martínez-Rica (1997), Purroy (1997), Rivera & Arribas (1993), Rodríguez (1993), Rodríguez & Sales (1999), Ruiz-Olmo & Aguilar (1995), Schilling *et al.* (1987), and Vives-Balmaña *et al.* (1987).

We only included well established exotic species which populations are capable to grow without direct support of humans, that is "naturalized species" sensu Williamson & Fitter (1996). Exotic plant species

listed as cultivated or planted were excluded, as well as those whose naturalization status was not certain. The following information for each naturalized plant species was gathered: family, Raunkiaer life-form (Raunkiaer 1934), origin and habitat. For vertebrates, the following information was gathered: family, common name, origin, habitat and date of introduction if known. We did not list exotic species if it was not known if they maintain self-sustaining populations (see examples in Purroy, 1997). That is, we did not include populations that failed to establish, populations that were too small to be considered viable or small populations for which there are no data on reproductive success. We did not include domestic vertebrates.

RESULTS

List and characteristics of naturalized species

Spain harbors 637 naturalized plant species distributed in 102 families, which represent 13% of the total flora. Less than 25% of these families have more than 10 naturalized species, whereas the majority only have one or two species (Appendix I).

The families with the most naturalized taxa are : Asteraceae, Poaceae, Brassicaceae and Fabaceae, followed by Solanaceae, Amaranthaceae and Lamiaceae (less than 4% of the total per family). Some families are completely naturalized: Agavaceae, Basellaceae, Phytolaccaceae, Pittosporaceae, Sapindaceae and Simaroubaceae. The majority of naturalized species are therophytes (40.98%), followed by hemycriptophytes (17.83%). Hydrophytes (0.85%), epiphytes (0.42%), parasites (0.42%) and helophytes are the least represented life-forms (Table 1).

The naturalized fauna of Spain comprises at least 20 fish species, 3 amphibians, 8 reptiles, 9 birds and 11 mammals (Appendix II). Date and reason for introduction for several of the species are uncertain. Several species such as the Turkish gecko (*Hemidactylus turcicus*) and the Mediterranean chameleon (*Chamaleo chamaleon*) are cryptogenic species, i.e. species that are not demonstrably native or introduced (Carlton, 1996). A few other species (e.g., collared turtedove: *Streptopelia decaocto*) have not been included in the Appendix II because they naturally invaded the Iberian Peninsula. The rock dove (*Columba livia*) has not been included because only part of the population is actually introduced. Some other species have been introduced in Spain (e.g. Californian quail: *Callipepla californica* and black-rumped waxbill: *Estrilda troglodytes*) but have failed to establish themselves in natural areas or their populations are too small to consider that the introduction has succeeded.

The percentage of European species that are native to Spain is the lowest for freshwater fishes (20-32%) and reptiles (30.1%), larger for mammals (34.3%) and amphibians (40.8%) and is highest for birds (52.5%) (Table 2). The percentage of the fauna that is naturalized is very high for freshwater fish (39%, excluding diadromous species), intermediate for reptiles (18%), amphibians (11%), and mammals (15%), and low for birds (3%). The apparent inverse relationship between fauna richness and percentage of naturalized species is not statistically significant ($r = -0.69$, $n = 5$, $P = 0.20$).

Origin of naturalized species

Exotic plants originated mainly from the Holarctic region (33%), most common being of the European origin. There are also a significant proportion of species coming from South America. Asian and African species also are numerous (Table 3). Although most naturalized animals originated also from the Holarctic region (Table 4), the region of origin significantly depends on the taxonomic group (Table 4: $G = 25.8$, d.f. = 12, $P = 0.01$). Exotics from North America are common within reptiles (50%) and fish (35%), and less frequent among mammals and birds, with only one species each. There are no naturalized fish from Africa, whereas for all the other groups of vertebrates more than 20% of species have an African origin.

Habitats with naturalized species

Most naturalized plants are found in ruderal communities, road-sides (44.67%) and crops (23.35%). Coastal and riparian communities are also highly invaded habitats (9.5 % and 5.7 %, respectively). In contrast, only 11 and 5 species invade forests and shrublands respectively (Table 5). Most naturalized birds, amphibians and reptiles have restricted distributions, in contrast to fish and

mammals. Exotic amphibians and mammals are common in natural habitats, whereas naturalized birds, reptiles, and fish occur in urban or human-altered habitats.

Life-form	Species (% of total)
Therophytes	40.98
Hemicryptophytes	17.83
Phanerophytes	11.89
Chamephytes	11.25
Geophytes	7.43
Nanophanerophytes	4.67
Macrophanerophytes	4.03
Hydrophytes	0.85
Epiphytes	0.42
Parasites	0.42
Helophytes	0.21

Table 1. Life-forms of Spanish naturalized plant species (exotics from Balearic and Canary islands are not included).

Phanerophyte (Ph): woody plant with buds located more than 40 cm above the ground; nanophanerophyte: Ph with buds located less than 2 m above the ground; macrophanerophyte: Ph with buds located more than 2 m above the ground; chamephyte: woody plant with buds located less than 40 cm above the ground; Biannual hemicryptophytes were considered perennials.

Taxonomic group	European native	Spanish native	Spanish naturalized	Reference
Plants	11557[a]	-	-	Tutin *et al.* 1993
	-	4900[a]	-	Simon (1994)
	-	-	637	this review
Freshwater fish	215[b]	-	-	Maitland & Linsell (1980)
	-	69[b], 32[c]	-	Elvira (1995)
	-	-	20	Elvira (1998), this review
Amphibians	45	21	-	Arnold & Burton (1995), Andrada (1985)
	59	24	3	Pleguezuelos & Martínez-Rica (1997) this review
Reptiles[d]	85	36	-	Arnold & Burton (1995)
	133	40	8	Pleguezuelos & Martínez-Rica (1997) this review
Birds	514[e]	270[e]	-	Hagemeijer & Blair (1997), Purroy (1997)
	-	-	9	this review
Mammals	181[f]	62[f]	-	Schilling *et al.* (1987)
	-	-	11	this review

Table 2. Number of European and Spanish species by taxonomic group according to several references. - = not considered.

a = total number of vascular plants
b = including diadromous species (i.e., migrating from/to the sea)
c = excluding diadromous species
d = excluding marine reptiles (5 turtle species)
e = excluding non-breeding species
f = excluding whales and dolphins

Origin	Species (% of total)
Southern America	21.68
Europe	20.22
Northern America	13.11
Northern Africa and Middle East	12.93
Central and Southern East Asia	10.75
Central and Southern Africa	9.65
America	4.01
Tropical	2.55
Australia and New Zealand	2.37
Other	1.64
Macaronesia	1.09

Table 3. Origin of Spanish naturalized plant species. Exotics from Balearic and Canary islands are not included.

Origin region	Fish	Amphibians	Reptiles	Birds	Mammals	Total
Eurasia	12	0	2	3	5	22 (44)
North America	7	1	4	1	1	13 (26)
South America	1	0	0	2	1	4 (8)
Africa	0	2	2	3	4	11 (22)

Table 4. Number of Spanish naturalized vertebrate species by origin and taxonomic group. The percentage of the total value is shown in parenthesis. Exotics from Balearic and Canary islands are not included.

Habitats	Species (% of total)
Crops	23.35
Ruderal	30.63
Roadsides	14.04
Littoral	8.97
Riparian woodlands	5.75
Herbaceous communities	4.06
Wetlands and moorlands	3.89
Sandy littoral habitats	3.05
Non-riparian woodlands	1.86
Salty shrublands	1.86
Shrublands	0.85
Sandy non-littoral habitats	0.68
Littoral cliffs and rocky areas	0.51
Non-littoral cliffs and rocky areas	0.34
Springs and streamlets	0.17

Table 5. Habitats invaded by Spanish naturalized plant species. Exotics from Balearic and Canary islands are not included.

Most Spanish freshwater courses are altered by pollution or regulation but naturalized fish are particularly common in reservoirs, where they are introduced by anglers.

DISCUSSION

Diversity of species in peninsular Spain and the naturalized component

Regional reviews of the number of native and naturalized species for a particular higher taxon are numerous. However, studies considering several higher taxa, particularly for large regions, are almost lacking (but see Vitousek *et al.*, 1997). This lack of integration, which was also the case for Spain, is unfortunate because only with detailed descriptions of the alien component at a regional scale can we establish patterns and correlates of naturalized species diversity at the global scale (Lonsdale, 1999). Our study unifies and updates the number of native and naturalized species currently present in Spain and can thus serve as a starting point for future hypothesis-oriented studies.

The naturalized component of the Spanish biota is quantitatively important. This probably reflects the many opportunities that humans have offered to exotics to reach the country. However, the number of naturalized species greatly varies among taxa. For example, naturalized plants are much more frequent than naturalized vertebrates, a pattern often found in the literature of biological invasions (Williamson, 1996). The families with the largest number of naturalized species belong also to the largest families worldwide because large families have more species available to invade, so more exotics are expected from large families (Pysek, 1998).

Compared to the figures given by Heywood (1989), Spain is one of the richest regions in Europe in naturalized plants, although the number of native species is also high. The proportion of naturalized plants in the Spanish flora is about 13%. According to Quézel *et al.* (1990) the mean in the Mediterranean Basin is 1% (Quézel *et al.*, 1990). However, this gap is undervaluated because taking only into account the naturalized flora of Spain it is of 2.24%. California, which is one of the most invaded temperate regions in the world, reported 20% exotic species (Hickman, 1993).

Among freshwater fish, the percentage of naturalized species is very high. This pattern is also found in some other regions (Vitousek *et al.*, 1997). On the contrary, relatively few amphibians and reptiles have become naturalised in Spain as well as around the world (di Castri, 1991; Lever, 1994). Birds are the only group that does not fit to the general pattern: the 8 species established in Spain are far from the 27 successfully introduced in Europe (Long, 1981; but see Hagemeijer & Blair 1997 for a more recent revision).

Habitat disturbance and naturalized species

Except for amphibians and mammals, Spanish naturalized vertebrates are generally more common in disturbed or man-made habitats than in pristine habitats. Higher plants also primarily concentrate in disturbed habitats; indeed, most taxa (68%) are pioneer species that colonize ruderal habitats or infest crops. The relationship between naturalized success and perturbation has already been pointed out for plants (Hobbs & Huenneke 1992), birds (Diamond & Veitch, 1981; Moulton & Pimm, 1983) and fish (Lever, 1996; Moyle & Light, 1996a,b). To some extent, this relationship may reflect a bias towards commensal species, which are more likely to be accidentally or unintentionally introduced. However, some authors hold that disrupted environments are especially vulnerable to invasions mainly due to their low richness of native species, which is thought to leave vacant niches or reduce the intensity of competition (Levine & D'Antonio, 1999; but see Moyle *et al.*, 1986; Moyle & Light, 1996a,b). The commonness of naturalized mammals in undisturbed habitats has also been attributed to the low number of native mammal species (Brown, 1989). Secular disturbance regimes and soil resource nutrients probably difficult invasion by exotic species of typical Mediterranean habitats such as woodlands and shrublands (Casasayas, 1989).

Impact of naturalized species

The impact of an invasive species is difficult to define because it depends on the ecological level

analysed and the spatial and temporal scales of the study (Parker *et al.*, 1999).

However, the need for impact assessment is urgent because even within the scientific and land-manager community the risks and costs of alien species are ignored and masked by alien species short term utilities and benefits (Daehler & Gordon, 1997). Major noxious species are weeds that cause problems in crop production and management. This is the case of several invaders from America, such as *Abutilon theophrastii*, *Sorghum halepense* and *Cuscuta campestris* (Masalles *et al.*, 1996). In natural areas some naturalized species when dominant may displace native species (e.g. *Carpobrotus edulis*, *Robinia pseudoacacia*). However, the magnitude of their impact at the community and ecosystem level needs further investigation.

The impact of naturalized vertebrates on the Spanish native biota also remains largely unknown. It is well known that most catastrophic impacts involve mammals or top predators (Taylor *et al.*, 1984; Lever, 1994; Moyle & Light, 1996a,b). Among freshwater fish, pike (*Esox lucius*) and largemouth bass (*Micropterus salmoides*) are top predators that have been suggested to be potentially more harmful (Elvira, 1998; García-Berthou & Moreno-Amich, 2000). Among herpetofauna, the bullfrog (*Rana catesbeiana*) and the three turtle species (Appendix II) seem more problematic. The bullfrog has been found to impact fishes and amphibians in the U.S. sites where it has been translocated (Lever, 1994). The ecological impact of birds should be of limited concern because they are only common in disturbed habitats. However, they may have an economic impact, such as the case of the monk parakeet which started to invade urban parks and are now invading natural habitats (Sol *et al.*, 1997). Among mammals, the mink (*Mustela vison*) is a predator that occupies natural habitats and apparently has affected the populations of the endangered Iberian desman (*Galemys pyrenaicus*) (see also Lever, 1994). The coypu (*Myocastor coypus*) has also been problematic elsewhere (Lever, 1994) but it is not yet widespread in Spain.

Further field surveys should investigate the distribution range and abundance of these species and their impact on the native biota. With regard to plants, the Database National Research Project is currently fulfilling this-gap (Dana *et al.*, 1999). The present review represents a preliminary analysis of the naturalized species in Spain. From this study some general conclusions can be drawn: (i) the naturalized component of the Spanish biota is quantitatively important; (ii) Spanish naturalized species are generally more common in disturbed or man-made habitats than in pristine habitats; (iii) some naturalized species are also naturalized elsewhere and (iv) the impact of naturalized vertebrates on the Spanish native biota can be potentially important but remains largely unknown. Mechanisms to stop the introduction of naturalized species and to control or reduce nuisance species should be implemented.

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Appendix I. Spanish naturalized plant species classified by families. For each family, the number of species and their percentage in respect to the total of naturalized species are shown. Exotics from Balearic and Canary islands are not included. Species list is available from the first author upon request.

FAMILY	*Species*	*% of total*
Asteraceae	104	14.59
Poaceae	67	9.40
Brassicaceae	48	6.73
Fabaceae	36	5.05
Solanaceae	26	3.65
Amaranthaceae	25	3.51
Lamiaceae	23	3.23
Rosaceae	21	2.95
Chenopodiaceae	19	2.66
Polygonaceae	18	2.52
Caryophyllaceae	16	2.24
Liliaceae	16	2.24
Aizoaceae	15	2.10
Onagraceae	14	1.96
Boraginaceae	13	1.82
Cactaceae	13	1.82
Convolvulaceae	12	1.68
Crassulaceae	11	1.54
Pinaceae	11	1.54
Cyperaceae	10	1.40
Scrophulariaceae	10	1.40
Euphorbiaceae	9	1.26
Mimosaceae	9	1.26
Apiaceae	8	1.12
Iridaceae	8	1.12
Oxalidaceae	8	1.12
Malvaceae	7	0.98
Ranunculaceae	7	0.98
Lythraceae	6	0.84
Papaveraceae	5	0.70
Gutiferae	4	0.56
Salicaceae	4	0.56
Asclepiadaceae	3	0.42
Balsaminaceae	3	0.42
Bignoniaceae	3	0.42
Caprifoliaceae	3	0.42
Cucurbitaceae	3	0.42
Cupressaceae	3	0.42
Dipsacaceae	3	0.42
Moraceae	3	0.42
Plumbaginaceae	3	0.42
Portulacaceae	3	0.42
Rubiaceae	3	0.42
Verbenaceae	3	0.42
Azollaceae	2	0.28
Betulaceae	2	0.28
Cesalpinaceae	2	0.28
Campanulaceae	2	0.28
Elatinaceae	2	0.28
Fagaceae	2	0.28
Haloragaceae	2	0.28
Hydrangeaceae	2	0.28
Juglandaceae	2	0.28
Juncaceae	2	0.28
Oleaceae	2	0.28
Phytolaccaceae	2	0.28
Pittosporaceae	2	0.28
Platanaceae	2	0.28
Saxifragaceae	2	0.28
Acanthaceae	1	0.14
Agavaceae	1	0.14
Alismataceae	1	0.14
Amaryllidaceae	1	0.14
Arecaceae	1	0.14
Baselaceae	1	0.14
Berberidaceae	1	0.14
Buddlejaceae	1	0.14
Capparaceae	1	0.14
Casuarinaceae	1	0.14
Ciperaceae	1	0.14
Cistaceae	1	0.14
Commelinaceae	1	0.14
Ebenaceae	1	0.14
Elaeagnaceae	1	0.14
Geraniaceae	1	0.14
Grossulariaceae	1	0.14
Hippocastanaceae	1	0.14
Hydrocaritaceae	1	0.14
Hydrophyllaceae	1	0.14
Lauraceae	1	0.14
Linaceae	1	0.14
Meliaceae	1	0.14
Molluginaceae	1	0.14
Myoporaceae	1	0.14
Najadaceae	1	0.14
Nyctaginaceae	1	0.14
Orobanchaceae	1	0.14
Passifloraceae	1	0.14
Plantaginaceae	1	0.14
Punicaceae	1	0.14
Resedaceae	1	0.14
Rutaceae	1	0.14
Sapindaceae	1	0.14
Sapotaceae	1	0.14
Selaginellaceae	1	0.14
Simaroubaceae	1	0.14
Tamaricaceae	1	0.14
Thymelaeaceae	1	0.14
Typhaceae	1	0.14
Ulmaceae	1	0.14
Urticaceae	1	0.14
Zygophyllaceae	1	0.14

Appendix II. Spanish exotic vertebrate species. A question mark before the species name indicates uncertain native/exotic status. Group: F = fish, A = amphibians, R = reptiles, B = birds, and M = mammals. Exotics from Balearic and Canary islands not included.

Group	FAMILY/ Species	Common name	Origin	Introduction date	Reference
F	CYPRINIDAE				
	Alburnus alburnus	Bleak	Europe	1990s?	1
	Blicca bjoerkna	White bream	Europe	1990s?	1
	Carassius auratus	Goldfish	Asia	17th cent.	1
	Cyprinus carpio	Common carp	Eurasia	17th cent.	1
	Gobio gobio	Gudgeon	Eurasia	19th cent.	1
	Rutilus rutilus	Roach	Eurasia	1910s?	1
	Scardinius erythrophthalmus	Rudd	Eurasia	1910s	1
	?Tinca tinca	Tench	Eurasia	Before 1735	1
F	ICTALURIDAE				
	Ameiurus (= Ictalurus) melas	Black bullhead	North America	1910s	1
F	SILURIDAE				
	Silurus glanis	Wels	Eurasia	1970s	1
F	ESOCIDAE				
	Esox lucius	Pike	Eurasia	1949	1
F	SALMONIDAE				
	Hucho hucho	Huchen	Europe	1968	1
	Oncorhynchus mykiss (=Salmo gairdneri)	Rainbow trout	North America	19th cent.	1
	Salvelinus fontinalis	Brook charr	North America	19th cent.	1
F	FUNDULIDAE				
	Fundulus heteroclitus	Mummichog	North America	1970s	1
F	POECILIIDAE				
	Gambusia holbrooki	Mosquitofish	North America	1921	1
F	PERCIDAE				
	Perca fluviatilis	Perch	Eurasia	1970s	1
	Stizostedion lucioperca	Pikeperch, Zander	Eurasia	1970s	1
F	CENTRARCHIDAE				
	Lepomis gibbosus	Pumpkinseed sunfish	North America	1910-1913	1
	Micropterus salmoides	Largemouth bass	North America	1955	1
F	CICHLIDAE				
	Cichlasoma facetum	"Chanchito"	South America	1940?	1
A	DISCOGLOSSIDAE				
	Discoglossus pictus	Painted frog	N Africa and S Mediterranean	19th cent.	2, 3, 4
A	RANIDAE				
	Rana catesbeiana	Bullfrog	E of North America	1987-1990	3

A	BUFONIDAE				
	Bufo mauritanicus	?	N Africa	1900s	3
R	EMYDIDAE				
	Pseudemys picta	Painted turtle?	North America	?	3
	Trachemys scripta	Read-eared slider?	North America	?	2, 3
R	TRIONYCHIDAE				
	Trionyx spiniferus	Eastern spiny softshell?	North America	1990s	3
R	GEKKONIDAE				
	Hemidactylus turcicus	Turkish gecko	Middle East	Neolithic	2, 5
	Tarentola mauritanica		Africa	4000 to 2400 B.C.	2
R	IGUANIDAE				
	Anolis carolinensis	Green anole	North America	?	3
R	CHAMAELEONTIDAE				
	Chamaeleo chamaeleon	Mediterranean chameleon	N Africa and Middle East	B.C.	3, 5, 6
R	LACERTIDAE				
	Podarcis sicula	Italian wall lizard	Italy, Greece, and Turkey	?	3, 4, 7
B	ANSERIFORMES	Ruddy duck	North & South America	1990s	8
	Oxyura jamaicensis				
B	PASSERIDAE				
	Estrilda melpoda	Orange-cheeked waxbill	Sub-Saharan Africa	1990	8, 9
	Estrilda astrild	Common waxbill	Sub-Saharan Africa	1960s?	8, 9
	Amandava amandava	Red avadavat	Asia	1974	8, 9
	Leiothrix lutea	Red-billed leiothrix	Southern Asia	1990	10
B	PSITTACIDAE				
	Myiopsitta monachus	Monk parakeet	South America	ca. 1975	8, 9
	Psittacula krameri	Rose-ringed parakeet	N Africa and Asia	ca. 1976	8, 9
	Aratinga mitrata	Mitret conure	South America	1992	D. Sol (per. obs.)
B	PHASIANIDAE				
	Phasianus colchicus	Ring-neeked pheasant	Eurasia	B.C.	11
M	CAPROMYDAE				
	Myocastor coypus	Coypu	South America	?	12, 13
M	MUSTELIDAE				
	Mustela vison	Mink	North America	1983	13
M	SCIURIDAE				
	Marmota marmota	Alpine marmot	Central Europe	1948	13 , 14
M	VIVERRIDAE				
	Genetta genetta	Common genet	Africa	ca. 16th cent.	13

M	CERVIDAE				
	Dama dama	Fallow deer	S Europe and Asia	B.C.	13, 15
M	BOVIDAE				
	Ovis musimon	Mouflon	Asia and Mediterranean islands	1954	13
	Ammotragus lervia	Barbary sheep	Africa	?	14
M	MURIDAE				
	Rattus norvegicus	Brown rat	SE Asia	16th cent.	14, 15, 16
	Rattus rattus	House rat	Asia	16th cent.	14, 16
M	ERINACIDAE				
	Erinaceus algirus	Algerian hedgehog	NW Africa	?	14
M	CERCOPITHECIDAE				
	Macaca sylvanus	Barbary ape	N Africa	711 B.C.?	17

References: 1 = modified from Lobón-Cerviá & Elvira (1989) and Elvira (1998), 2 = Llorente *et al.* (1995), 3 = Pleguezuelos & Martínez-Rica (1997), 4 = Vives-Balmaña *et al.* (1987), 5 = Rivera & Arribas (1993), 6 = Arnold & Burton (1995), 7 = Andrada (1985), 8 = Hagemeijer & Blair (1997), 9 = Purroy (1997), 10 = Long (1981), 11 = Rodríguez & Sales (1999), 12 = Gosàlbez (1985), 13 = Ruiz-Olmo & Aguilar (1995), 14 = Rodríguez (1993), 15 = Lever (1985), 16 = McDonald & Barrett (1993), and 17 = Schilling *et al.* (1987).

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The seed bank and the between years dynamics of the vegetation of a Mediterranean temporary pool (NW Morocco)

Le stock de semences et la dynamique inter-annuelle de la végétation d'une mare temporaire méditerranéenne (N.O. du Maroc)

Laïla RHAZI [1], Patrick GRILLAS [2], Laurine TAN HAM [2] & Driss EL KHYARI [1]

[1] Université Hassan II, Faculté des Sciences Aïn Chock, Laboratoire de Biologie et de Physiologie Végétale, BP 5366 Maarif Casablanca, Maroc.

[2] Station Biologique de la Tour du Valat, Le Sambuc 13200 Arles, France.
Tel : (33) (0)4 90 49 86 21, Fax: (33) (0)4 90 97 20 19. E-mail : grillas@tour-du-valat.com

RESUME

La dynamique de la végétation a été étudiée pendant 3 années consécutives sur des quadrats disposés le long de transects permanents et les stocks semenciers dénombrés (1 année) par la méthode de mise en germination dans chacune des 3 ceintures identifiées (centre : B1, intermédiaire : B2 et périphérique : B3). Dans les stocks semenciers, la richesse spécifique, la densité totale des semences et le pourcentage des annuelles différent significativement entre ceintures, augmentant du centre (B1) vers la périphérie (B3). Les espèces dominantes dans les stocks semenciers de la ceinture intermédiaire sont plus semblables à ceux de la ceinture interne (B1) que de la périphérique (B3). La composition spécifique de la végétation varie avec le gradient topographique, la végétation de la ceinture B2 étant plus semblable à celle de B3 qu'à celle de la ceinture interne (B1). Les annuelles dominent les ceintures B1 et B3 (sauf l'année 3) et les vivaces en B2. L'abondance des espèces dans la végétation est généralement peu corrélée à leur abondance dans les stocks semenciers (végétation totale). Elle est généralement forte pour les annuelles dans les ceintures périphériques sauf lorsque les vivaces dominent la végétation (B2 et B3 pour l'année 3). La zonation de la végétation est interprétée comme le résultat de la superposition de différentes contraintes dans l'espace. En position intermédiaire le long des gradients topographiques, les vivaces limitent l'expression des stocks semenciers des annuelles. La comparaison des données inter-annuelles sur la végétation et des données sur les stocks semenciers suggèrent que la localisation et la composition spécifique de la ceinture intermédiaire peut varier dans le temps. La ceinture périphérique est enrichie par les espèces des écosystèmes voisins pendant les années sèches.

Mots clés : stock de semences, zonation, gradient de stress, dynamique de la végétation, mare temporaire méditerranéenne, Maroc

ABSTRACT

The vegetation dynamics were studied for 3 consecutive years on quadrats arranged along permanent transects and the seed bank stocks were counted (1 year) using the germination method in each of the 3 vegetation belts identified (centre: B1, intermediate: B2 and margin: B3). The number of species, the total density of seeds and the percentage of annuals in the seed banks differed significantly between belts, increasing from the centre (B1) toward the margin (B3). The dominant species in the seed banks of the intermediate belt were more similar to those of the centre (B1) than of the margin (B3). The species composition of the vegetation varied with the topographical gradient, the vegetation of the belt B2 being more similar to that of B3 than to that of the centre (B1). Annuals dominated belts B1 and B3 (except in year 3) whereas perennials dominated in B2. The abundance of species in the vegetation was usually poorly correlated with their abundance in the seed banks (total vegetation). There was usually a stronger correlation with the annuals in the outer belts except when perennials dominated the vegetation (B2 and B3 for year 3). The zonation of the vegetation is interpreted as the result of a combination of various spatial constraints. In an intermediate position along the topographical gradients perennials limit the expression of the seed banks of annual species. The comparison of vegetation and seed bank data between years suggests that the location and species composition of the intermediate belt can vary with time. The marginal belt is enriched by species from neighbouring ecosystems in dry years.

Key words: seed bank, zonation, stress gradient, vegetation dynamics, Mediterranean temporary pool, Morocco

INTRODUCTION

Temporary pools under Mediterranean climates are ecosystems subjected to severe environmental stresses, resulting from the alternation during the annual cycle of an aquatic stage and a dry stage during which there is severe soil drought. The great climatic variability between years under a Mediterranean climate makes this succession of wet and dry stages irregular, both in timing and intensity (Grillas, 1992; Bonis, 1993). The vegetation in temporarily flooded habitats is composed mainly of annual species (Poiani & Johnson, 1989; Haukos & Smith, 1993) and the survival of species from one year to another depends mainly on germination from the persistent seed bank (Zedler, 1987; Bonis *et al.*, 1995; Brock & Britton, 1995). The amount of rainfall and its distribution over the annual cycle play a major role in determining the species composition of the vegetation (Holland & Jain, 1981; Grillas & Battedou, 1998).

Marked concentric zonations are known to occur in many aquatic ecosystems (Hutchinson, 1975; Wilson *et al.*, 1993; Shipley *et al.*, 1991), these being attributed to differences in flooding tolerance along the hydromorphic gradient (Brewer *et al.*, 1997; Lenssen *et al.*, 1999) and to the interaction with biotic factors, especially through competition (e.g. Grime, 1973), which is strengthened by the clonal nature of the dominant species (Grace, 1997). Disturbances favour less competitive species and a greater species richness (e.g. Pickett, 1980; Chesson, 1986). The temporal and spatial stability of the vegetation of temporary pools (Boutin *et al.*, 1982; Metge, 1986; Bonis, 1993; Crowe *et al.*, 1994) and the role of the seed bank in structuring the vegetation have been little studied (Keddy *et al.*, 1982, Pederson & Van der Valk, 1984; Wisheu & Keddy, 1991). The species composition of the seed bank is well correlated with that of the vegetation when it is dominated by annuals (Leck, 1989; Haukos & Smith, 1993; Marañòn 1998), but is poor when it is dominated by perennials (Van der Valk, 1981; Wilson *et al.*, 1993). However an absence of correlation between the seed bank of wetlands and their existing vegetation was reported by Leck & Simpson (1995) and by Bonis *et al.* (1996) for some species only. A number of factors can lead to differences between species for the correlation between the vegetation and seed banks (Grillas *et al.*, 1993) such as strategies for recruitment or for the allocation of resources to seeds, i.e. many small seeds versus few large seeds (Van der Valk & Davis, 1978; Van der Valk, 1981; Bonis *et al.*, 1996; Grillas & Battedou, 1998).

The aims of this study were (1) to assess the size of the seed bank in a daya (local name for a seasonal pool in North-West Morocco) and to answer the following questions (2) does the seed bank reflect the existing vegetation, (3) is the spatial distribution of the vegetation similar to that of the seed bank, (4) are the vegetation dynamics the same all along the hydromorphic gradient and (5) do annual and perennial species exhibit the same pattern of variability between years ?

MATERIALS AND METHODS

Study area

The study area is the Benslimane Province (N-33°38, W-7°07, 268 000 ha) on the Atlantic seaboard of Morocco. It has a large number of dayas covering ca. 2% of the total land area of the province (Rhazi, 1990). This region belongs to the northern coastal meseta domain or the low North Atlantic plateau (Destombes & Jeannette 1966) and lies within the upper semi-arid Mediterranean bioclimatic zone with mild winters. The mean annual rainfall is 462 mm, falling mainly in winter (Zidane, 1990). During the study the annual rainfall in Rabat was 748 mm in 1996, 564 mm in 1997, 499 mm in 1998 and 344 mm in 1999.

Choice of pool

The chosen pool, with an area of about of 0.5 ha, is situated in the semi-arid cork oak forest of Benslimane, on an underlying Palaeozoic sandstone-quartzite bedrock (Destombes & Jeannette, 1966). The soil is rich in clay in the centre (68% clay) and sandy at the margin (31.6% sand). This daya is typical of oligotrophic relatively undisturbed dayas in forested areas (Rhazi *et al.*, 2001); it is used for grazing and as a watering hole for livestock. The vegetation contains several rare and endangered species for Morocco including *Elatine brochonii, Lythrum thymifolia, Pilularia minuta, Exaculum pusillum, Isoetes setacea, Isoetes velata* and *Myriophyllum alterniflorum.*

Study of the vegetation

The vegetation of the pool was studied in 3 consecutive years: 1997, 1998 and 1999 with two surveys per year (April and June in 1997, February and June in 1998 and February and May in 1999). The vegetation was measured on 79 quadrats arranged every 2 m along 2 permanent transects at right angles to one another (T1 and T2 of 80 metres and 74 metres long respectively) passing through the deepest point of the pool. The quadrats used (0.3 x 0.3 m) were divided into 9 squares of 0.1 x 0.1 m. The water depth was recorded on each quadrat, plus the abundance of each species recorded as the number of squares in which it occurred (value between 0 and 9).

Three concentric belts of vegetation of different widths were distinguished: the centre (B1), intermediate (B2) and margin (B3). The belts were distinguished from one another on the basis of their vegetation and always occurred at the same altitude on the transects.

The limit between B3 and B2 was based on the occurrence of terrestrial plants in the vegetation of B3 (*Plantago coronopus, Asphodelus microcarpus, Cynara humilis, Leontodon saxatilis, Erodium cicutarium, Cerastium glomeratum, Anthoxanthum odoratum* and *Isoetes histrix*). Belt B3 is very rarely flooded.

The limit between B1 and B2, separating mostly aquatic vegetation (*Myriophyllum alterniflorum, Callitriche brutia*) from amphibious plants (*Scirpus maritimus, Lythrum biflorum, Exaculum pusillum*), occurred at an altitude of about 10 cm above the deepest part of the pool, corresponding to a maximum water depth of 32 cm.

In the analyses per belt, the quadrats of the two vegetation transects were lumped together per belt to give 31 quadrats in B1, 35 quadrats in B2 and 13 quadrats in B3. The mean abundance of each species was calculated per belt in 1997, 1998 and 1999. The longevity of the species (annual or perennial) was recorded on the basis of the catalogue of plants of Morocco (Jahandiez *et al.*, 1931-1934) and the flora of North Africa (Maire, 1952-1987).

Study of the seed bank

Twenty soil samples, consisting of 4 cm diameter cores 4 cm deep were collected from the centres of each of the three belts (a total of 60 samples). Sampling was conducted in August 1997 after the end of seed production. The total area sampled in each belt was 0.025 m^2. The samples were stored dry until the start of experimentation.

The samples were soaked in water (10 October 1997) overnight and then spread into a layer about 1 cm thick in a perforated dish 15.5 cm in diameter on a layer of synthetic absorbent tissue on top of a 1 cm layer of previously washed and sterilised sand. The samples were arranged at random in a greenhouse and watered every day until 30 June 1998. The seedlings that germinated were counted every 2 weeks and were removed after identification. Unidentified seedlings were transplanted into pots until they reached adult size and could be definitively identified. After each count and throughout the germination stage, the samples were randomly redistributed in the greenhouse. The same samples were again set to germinate from 5 October 1998 to 9 July 1999 by dividing the samples from each belt between two treatments: irrigated (10 samples) and flooded (10 samples) under about 5 cm of water. At the end of the experiment the differences between the 2 treatments (flooded and irrigated in the second period of germination) were tested (ANOVA) for each species. When the differences were not significant ($p>0.05$) the mean number of germinations per species was calculated using all 20 samples. When the differences were significant the number of germinations in the second year was calculated using the treatment (n=10) with the highest number of germinations. The cumulative number of germinations for the 2 years and the resulting density per m^2 were calculated.

Data analysis

A correspondence analysis (CA) was conducted on all the data from the three years of observation by taking, for each species and for each year, the maximum abundance value recorded per quadrat (2 surveys per year). The CA was conducted with 59 species by excluding those that were encountered less than 4 times in the three years. The centres of gravity of the distributions of the quadrats in each belt for each year were plotted on the plot of the first two axes of the analysis The centres of gravity of the seed banks per sample were superimposed (individuals inactive in the analysis) on the same plot.

The effect of the number of sediment samples on the total number of species germinating from the seed banks was tested by calculating the number of new species obtained for each new sediment sample (Forcella, 1984). A linear regression between the number of new species and the cumulative area of the samples (Log transformed) was conducted by comparing the 3 belts (ANCOVA). The comparison of the density of the seed bank between the three belts was tested by analysis of variance (ANOVA) followed by a pairwise comparison of means using the Tukey-Kramer test. Differences in the relative frequency of annual species in the seed banks of the three belts were tested by χ^2. The similarity between the seed banks of the 3 belts was tested by linear regression using the numbers of seeds per species.

The relations between the number of species per quadrat and the maximum water depth on each quadrat for the three years of observation were tested by analysis of variance for repeated measurements (MANOVA). The differences in the abundances of annuals and perennials between the belts and between years of observation were tested by analysis of variance for repeated measurements (MANOVA), using for each year the maximum values of abundance per species and per quadrat (two measurement dates/year).

Linear regression coefficients (r^2) were used to quantify the similarities between years, between belts and compartments (vegetation and seeds) for the vegetation and the seed banks. These regressions were calculated by excluding those species that were absent in the two series studied. The relations between these regression coefficients and the abundance of perennials was tested by linear regression. The parametric statistical analyses were conducted using "Jump™" software and the multivariate analyses using the "ADE™" package.

RESULTS

The three years of vegetation monitoring differed greatly in terms of rainfall and pool flooding period. The three consecutive years were increasingly dry (Table 1) with similar flooding periods in 1997 and 1998 with 23 and 20 weeks of flooding respectively in the centre of the pool but only 11 weeks in 1999.

The seed bank

During the experiments a total number of 8466 seedlings germinated (all samples cumulated), among which 89% were obtained during the first year (1998) and 11% in the second year (1999).

On average 112 341 ± 56 826 seeds/m^2 emerged from the sediment of the studied daya (maximum: 328 026 seeds/m^2 and minimum: 23 885 seeds/m^2) with 42 species including 30 annuals. Ten species (*Isoetes velata, Juncus bufonius, Juncus pygmaeus, Ranunculus baudotii, Elatine brochonii, Exaculum pusillum, Lythrum hyssopifolia, Polypogon monspeliensis, Callitriche brutia* and *Glyceria fluitans*) occurred in more than half the samples (30 samples out of 60) accounting for 84% of the total seed bank. In contrast, 13 species were found in less than 3 samples and only accounted for 1% of the total seed bank. The number of new species encountered in each new sediment sample decreased very quickly (Figure 1). After 7 samples the probability of finding a new species in a sediment sample became very low. The number of new species per sample was linearly correlated with the Log of the cumulative area of the samples ($F= 116.92$, $dF=1$, $p< 0.0001$) and this relation did not differ significantly between belts ($F=2.14$, $dF=2$, $p=0.13$). The mean total number of seeds/m^2 increased along the topographical gradient (Belt 1 : 91 600 ± 44 450; Belt 2 : 109 355 ± 44 448; Belt 3 : 136 066 ± 70 861 seeds /m^2: Tables 2a,b,c) and differed significantly between the margin and the centre of the daya (ANOVA $F = 3.37$, $dF = 2$, $p = 0.041$). The densities were only significantly different (pairwise comparison $p<0.05$) between B1 and B3.

The dominant species in the seed bank in the centre of the daya (B1) were *Isoetes velata* accounting for 57% of the total, *Ranunculus baudotii* (14%), *Myriophyllum alterniflorum* (10%) and *Nitella translucens* (9%). In the intermediate belt (B2) *Elatine brochonii* (24%), *Isoetes velata* (17%), *Juncus bufonius* (16%) and *Juncus pygmaeus* (13%) dominated. In the marginal belt (B3) *Juncus bufonius, Juncus pygmaeus, Polypogon monspeliensis* and *Elatine brochonii* accounted for 39%, 11%, 10%, and 9% of the seeds, respectively.

	Rainfall (mm)	B_1	B_2	B_3
1997	564.1	23	18	1
1998	499.2	20	15	0
1999	343.7	11	5	0

Table 1. Duration of flooding (in weeks) of the three vegetation belts (B1: centre, B2: intermediate and B3: margin) for the three years of observation.

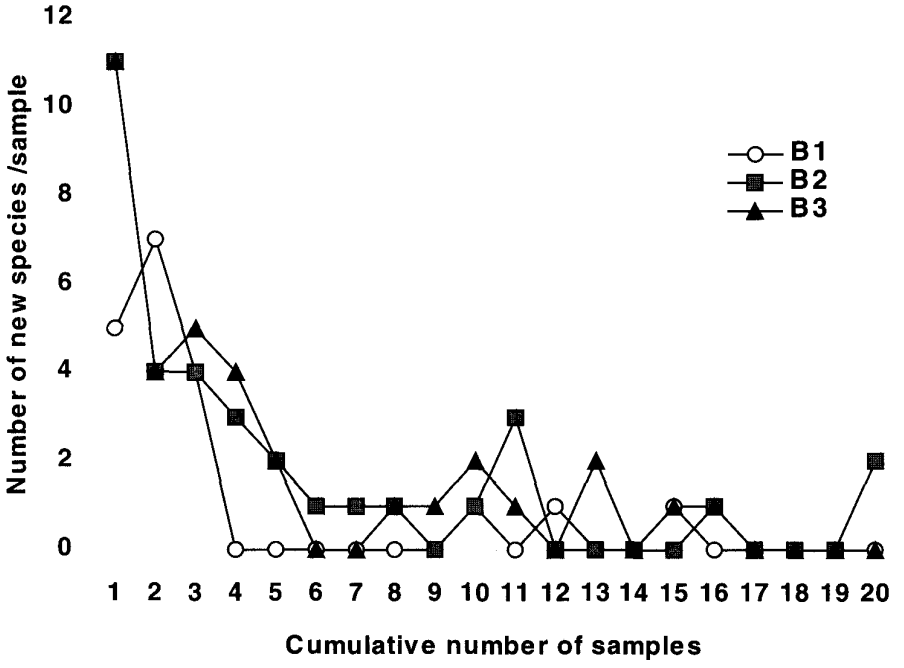


Figure 1. Number of new species encountered in the seed bank in relation to the number of samples for the 3 belts (B1: centre, B2: intermediate, B3: margin).

Species (B1)	Seed bank n=20 Density (seeds/m²) Mean	Freq.%	Vegetation 1997 n=31 Abundance Mean	Freq.%	Vegetation 1998 n=31 Abundance Mean	Freq.%	Vegetation 1999 n=31 Abundance Mean	Freq.%
Isoetes velata	52468 ± 37647	100	3.71 ± 3.37	68	2.19 ± 3.15	39	8.58 ± 1.63	97
*Ranunculus baudotii**	13250 ± 9250	100	8.03 ± 1.43	100	9.00 ± 0.00	100	9.00 ± 0.00	100
*Myriophyllum alterniflorum**	8913 ± 4675	95	7.58 ± 1.86	97	7.29 ± 1.99	100	- -	-
*Nitella translucens**	8594 ± 5342	95	- -	-	- -	-	- -	-
*Chara sp**	4576 ± 4067	45	- -	-	- -	-	- -	-
Glyceria fluitans	4459 ± 6527	80	8.06 ± 1.59	100	8.68 ± 1.62	97	8.39 ± 1.75	100
Callitriche brutia	3145 ± 3989	85	2.58 ± 3.11	55	2.10 ± 2.20	68	5.42 ± 2.46	97
Juncus bufonius	1473 ± 3468	25	- -	-	- -	-	0.16 ± 0.58	10
Heliotropium supinum	1154 ± 1581	50	5.61 ± 3.20	87	0.77 ± 1.28	42	0.39 ± 0.88	23
Illecebrum verticillatum	557 ± 1828	15	- -	-	0.29 ± 0.78	13	0.13 ± 0.34	13
*Erigeron canadensis**	557 ± 604	35	- -	-	- -	-	- -	-
Juncus pygmaeus	438 ± 1252	15	- -	-	- -	-	0.77 ± 1.26	42
Pulicaria arabica	398 ± 483	45	0.03 ± 0.18	3	2.32 ± 2.44	65	1.39 ± 2.17	35
Equisetum arvense	279 ± 1246	5	- -	-	- -	-	- -	-
Elatine brochonii	199 ± 354	25	- -	-	- -	-	- -	-
Lythrum borysthenicum	199 ± 508	15	- -	-	- -	-	0.13 ± 0.56	6
Baldellia ranunculoides	159 ± 417	15	1.52 ± 3.05	23	0.03 ± 0.18	3	0.42 ± 0.89	23
Polypogon monspeliensis	159 ± 554	10	- -	-	- -	-	0.65 ± 1.20	29
Lythrum hyssopifolia	119 ± 292	15	- -	-	- -	-	- -	-
Corrigiola littoralis	40 ± 178	5	- -	-	- -	-	- -	-
Cynodon dactylon	- -	-	0.10 ± 0.54	3	- -	-	- -	-
Scirpus maritimus	- -	-	3.87 ± 3.57	68	4.29 ± 3.14	74	3.65 ± 3.23	77
Eleocharis palustris	- -	-	2.39 ± 3.63	35	2.03 ± 3.34	32	2.48 ± 3.97	29
Carex divisa	- -	-	1.03 ± 2.76	13	- -	-	- -	-
Antinoria agrostidea	- -	-	- -	-	- -	-	0.32 ± 1.28	13
Polygonum aviculare	- -	-	- -	-	- -	-	0.32 ± 1.47	6
Ranunculus sardous	- -	-	- -	-	- -	-	0.06 ± 0.25	6
Rumex pulcher	- -	-	- -	-	- -	-	0.10 ± 0.54	3
Total density	**91600 ± 44450**							
Species richness	**20**		**12**		**11**		**18**	

Table 2a. Density of the seed bank (mean ± standard deviation, frequency, *: mean calculated with n=10) and abundance of the vegetation (mean ± standard deviation, frequency) in the centre (B1) in the three consecutive years (1997-1998-1999); - : species not found.

Species (B2)	Seed bank n=20 Density (seeds/m²)		Vegetation 1997 n= 35 Abundance		Vegetation 1998 n = 35 Abundance		Vegetation 1999 n = 35 Abundance	
	Mean	Freq.%	Mean	Freq.%	Mean	Freq.%	Mean	Freq.%
Elatine brochonii	25756 ± 24007	95	1.14 ± 2.17	26	- -	-	- -	-
Isoetes velata	18272 ±14444	100	6.20 ± 2.79	91	6.91 ± 3.63	80	4.63 ± 3.96	66
Juncus bufonius	17994 ±14956	100	0.17 ± 1.01	3	0.40 ± 1.72	6	- -	-
Juncus pygmaeus	14252 ± 9420	100	0.06 ± 0.34	3	0.77 ± 2.56	9	- -	-
Polypogon monspeliensis	7962 ± 9140	80	0.89 ± 2.14	17	1.03 ± 2.91	11	5.00 ± 2.92	94
Exaculum pusillum	5494 ± 4436	95	0.17 ± 0.86	6	0.57 ± 1.52	14	- -	-
Lythrum hyssopifolia	5454 ± 5824	70	- -	-	- -	-	- -	-
Ranunculus baudotii	2588 ± 3204	75	6.57 ± 2.45	100	8.89 ± 0.53	100	5.34 ± 4.07	77
*Glyceria fluitans**	2348 ± 4484	60	2.46 ± 3.34	43	1.89 ± 3.34	29	1.37 ± 2.90	23
Lythrum borysthenicum	2150 ± 3832	45	0.34 ± 1.00	11	0.51 ± 1.85	9	- -	-
Illecebrum verticillatum	1154 ± 1495	60	- -	-	2.83 ± 3.05	57	1.46 ± 2.98	29
Pulicaria arabica	836 ± 912	55	2.43 ± 3.67	46	5.86 ± 3.02	94	2.46 ± 2.92	60
Juncus tenageia	796 ± 1155	40	- -	-	- -	-	- -	-
Callitriche brutia	677 ± 1374	40	0.43 ± 1.09	14	0.43 ± 1.31	14	0.40 ± 1.19	14
Hypericum tomentosum	597 ± 1092	40	0.17 ± 0.62	9	0.11 ± 0.32	11	0.51 ± 1.09	23
Heliotropium supinum	557 ± 1345	25	1.40 ± 1.94	54	0.20 ± 1.02	6	0.11 ± 0.32	11
Lythrum thymifolia	557 ± 1969	15	0.03 ± 0.17	3	- -	-	- -	-
*Erigeron canadensis**	517 ± 534	25	- -	-	- -	-	- -	-
Damasonium stellatum	358 ± 1110	15	0.69 ± 1.64	20	- -	-	- -	-
Equisetum arvense	239 ± 1068	5	- -	-	- -	-	- -	-
Baldellia ranunculoides	199 ± 725	10	3.00 ± 3.48	60	0.97 ± 1.82	31	0.89 ± 1.73	37
Chara sp	159 ± 417	15	- -	-	- -	-	- -	-
Corrigiola littoralis	119 ± 390	10	0.97 ± 1.71	37	0.46 ± 1.01	29	1.29 ± 2.22	46
Isoetes histrix	119 ± 390	10	- -	-	- -	-	0.11 ±0.68	3
Sagina apetala	119 ± 390	10	- -	-	- -	-	- -	-
Scirpus pseudosetaceus	119 ± 292	15	- -	-	- -	-	- -	-
Isoetes setacea	80 ± 356	5	- -	-	- -	-	- -	-
Juncus capitatus	80 ± 245	10	- -	-	- -	-	- -	-
Mentha pulegium	80 ± 356	5	0.23 ± 0.69	11	- -	-	0.03 ± 0.17	3
Anagallis arvensis	40 ± 178	5	- -	-	- -	-	- -	-
Filago gallica	40 ± 178	5	- -	-	0.20 ± 0.68	9	0.37 ± 0.88	20
Myriophyllum alterniflorum	40 ± 178	5	1.46 ± 2.67	31	0.71 ± 2.02	14	- -	-
Pilularia minuta	40 ± 178	5	0.66 ± 1.78	17	- -	-	- -	-
Spergularia rubra	40 ± 178	5	- -	-	- -	-	0.26 ± 1.20	9
Cistus salviifolius	- -	-	- -	-	0.03 ± 0.17	3	- -	-
Crassula tillaea	- -	-	- -	-	0.09 ± 0.51	3	- -	-
Cynodon dactylon	- -	-	0.06 ± 0.34	3	0.40 ± 1.65	6	0.29 ± 0.99	11
Scirpus maritimus	- -	-	4.49 ± 3.88	66	3.14 ± 3.46	54	4.46 ± 3.93	66
Eleocharis palustris	- -	-	1.43 ± 2.66	31	0.91 ± 1.85	23	1.49 ± 2.86	29
Carex divisa	- -	-	1.09 ± 1.99	29	0.11 ± 0.47	6	0.43 ± 1.77	6
Narcissus viridiflorus	- -	-	- -	-	0.94 ± 1.59	34	0.57 ± 1.22	26
Scilla autumnalis	- -	-	- -	-	1.57 ± 2.69	31	2.49 ± 3.44	40
Trifolium tomentosum	- -	-	- -	-	0.11 ± 0.68	3	- -	-
Carlina racemosa	- -	-	- -	-	0.06 ± 0.34	3	0.17 ± 0.75	6
Spergula arvensis	- -	-	- -	-	0.26 ± 0.95	9	0.03 ± 0.17	3
Lotus hispidus	- -	-	- -	-	0.06 ± 0.34	3	- -	-
Bellis annua	- -	-	- -	-	0.06 ± 0.34	3	0.11 ± 0.68	3
Scorpiurus vermiculatus	- -	-	- -	-	0.11 ± 0.68	3	0.06 ± 0.24	6
Leontodon saxatilis	- -	-	- -	-	0.06 ± 0.34	3	1.17 ± 2.08	34
Kickxia commutata	- -	-	- -	-	0.23 ± 1.06	6	0.29 ± 0.83	14
Tolpis barbata	- -	-	- -	-	- -	-	0.09 ± 0.37	6
Antinoria agrostidea	- -	-	- -	-	- -	-	0.31 ± 0.80	17
Cistus monspeliensis	- -	-	- -	-	- -	-	0.26 ± 0.98	9
Lolium rigidum	- -	-	- -	-	- -	-	0.11 ± 0.53	6
Trifolium lappaceum	- -	-	- -	-	- -	-	0.06 ± 0.24	6
Total density	**109355 ± 44448**							
Species richness	**34**		**24**		**33**		**32**	

Table 2b. Density of the seed bank (mean ± standard deviation, frequency, * : mean calculated with n=10) and abundance of the vegetation (mean ± standard deviation, frequency) in the intermediate belt (B2) in the three consecutive years (1997-1998-1999); - : species not found.

Species (B3)	Seed bank n=20 Density (seeds/m²)		Vegetation 1997 n = 13 Abundance		Vegetation 1998 n= 13 Abundance		Vegetation 1999 n = 13 Abundance	
	Mean	Freq%	Mean	Freq.%	Mean	Freq.%	Mean	Freq.%
Juncus bufonius	53424 ± 42092	100	3.31 ± 3.40	62	4.00 ± 2.83	85	0.08 ± 0.28	8
Juncus pygmaeus	14729 ± 8211	100	1.77 ± 2.62	46	2.54 ± 3.71	38	- -	-
Polypogon monspeliensis	12978 ± 21561	90	2.69 ± 3.52	46	4.00 ± 4.42	54	3.00 ± 3.79	54
Elatine brochonii	12699 ± 22406	80	3.00 ± 2.77	69	- -	-	- -	-
Lythrum hyssopifolia	10748 ± 12956	100	2.46 ± 2.18	77	- -	-	0.08 ± 0.28	8
Isoetes histrix	7166 ± 6422	100	0.31 ± 0.75	15	1.08 ± 2.53	31	0.62 ± 1.19	31
Illecebrum verticillatum	4658 ± 7673	55	- -	-	0.92 ± 1.98	31	0.54 ± 1.45	15
Juncus capitatus	3861 ± 6196	65	- -	-	- -	-	- -	
Exaculum pusillum	2906 ± 2508	95	0.08 ± 0.28	8	0.23 ± 0.60	15	- -	-
Isoetes velata	2627 ± 5553	30	0.15 ± 0.55	8	0.38 ± 1.39	8	0.38 ± 1.39	8
Lythrum borysthenicum	1911 ± 2938	45	0.54 ± 1.33	15	0.38 ± 0.96	15	- -	-
Juncus tenageia	1314 ± 2119	45	- -	-	- -	-	- -	-
Scirpus pseudosetaceus	1194 ± 2259	35	- -	-	- -	-	- -	-
Crassula tillaea	835 ± 3027	5	- -	-	0.31 ± 1.11	8	- -	-
Pulicaria arabica	637 ± 1020	40	2.69 ± 3.17	62	0.38 ± 0.65	31	0.08 ± 0.28	8
Hypericum tomentosum	518 ± 1219	25	1.15 ± 1.46	46	0.92 ± 1.61	31	1.00 ± 1.29	46
Ranunculus baudotii	518 ± 1104	30	2.92 ± 2.96	69	5.38 ± 3.75	77	1.23 ± 2.05	38
Erigeron canadensis	438 ± 657	35	- -	-	- -	-	- -	-
Solenopsis laurentia	398 ± 1427	15	- -	-	- -	-	- -	-
Sagina apetala	398 ± 796	30	- -	-	- -	-	- -	-
Callitriche brutia	358 ± 657	30	-		0.69 ± 2.21	15	0.38 ± 1.12	15
Pilularia minuta	358 ± 1016	15	1.38 ± 2.47	31	- -	-	- -	-
Filago gallica	199 ± 438	20	- -	-	0.38 ± 0.87	23	1.00 ± 1.22	46
Helianthemum guttatum	199 ± 725	10	- -	-	- -	-	- -	-
Heliotropium supinum	199 ± 354	25	0.23 ± 0.60	15	- -	-	- -	-
Equisetum arvense	159 ± 712	5	- -	-	- -	-	- -	-
Stachys arvensis	159 ± 417	15	- -	-	- -	-	- -	-
Corrigiola littoralis	119 ± 390	10	0.31 ± 0.63	23	0.23 ± 0.83	8	0.23 ± 0.44	23
Glyceria fluitans	80 ± 245	10	- -	-	- -	-	- -	-
Lythrum thymifolia	80 ± 245	10	- -	-	- -	-	- -	-
Mentha pulegium	80 ± 245	10	0.69 ± 1.03	38	1.15 ± 1.91	38	0.77 ± 1.30	31
Cerastium glomeratum	40 ± 178	5	- -	-	0.08 ± 0.28	8	- -	-
Cistus salviifolius	40 ± 178	5	- -	-	0.38 ± 0.96	15	0.15 ± 0.55	8
Cynodon dactylon	40 ± 178	5	- -	-	0.77 ± 1.92	15	1.62 ± 3.12	38
Baldellia ranunculoides	- -	-	0.23 ± 0.60	15	0.23 ± 0.60	15	- -	-
Anagallis arvensis	- -	-			0.08 ± 0.28	8	0.23 ± 0.83	8
Damasonium stellatum	- -	-	2.23 ± 2.13	62	- -	-	- -	-
Spergularia rubra	- -	-	- -	-	- -	-	0.23 ± 0.60	15
Carex divisa	- -	-	0.23 ± 0.83	8	0.38 ± 0.96	15	0.54 ± 1.33	15
Kickxia commutata	- -	-	0.62 ± 1.26	23	- -	-	- -	-
Asphodelus microcarpus	- -	-	0.85 ± 2.15	15	0.92 ± 2.40	15	1.31 ± 1.84	38
Plantago coronopus	- -	-	0.69 ± 1.80	15	0.31 ± 0.85	15	- -	-
Spergula arvensis	- -	-	0.08 ± 0.28	8	0.31 ± 0.85	15	0.08 ± 0.28	8
Scilla autumnalis	- -	-	- -	-	2.08 ± 2.43	54	3.69 ± 2.93	77
Anthoxantum odoratum	- -	-	- -	-	2.69 ± 3.82	46	- -	-
Trifolium tomentosum	- -	-	- -	-	1.23 ± 2.28	38	0.08 ± 0.28	8
Carlina racemosa	- -	-	- -	-	1.23 ± 2.20	31	0.23 ± 0.83	8
Lotus hispidus	- -	-	- -	-	0.62 ± 1.26	23	- -	-
Bellis annua	- -	-	- -	-	0.31 ± 0.85	15	0.54 ± 1.66	15
Scorpiurus vermiculatus	- -	-	- -	-	0.54 ± 1.66	15	- -	-
Leontodon saxatilis	- -	-	- -	-	0.23 ± 0.83	8	1.15 ± 2.08	38
Cynara humilis	- -	-	- -	-	0.23 ± 0.83	8	0.54 ± 1.05	23
Erodium cicutarium	- -	-	- -	-	0.08 ± 0.28	8	- -	-
Sherardia arvensis	- -	-	- -	-	0.15 ± 0.55	8	0.15 ± 0.55	8
Tolpis barbata	- -	-	- -	-	0.23 ± 0.83	8	0.77 ± 1.36	31
Narcissus viridiflorus	- -	-	- -	-	0.69 ± 1.11	31	0.85 ± 1.52	38
Antinoria agrostidea	- -	-	- -	-	- -	-	0.15 ± 0.55	8
Cistus monspeliensis	- -	-	- -	-	- -	-	0.38 ± 0.65	31
Euphorbia exigua	- -	-	- -	-	- -	-	0.15 ± 0.38	15
Lolium rigidum	- -	-	- -	-	- -	-	0.54 ± 1.05	23
Total density	**136066**	**± 70861**						
Species richness	**34**		**23**		**38**		**33**	

Table 2c. Density of the seed bank (mean ± standard deviation, frequency, * : mean calculated with n=10) and abundance of the vegetation (mean ± standard deviation, frequency) in the marginal belt (B3) in the three consecutive years (1997-1998-1999); - : species not found.

The total number of species in the seed bank was lower in the centre (20 species) than in B2 and B3 (34 species) (Tables 2a, b, c). Among these species, 16 occurred in all 3 belts, only a single species (*Nitella tanslucens*) was found only in belt 1, 5 were exclusive to belt 2 and 8 to belt 3. There was no difference in the frequency of annual species between the belts (17/20 in B1, 26/34 in B2 and 25/34 in B3, χ^2=0.24, p = 0.89, dF= 86). However the proportion of annuals in the seeds germinating per sample did differ significantly between the 3 belts, increasing from centre (B1= 42%) toward the margin (B2= 82% and B3= 92% ; ANOVA F=49.34, dF= 59, p<0.0001). The similarity between the seed banks of the 3 belts was tested by linear regression using the number of seeds per species. The similarity was high between B3 and B2 (r^2= 0.43, n= 42, p<0.001) and lower between B1 and B2 (r^2= 0.14, n= 36, p< 0.05). The correlation between B1 and B3 was very low and not significant (r^2= 0.002, n= 38, p>0.05).

The vegetation

In the three years of observation, a total of 59 species were recorded in the vegetation (on the transects) with 29 species in 1997, 43 in 1998 and 47 in 1999 (Table 3). There were more annuals (66-67%) than perennials in the vegetation in all three years with 19, 29 and 31 species, respectively.

The zonation

The first three axes of the CA conducted on the quadrats explained 7.4%, 5.4% and 5.1% (total 17.9%) of the total variance. Axis 1 (Figure 2a) separated the aquatic and amphibious species (*Myriophyllum alterniflorum, Callitriche brutia, Ranunculus baudotii, Isoetes velata, Eleocharis palustris* and *Scirpus maritimus*) from terrestrial species (*Tolpis barbata, Leontodon saxatilis, Bellis annua* and *Hypericum tomentosum*). Axis 2 separated spring flowering species (*Mentha pulegium, Cynodon dactylon, Anthoxantum odoratum* and *Cynara humilis*) from summer flowering species (*Pulicaria arabica, Kickxia commutata* and *Exaculum pusillum*).

The coordinates of the vegetation quadrats on axis 1 of the CA differed significantly according to the maximum water depths on the quadrats (MANOVA F = 52.47, dF = 1, p < 0.0001) and between years (F = 5.57, dF = 2, p = 0.004).

The centres of gravity of the vegetation belts were distributed along axis 1 of the CA (Figure 2b).

The similarity between the vegetation of the 3 belts in 1997 was tested by linear regression using the mean abundances of each species per quadrat in each belt. B1 and B2 were very similar (r^2= 0.52, n= 24, p<0.001) but the similarity between B2 and B3 was lower (r^2= 0.09, n= 30, p<0.05). In contrast the correlation between B1 and B3 was very low and not significant (r^2= 0.005, n= 27, p>0.05).

- Belt 1: centre

In the centre of the pool a total of 21 species were recorded in the vegetation: 12, 11 and 18 species in each 3 consecutive years (Table 2a). Annual species were the most abundant, accounting for 74%, 72% and 62% of the cover in 1997, 1998 and 1999 respectively (Figure 3).

Ranunculus baudotii and *Glyceria fluitans* were the most abundant, accounting for 18% to 23% of total abundance in the 3 years. *Myriophyllum alterniflorum* was very abundant in 1997 and 1998 (17% and 19% respectively) but was totally absent in 1999, whereas *Isoetes velata* became dominant in 1999 (20% compared to 8% and 6% in 1997 and 1998, respectively).

- Belt 2: intermediate

In the intermediate belt B2 (Table 2b), a total of 45 species were recorded in the vegetation: 24, 33 and 32 species the 3 consecutive years respectively. The relative abundance of annuals and perennials in the vegetation was quite stable in the three consecutive years, the cover of annuals being between 47% and 49% and that of perennials being between 51% and 53% (Figure 3).

Ranunculus baudotii, Isoetes velata and *Scirpus maritimus* dominated (on average 18%, 15% and 11% total plant cover in the three years combined). *Pulicaria arabica* was about twice as abundant in 1998 (14%) as in 1997 (7%) and 1999 (7%). *Polypogon monspeliensis* was rather rare in 1997 and 1998 (2-3%) but became abundant in 1999 (14%).

		Frequency of occurence				
Species	**Longevity***	**1997**	**1998**	**1999**	**Total 97-98-99**	**Annual occurrence**
Ranunculus baudotii	a	75	76	63	76	3
Polypogon monspeliensis	a	12	11	49	53	3
Glyceria fluitans	a	46	40	40	52	3
Heliotropium supinum	a	48	15	11	52	3
Callitriche brutia	a	22	28	37	46	3
Baldellia ranunculoides	a	30	14	20	34	3
Corrigiola littoralis	a	16	11	21	28	3
Juncus pygmaeus	a	7	8	13	25	3
Juncus bufonius	a	9	13	4	16	3
Kickxia commutata	a	3	2	5	9	3
Lythrum borysthenicum	a	6	5	2	8	3
Spergula arvensis	a	1	5	1	7	3
Isoetes velata	v	54	41	54	67	3
Pulicaria arabica	v	25	57	33	65	3
Scirpus maritimus	v	44	42	47	55	3
Eleocharis palustris	v	22	18	19	29	3
Hypericum tomentosum	v	9	8	14	19	3
Carex divisa	v	15	4	4	17	3
Mentha pulegium	v	9	5	5	14	3
Cynodon dactylon	v	2	4	9	12	3
Isoetes histrix	v	2	4	5	6	3
Myriophyllum alterniflorum	a	41	36	0	42	2
Illecebrum verticillatum	a	0	28	16	33	2
Leontodon saxatilis	a	0	2	17	17	2
Filago gallica	a	0	6	13	15	2
Lythrum hyssopifolia	a	10	0	11	11	2
Exaculum pusilum	a	3	7	0	10	2
Trifolium tomentosum	a	0	6	1	7	2
Tolpis barbata	a	0	1	6	6	2
Bellis annua	a	0	3	3	5	2
Scorpiurus vermiculatus	a	0	3	2	5	2
Anagallis arvensis	a	0	1	1	2	2
Plantago coronopus	a	2	2	0	2	2
Sherardia arvensis	a	0	1	1	1	2
Narcissus viridiflorus	v	0	16	20	25	2
Scilla autumnalis	v	0	18	24	24	2
Carlina racemosa	v	0	5	3	7	2
Cistus salviifolius	v	0	3	1	3	2
Cynara humilis	v	0	1	3	3	2
Elatine brochonii	a	18	0	0	18	1
Damasonium stellatum	a	15	0	0	15	1
Antinoria agrostidea	a	0	0	11	11	1
Anthoxantum odoratum	a	0	6	0	6	1
Spergularia rubra	a	0	0	6	6	1
Lolium rigidum	a	0	0	5	5	1
Lotus hispidus	a	0	4	0	4	1
Crassula tillaea	a	0	2	0	2	1
Euphorbia exigua	a	0	0	2	2	1
Polygonum aviculare	a	0	0	2	2	1
Ranunculus sardous	a	0	0	2	2	1
Trifolium lappaceum	a	0	0	2	2	1
Antirrhinum orontium	a	0	0	1	1	1
Cerastium glomeratum	a	0	1	0	1	1
Erodium cicutarium	a	0	1	0	1	1
Lythrum thymifolia	a	1	0	0	1	1
Plantago lagopus	a	0	0	1	1	1
Pilularia minuta	v	10	0	0	10	1
Cistus monspeliensis	v	0	0	7	7	1
Rumex pulcher	v	0	0	1	1	1
Total		**29**	**43**	**47**	**59**	**59**

Table 3. Number of quadrats occupied (frequency of occurrence) and number of years the species were present during the three consecutive years 1997, 1998 and 1999
*Longevity: annual (a) or perennial (v), according to the catalogue of plants of Morocco and the flora of North Africa

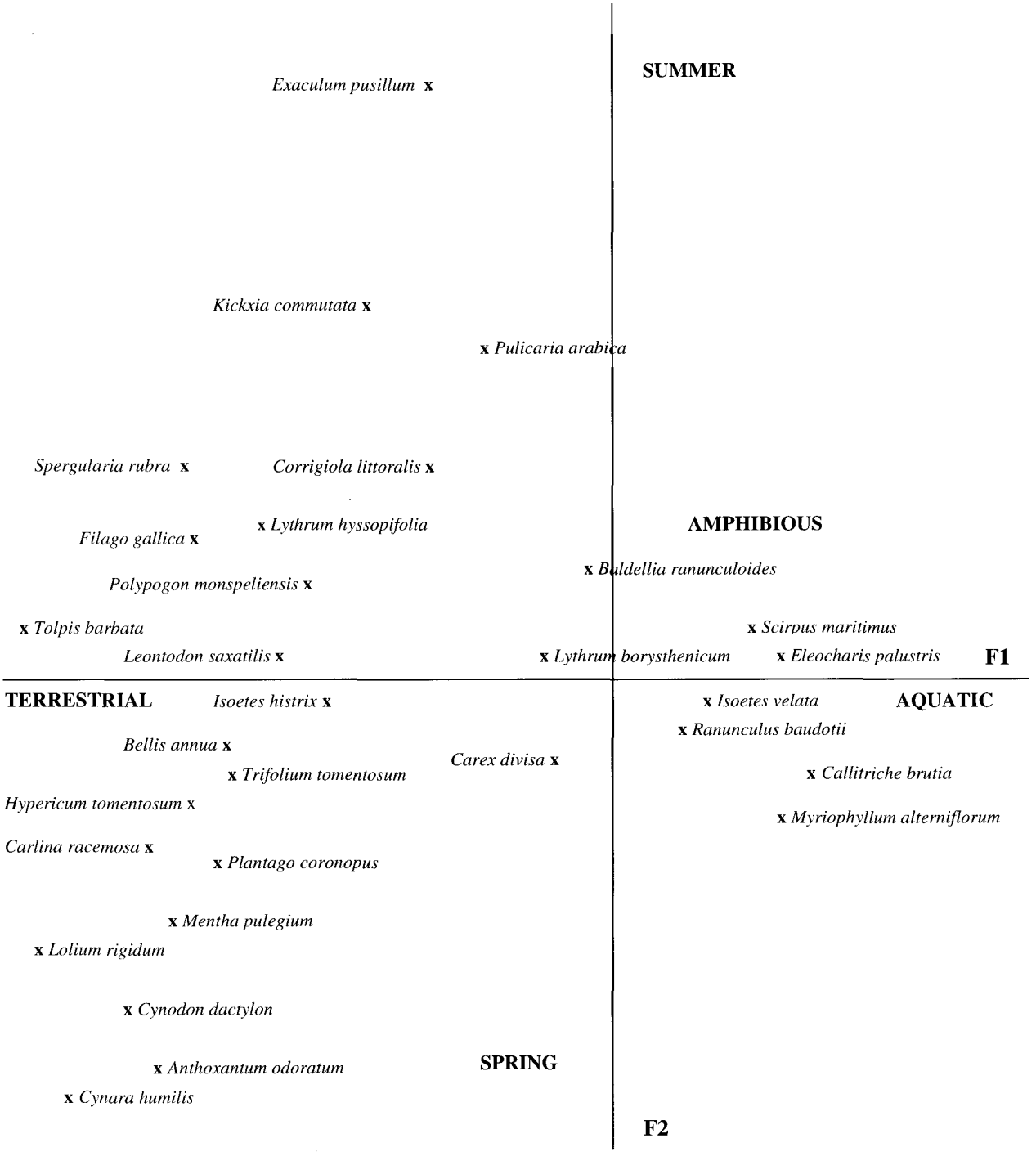


Figure 2a. Plot of axes 1 and 2 of the correspondence analysis (CA) conducted on the plant abundances in the three years of observation 1997, 1998 and 1999. Species with a low contribution, located at the centre of the graph, are not shown to improve legibility.

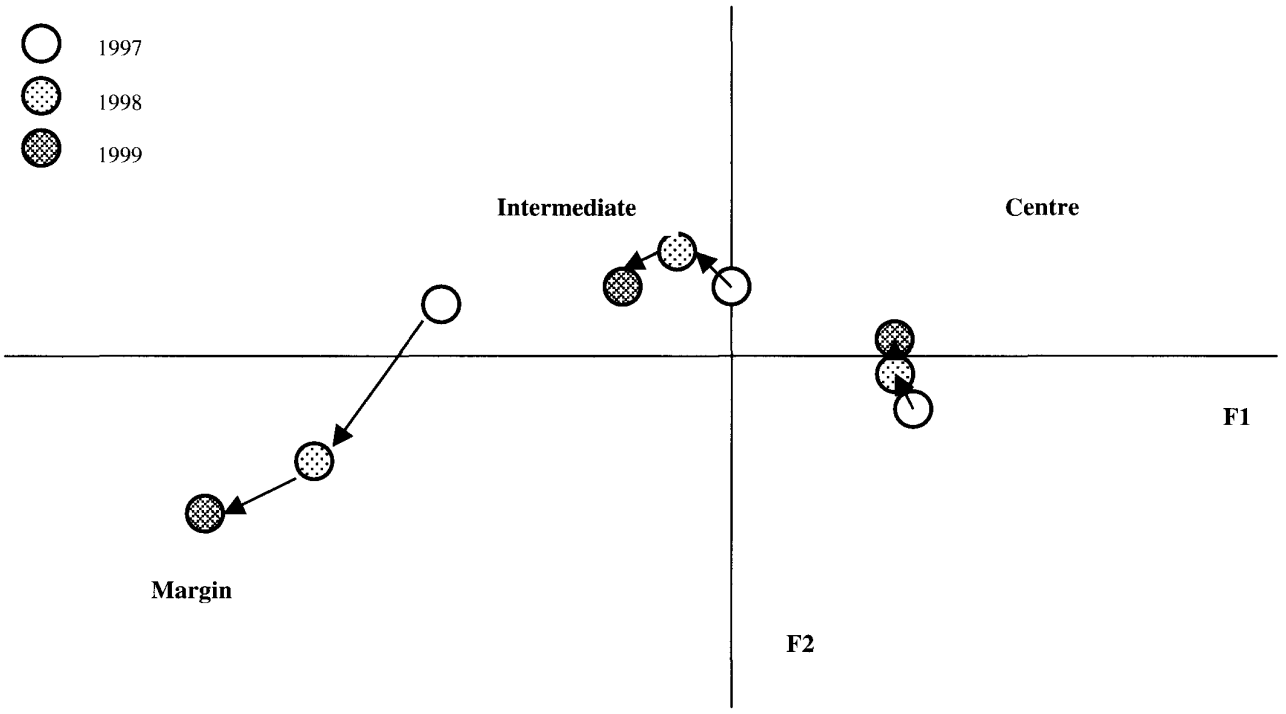


Figure 2b. Shifts in the centres of gravity of the vegetation belts in the pool during the three consecutive years (1997-1998-1999) on the plot of axes 1 and 2 of the CA.

- Belt 3: marginal

In the marginal belt B3 (Table 2c), a total of 49 species were recorded in the vegetation: 23, 38 and 33 species in 1997, 1998 and 1999 respectively. Perennials were not abundant in 1997 (27%) and 1998 (29%) but became dominant in 1999 (54%) (Figure 3).

The dominant species in 1997 were *Juncus bufonius* (12% of the total plant cover), *Elatine brochonii* (11%) and *Ranunculus baudotii* (10%). In 1998, *Elatine brochonii* was totally absent and *Ranunculus baudotii* (15%) was the most abundant together with *Juncus bufonius* (11%) and *Polypogon monspeliensis* 11%. In 1999, *Scilla autumnale* (16%) was the most abundant together with *Polypogon monspeliensis* (13%).

Vegetation dynamics between years

Of the 59 species recorded during the three years in the vegetation (Table 3), 21 occurred in all 3 years (12 annuals and 9 perennials), 18 only in 2 years (13 annuals and 5 perennials) and 20 were only recorded in one of the years of observation (17 annuals and 3 perennials).

The mean abundance of species per quadrat was highly correlated between years (all species except those absent during both years considered in the same regression). The correlations were higher between consecutive years (1997-98: r^2= 0.80, n=52, p<0.001; 1998-99: r^2=0.75, n=59, p< 0.001) than between 1997 and 1999 (r^2=0.65, n=58, p< 0.001).

On the plot of axes 1 and 2 of the CA (Figure 2b) the centre of gravity of each belt occurred in a different position each year, with a shift toward the left of axis 1 for the belts B1 and B2. The shift in the centre of gravity of the belts increased from centre toward the margin. There was also a shift in the centre of gravity of B3 on axis 2 corresponding to a relative increase in spring species (*Bellis annua, Trifolium tomentosum, Hypericum tomentosum, Plantago coronopus, Mentha pulegium, Lolium rigidum*) compared to summer species (*Kickxia commutata, Pulicaria arabica*) and by the arrival of additional species in 1998 and 1999 as compared to 1997 (e.g. *Cynara humilis, Anthoxanthum odoratum, Cynodon dactylon*, see also Table 2c).

The mean cover of annuals per quadrat differed significantly (MANOVA) between belts (F= 16.19, dF= 2, p< 0.001), decreased significantly between

years (F=24.64, dF = 2, p< 0.001) and the interaction between these factors was also significant (F=9.13, dF = 4, p< 0.001). The abundance of perennials also differed significantly, being higher in belt 2 (F= 15.09, dF = 2 ; p < 0.0001), increasing between 1997 and 1999 with a significant interaction (F = 3.26, dF = 4, p = 0.013) showing that the temporal changes differed between belts.

The similarity between pairs of years in the vegetation of the belts was also measured by the linear regression coefficient between the species abundances (Figure 4). The values of this coefficient (r^2) were higher for belts B1 (0.48 - 0.82) and B2 (0.74 - 0.80) than for B3 (0.01 - 0.29) when the total vegetation was taken into account. This pattern was also evident when annual and perennial species were analysed separately (Figure 4). The regression coefficients between years for the total vegetation (B1 and B3) and for the annuals (B1 and B3) were higher for 2 consecutive years (1997-98 and 1998-99) than for 2 years apart (1997-99). Belt B2 always had higher regression coefficients for all pairs of years, for total vegetation, for annuals and perennials. The contribution of perennials to total plant cover (measured by the frequencies in the quadrats) was high and stable between years in belt B2 (51-53%). In the belts B1 and B3 the perennials were less abundant in the first two years (< 29%) but increased in 1999 to reach 38% in B1 and 54% in B3.

Correlation between the vegetation and the seed bank

For the whole of the pool, 12 species (3 perennials and 9 annuals) were only found in the seed bank and 30 species (10 perennials and 20 annuals) were only found in the existing vegetation.

In the centre of the pool B1 (Table 2a), 7 species including only one perennial (*Equisetum arvense*) were only found in the seed bank (*Nitella translucens, Elatine brochonii, Erigeron canadensis, Lythrum hyssopifolia, Corrigiola littoralis* and *Chara sp.*). On the other hand, 8 species including 5 perennials (*Scirpus maritimus, Eleocharis palustris, Carex divisa, Cynodon dactylon and Rumex pulcher)* and 3 annuals *(Antinoria agrostidea, Polygonum aviculare, Ranunculus sardous)* were only found in the existing vegetation. In the intermediate belt B2 (Table 2b), 55

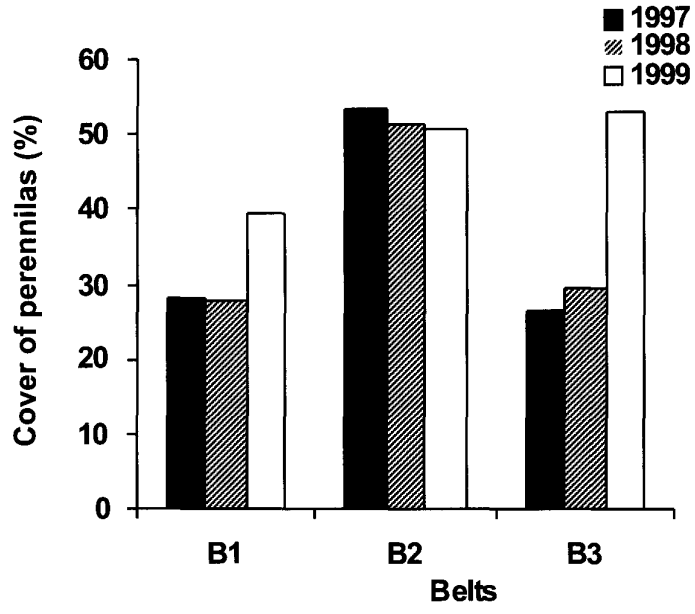


Figure 3. Proportion of perennials in the three vegetation belts (B1: centre, B2: intermediate, B3: margin) during the three years of observation (1997, 1998, 1999).

species were recorded, 34 in the seed bank and 45 in the vegetation. Among these, 10 species including 2 perennials were only found in the seed bank and 21, including 7 perennials, only in the vegetation. In the marginal belt B3 (Table 2c), 11 species, including only a single perennial, were found only in the seed bank and 26 species, including 5 perennials, only in the existing vegetation.

The correlation between the seed banks (sampled in summer 1997) and the vegetation occurring in the 3 consecutive years (1997-99) was very variable between years and between belts, with values of r^2 between <0.001 and 0.37 (Figure 4a). These correlations were always low and not significant in the intermediate belt (B2), being between 0.02 and 0.07. In the margin (B3) these correlations were significant ($p< 0.001$) in 2 years out of 3: in 1997 (r^2=0.36) and 1998 (r^2=0.25). In the centre of the daya (B1) the correlation was only significant in the third year (r^2= 0.37, $p< 0.001$).

When only the annuals were taken into consideration (Figure 4b) the correlation coefficients between the vegetation and the seed banks were generally higher than for the total vegetation in B1 and B3. The correlations between the abundance of annuals in the seed banks and in the vegetation were significant for each year in the centre (Figure 4b, B1 : r^2 = 0.46, 0.55 and 0.31 respectively for 1997, 1998 and 1999) and for 2 years out of three (1997 and 1998) for the marginal belt (B3: r^2 = 0.45, 0.27 and 0.07 respectively, for 1997, 1998 and 1999).
In contrast, the correlations were not significant in the intermediate belt (Figure 4b, B2 : r^2= 0.01, 0.002 and 0.004).

The correlation coefficient (r^2) between the abundance of annuals in the vegetation each year and in the seed banks was negatively correlated with the mean abundance of perennials in the vegetation of each belt (r^2=0.71, n=9, $p<0.01$).

The abundance of perennial species in the vegetation was generally not significantly correlated with their density in the seed banks except in the third year in the centre (Figure 4c, $B1_{1999}$: r^2=0.78) and the second year for the intermediate belt ($B2_{1998}$: r^2= 0.32).

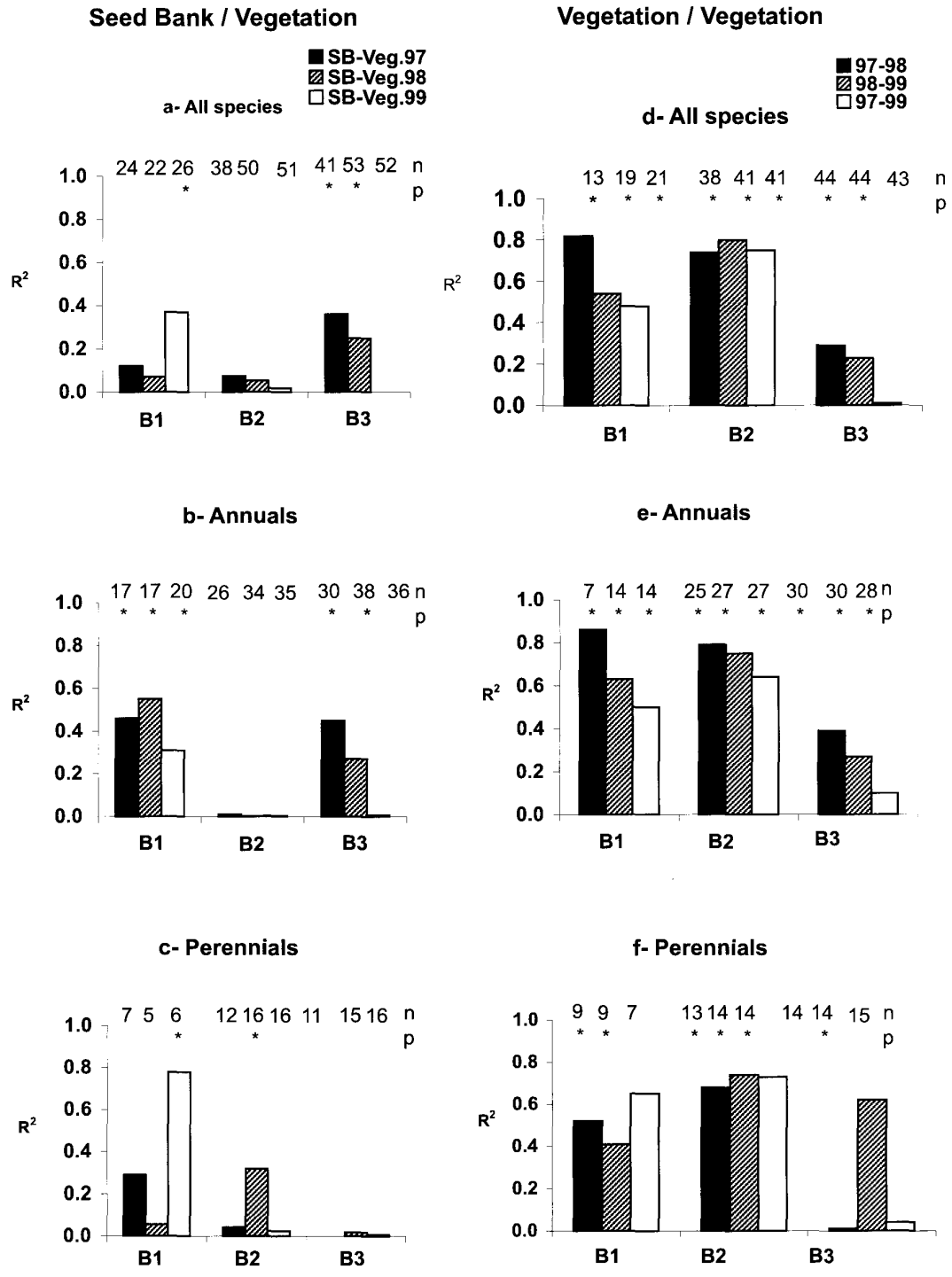
DISCUSSION

The seed bank

Size of the seed bank

It is difficult to compare the seed banks between different sites and different authors because the methods used can vary greatly both in terms of sampling methods in the field (size and number and depth of samples) and in the techniques of counting buried seeds (direct counting, germination tests, the length of test time, light and temperature conditions for germination, etc.) (Forcella, 1984; Poiani & Johnson, 1988; Leck, 1989; Gross, 1990; Brock *et al.*, 1994). Furthermore the numbers of seeds in the sediment varies greatly between years (Leck & Simpson, 1995). The method used in this study tends to underestimate the size of the seed bank because the experimental conditions are not necessarily suitable for the germination of all species and only the non-dormant fraction of the seeds germinates. The area sampled (a total of 2370 cm^2) and the number of samples used (60) were sufficient to describe the seed bank (Forcella, 1984; Brock *et al.*, 1994). The detailed analysis of results per species should however be avoided when they exhibit a low frequency of occurrence (Grillas *et al.*, 1991)
The densities of seeds measured in the Moroccan dayas are greater than those reported for most other wetlands (e.g. Van der Valk & Davis, 1976; Leck & Simpson, 1995) including the 8 000 – 15 000 seeds/m^2 found in an Australian floodplain (Finlayson *et al.*, 1990). The density of seeds is within the range reported for other Mediterranean temporary pools. Values of 37 000 to 808 000 seeds/m^2 were found in temporary marshes in the Rhône delta (Bonis *et al.*, 1995) and 433 000/m^2 in the brackish marshes of the Coto Doñana, in southern Spain (Grillas *et al.*, 1993) using the direct counting method, which tends to over-estimate the viable part of the seed bank. The densities of seeds measured in annual vegetation in the Mediterranean region (49 000 – 126 000 seeds /m^2, using the germination method) are also of the same order of magnitude (Marañon, 1998). Similar values have been found in Australian ricefields (177 000 seeds/m^2), that are similar to seasonally flooded natural marshes (McIntyre, 1985).

Figure 4. Coefficients of similarity (R^2) for each belt between the vegetation and the seed bank for (a) the total vegetation, (b) annual species, (c) perennial species occurring during the 3 years of observation (1997, 1998 and 1999) and coefficients of similarity between years of the vegetation for (d) total vegetation, (e) annual species, (f) perennial species.



The contribution of pteridophytes and charophytes is not always taken into account in studies on seed banks (Wisheu & Keddy, 1991). The high abundance of charophytes in the coastal wetlands of the Rhône delta (Bonis *et al.*, 1995: 86-94 %) and the Guadalquivir estuary (Grillas *et al.*, 1993: 97%) compared to this study (2%) can be explained by (i) the salt tolerance of charophytes (Grillas *et al.*, 1993), (ii) the longer flooding period and (iii) the high carbonate concentrations in the water that are needed by the genus *Chara* (Corillion, 1957). In contrast, the pteridophytes that were abundant in our study, where they accounted for 24% of germinations, were totally absent in the Mediterranean coastal wetlands.

Structure of the seed bank

The seed banks in the three belts studied differed in their seed densities, number of species and relative abundance of the various species (Table 2a, 2b, 2c). The species composition of the belts varied along the gradient between the centre and the margin. The greater similarity between the marginal and intermediate belts than with the centre is explained by overwhelming influence of winter flooding in B1. The decrease in the density of seeds from the margin (Table 2a, 2b, 2c) toward the centre is similar to the findings of Wisheu & Keddy (1991) but contradicts those of Keddy & Reznicek (1982, 1986) and Pederson & Van der Valk (1984) who found the highest densities at intermediate positions along the topographical gradient. The hypothesis that Wisheu & Keddy (1991) gave for the difference between their result and that of other studies was that seeds would be preferentially deposited at high levels during periods of high water level. This explanation cannot apply in our case because the water level was very low or the pool was even dry during seed production so that dispersal by water could not take place. It is more likely that the decrease in the density of seeds with increasing depth is related to the reduction in the number of species in the seed bank (Table 2a, 2b, 2c).

The contribution of annuals to the total seed bank differed between belts, being higher at the margin (81%) and at intermediate levels (91%) in the pool than at the centre (47%). This spatial distribution of perennials and annuals is somewhat different from that described for vernal pools (Holland & Jain, 1977) and in Washington State (Crowe *et al.*, 1994) where perennials dominated at the margin and annuals in the centre. It seems that the physical conditions in the B3 belt were unfavourable for the dominance of perennials, either because of excessive summer drought, or because of exceptionally severe flooding in the year preceding the study. Annuals also accounted for 79% to 93% of the seed banks in saline marshes in the Guadalquivir estuary and in annual grasslands in south-west Spain (Marañon, 1998). The lower relative abundance of annuals in the centre of the daya could in part be an artefact, because *Isoetes velata,* which was considered to be a perennial and which accounted for 52% of the seed bank in B1, can become a facultative annual in exceptionally dry years such as 1999. This species germinated abundantly from spores in the dry year (1999) in the centre of the pool and behaved like a facultative annual. The plasticity of the life cycle of *Isoetes velata* has also been observed in the rock pools in the rhyolites at Colle-du-Rouet (Poirion & Barbero, 1965).

The vegetation

Similarity with the seed banks

Widely varying results have been published concerning the similarity between the vegetation and the seed bank. There is often a close similarity when the vegetation is dominated by annuals (Leck, 1989; Leck & Simpson, 1995; Marañòn, 1998). Leck & Simpson (1995) listed a series of factors explaining the absence of similarity such as dominance by a species producing few or no viable seeds, inappropriate germination conditions, low seedling survival and differences in the seasonal timing of germination. The results of our study showed that the correlation between the seed bank and the vegetation varied spatially (between belts) and between annuals and perennials. In all three belts the stocks of seeds showed little resemblance to the vegetation as a whole. The similarity was on the whole rather low for the total vegetation, high for the annuals in B1 and B3 and usually low for perennials with the notable exception of B1. The low similarities found can be explained by several factors that vary in importance between belts and years:

(1) There is a great diversity of resource allocation strategies, between the production of a few large-sized seeds and large numbers of tiny seeds (Thompson &

Grime, 1979; Grillas *et al.*, 1993) with important ecological implications. The difference seems to be particularly pronounced between the angiosperms and pteridophytes (in this case *Isoetes velata* in B1). The same difference in the abundance of "seeds" has also been recorded between charophytes and angiosperms in coastal marshes (Bonis, 1993; Grillas *et al.*, 1993). This difference also occurs among the angiosperms and helps explain the poor correlations in B2 between the abundance of species in the vegetation and in the seed bank (Table 2b in B2: *Elatine brochonii*, *Juncus bufonius*, and *J. pygmaeus* have very large seed banks consisting of very small seeds). Using the weight of the seeds instead of their density would overcome this problem (Grillas *et al.*, 1993) but information on seed weights is only available for a small proportion of species.

(2) The importance of vegetative reproduction also varies greatly between species. Those that practice such a strategy are more abundant in the vegetation than in the seed bank (*Glyceria*, *Callitriche* in B1).

(3) The presence of perennials that produce few or no seeds and which survive from one year to another by their vegetative structures. The isolation of the pool among an arid landscape could also explain the absence of seed production by *Scirpus maritimus* (abundant in B2) resulting from a lack of allo-pollen (Charpentier *et al.*, 2000).

(4) Unfavourable weather conditions are also probably responsible for the absence of some species in the vegetation whereas they have large seed banks (e.g. *Elatine brochonii, Lythrum thymifolia* and *Damasonium stellatum* only germinated in 1997, the wettest year). Therefore in each year only a part of the species having a seed bank appears in the vegetation (Thompson & Grime, 1979; Marañòn, 1998; Bliss & Zedler, 1998).

(5) Competitive exclusion by perennials could help to explain the poor correlation obtained for annuals, since the similarity was negatively correlated with the cumulative cover of perennials.

(6) The correlations between the vegetation and the seed bank were generally lower with the vegetation in 1999, which can be explained by the single sampling date for the seed bank. It is likely that the species composition of the vegetation and the seed bank are continually changing under the cumulative effects of germination, plant growth and reproduction (Bonis *et al*, 1995; Leck & Simpson, 1995). Terrestrial species appeared in the vegetation of B3 in 1999 (*Cistus salviifolius, Cistus monspeliensis* and *Lolium rigidum)* sometimes with a high abundance (*Cynodon dactylon, Asphodelus microcarpus*) probably coming from the nearby matorral and favoured by the drought in 1999.

The zonation

Zonations have long been recognised in aquatic vegetation (e.g. Hutchinson, 1975; Wilson & Keddy, 1985; Shipley *et al.*, 1991) and have been attributed to flooding tolerance along the hydromorphic gradient (Lenssen *et al.*, 1999) and to the interaction with biotic factors, mainly through competition (e.g. Grace & Pugesek, 1997). The effect of competition is reinforced by the clonal nature of the dominant species favouring vegetative reproduction. In Moroccan pools 3 belts are generally recognised (Nègre, 1956; Boutin *et al.*, 1982; Metge, 1986). According to Brewer *et al.* (1997) and Lenssen *et al.* (1999), competition plays an important role only in the parts that are rarely flooded, the tolerance of the physical conditions prevailing in the parts that are flooded for long time.

This study suggests that in Moroccan pools the zonation is the result of the distribution of the species along the topographical gradient in relation to their tolerance of winter flooding and spring and summer drought. On top of this gradual discernible pattern in the seed bank there is a discontinuity created by competitive exclusion exerted by perennials especially in belt B2. The extension of the model of Brewer *et al.* (1997) to Moroccan temporary pools leads to different explanations being given for the mechanisms in each belt that determine the zonation. In B1, flood tolerance is probably the determining factor, in B2 the stress caused by flooding is less and competitive exclusion becomes dominant. In B3, summer drought could be the main factor. This spatial distribution pattern of constraints probably changes from year to year in relation to variations in water level and the processes of vegetation dynamics.

Vegetation dynamics

Vegetation dynamics are the result of environment constraints and biotic processes. In this study the dynamics of the vegetation between years was

measured by the decrease in the coefficients of similarity between the 3 years of observation (Figure 4). The vegetation changed more at the margin than in the centre where the submersion constraints were probably a more stable stress factor than in the other belts. The dynamics were also expressed by the increase in the cover of perennials in B3 (Figure 3). We think that the observed changes in the vegetation were the result of the impact of recent fluctuations in weather conditions between years leading to reduced durations of flooding. The different degrees of similarity between belts in terms of their vegetation and their seed banks could also be interpreted as the result of longer term vegetation changes induced by rainfall fluctuations. The changes observed in the vegetation in B2 and B3 are mainly explained by recolonisation by more terrestrial vegetation (especially mattoral perennials in B3 such as *Cistus*, and *Asphodelus*, Table 2c) which is in agreement with the decreasing rainfall during the period 1997-1999 (Table 1). These changes occurred after an exceptionally wet year (1996: 748.2 mm) which probably greatly reduced the terrestrial component of the vegetation. In the belt B1, the between-years vegetation dynamics resulted more from a direct effect of weather conditions on the germination of the seed banks and the differential growth of species with few new species.

The similarity between belt B2 and the two neighbouring belts differed depending on whether the vegetation or the seed bank was being analysed. The vegetation of B2 was similar to that of B1 ($r^2 = 0.52$) in 1997 but differed greatly from the vegetation of B3 ($r^2 = 0.09$), whereas for the seed banks the similarity was greater between B2 and B3 ($r^2 = 0.46$) than between B2 and B1 ($r^2 = 0.17$). Because of dormancy, the seed bank in B2 integrated meteorological changes over a longer time period than the vegetation. Seed banks would be less affected than the vegetation by recent wet years (1996-1998) and could reflect the drought of the period 1990-1995 (mean rainfall 336 mm/year). This interpretation is in agreement with the results of the hypothesis that direct linear succession is absent in wetlands (Mitsch & Gosselink, 1986).

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Tree ring to climate relationships of Aleppo pine (*Pinus halepensis* Mill.) in Greece

Relations cernes– climat chez le pin d'Alep *(Pinus halepensis* Mill.) en Grèce

A. Papadopoulos[1], F. Serre-Bachet[†], & L. Tessier[2]

[1]: Technological Education Institute of Lamia, Department. of Forestry, GR- 36100 Karpenissi, Greece.

[2]: I.M.E.P., case 451, Université d'Aix-Marseille III, Faculté des Sciences de St Jérôme, F-13397 Marseille Cedex 20, France.

DEDICATION

This article is dedicated to the memory of Mme Françoise Serre-Bachet who greatly contributed to the dendroclimatological study of Aleppo pine in Greece.

ABSTRACT

The relationship between radial growth of Aleppo pine (*Pinus halepensis* Mill.) in Greece and climate is calculated for the period 1955-1989. Fourteen populations are selected to represent at best the distribution area of Aleppo pine in Greece. The climate parameters used are monthly precipitation and mean monthly minimum and maximum temperatures, from four meteorological stations chosen, after principal component analysis, for their suitability to express the local climate of the forest sites. Response functions are used to express the relationship between tree-ring width and climate, and were computed using Bootstrapped Orthogonal Regression.
Results show that ring width correlates positively to winter precipitation, (December, January), and spring (April, May) precipitation, and negatively to spring temperature (April, May). These relationships slightly differ according to geographical location of the populations. They emphasise the role of water storage during winter dormancy and that of evapotranspiration processes during the initial growth period in spring.

Key words: Dendroclimatology, dendroecology, response function

RESUME

La relation entre la croissance radiale annuelle du pin d'Alep (*Pinus halepensis* Mill.) et le climat est calculée pour la période 1955-1989 sur 14 populations représentatives de l'ensemble des forêts de pin d'Alep de Grèce. Les paramètres climatiques pris en compte associent les valeurs mensuelles des précipitations et des températures minimales et maximales. Ces données climatiques sont fournies par quatre stations météorologiques sélectionnées, après analyse en composantes principales, pour leur représentativité des climats régionaux auxquels sont soumis les différents sites forestiers. La relation cerne-climat mise en évidence par le calcul des fonctions de réponse met en oeuvre des régressions multiples orthogonalisées.
Les résultats montrent que l'épaisseur du cerne annuel est globalement corrélée, positivement aux précipitations hivernales (décembre, janvier) et printanières (avril, mai), négativement aux températures printanières (avril, mai). Ces relations se nuancent en fonction de la distribution régionale des différentes populations. Les résultats confirment le rôle important de la constitution des réserves hydriques pendant la phase de repos hivernal et l'importance de la régulation de l'évapotranspiration pendant la phase printanière de mise en place du cerne.

Mots-clés: Dendroclimatologie, Dendroécologie, fonction de réponse

INTRODUCTION

Aleppo pine (*Pinus halepensis* Mill.) is a typical Mediterranean species that has been the object of dendrochronological analyses in various Mediterranean countries such as France (Serre, 1976; Serre-Bachet, 1985, 1991, 1992; Nicault, 1999), Morocco (Mokrim, 1989), Algeria (Mederbal, 1992; Safar, 1994), and Israel (Lev-Yadun *et al.*, 1981). Many of these studies deal with the relationships between annual ring width and climate variables such as monthly precipitation and temperature, or climate and bioclimate indexes. As mentioned by Hughes *et al.* (1982) and Schweingruber (1996), tree ring to climate relationships involve not only climate but also the whole tree-site complex. The site characteristics (topography, substratum nature, soil components and structure, surrounding vegetation, etc) play the role of modulators of the climatic factor considered as input. They can amplify or reduce the contribution of some factors in limiting annual growth. On a homogeneous climatic area, site characteristics variability introduces most of the spatial variation in tree growth rates. A *posteriori* analysis of relationships between the tree-ring sequences and the synchronous sequences of monthly climate parameters makes it possible to characterise ecologically tree populations within their habitat (Tessier, 1989; Tessier *et al.*, 1994). The purpose of this study is to determine the growth response of Aleppo pine to climate inter-annual variability over its whole distribution area in Greece.

MATERIALS AND DATA

Dendrochronological data

The data used in the present study come from fourteen Aleppo pine populations representing most of the species distribution area (Figure 1). Table 1 shows the environmental and site features of the 14 sampled populations. For each population, ten to fifteen mainly dominant trees were selected from a homogeneous, as to environmental features, area of approximately 1 Ha. Three, breast-height cores were sampled per tree resulting to 30-45 samples per population. After crossdating (Kaennel & Schweingruber, 1995) and ring width measurement, 30 to 36 elementary series were built for each population (Papadopoulos, 1992).

Climate Data

The following monthly climate factors were used: sum of precipitation (P), mean of minimum (Tmin), mean of maximum (Tmax) and mean (Tm) temperatures. These data are relative to the meteorological stations of Pirgos, Observatory of Athens, Kimi, and Thessaloniki (Figure 1); they cover the period 1955-1989, the longest for which reliable meteorological data are available. Stations co-ordinates and tree populations related with are given in Table 2. The four stations were selected from 37 operating within four isoclimatic regions. These regions overlay Aleppo pine's natural distribution in Greece and were determined from a principal component analysis of the interannual variability of precipitation and temperature over the period 1955- 1989 (Papadopoulos, 1992, 1993).

The criteria for the selection of the stations were their proximity to the tree sites as well as the completeness, accuracy, homogeneity of observations and the length of the series (Schweingruber, 1996). The time window used to correlate ring width and monthly climate parameters refers to the biological year defined as the period from October of the year prior to growth to September of the year of ring formation. This period is generally accepted for dendroclimatological and dendroecological appli-cations in the Mediterranean basin (Berger *et al.*, 1979; Serre-Bachet, 1985; Till, 1985; Tessier, 1986, 1989; Schweingruber, 1988; Nola, 1992; Safar, 1994; Gadbin-Henry, 1994; Romagnoli & Codipietro, 1996). Such a calendar has been confirmed for *Pinus halepensis* in Southern France by recent monitoring of radial growth (Nicault, 1999).

METHODOLOGY

For each population, calculation of tree-ring to climate relationships included four steps. The first step is the standardisation of the elementary chronologies corresponding to each core in order to minimise the non-climatic signal. The second step is the calculation of the tree-ring to climate relationships for all the previously standardised elementary chronologies. The chronologies that gave the strongest relationships are used to build up a mean chronology in the third step.

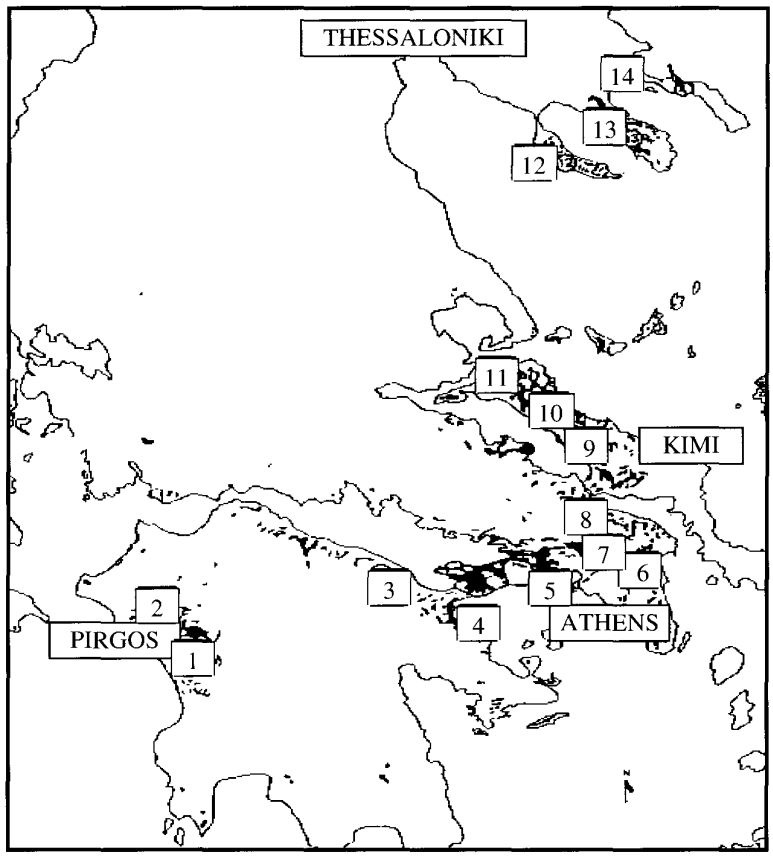

Figure 1. Location of the 14 Aleppo pine populations and the 4 meteorological stations. White areas represent the Aleppo pine distribution in Greece.

Population	Site	Altitude (m)	Bioclimatic type	Substrate	Crown coverage (%)
1	Pirgos	150	Subhumid	Marls	100
2	Ámaliada	180	Subhumid	Marls	100
3	Xylokastro	100	Semiarid	Marls	100
4	Korinth	70	Semiarid	Limestone	80
5	Salamina	50	Semiarid	Limestone	75
6	Pendeli	320	Semiarid	Schist	85
7	Tatoi	550	Semiarid	Limes & marls	85
8	Chalkida	150	Semiarid	Limes & marls	80
9	Prokopi (Evia)	190	Subhumid	Peridotites	75
10	Agia Anna (Evia)	90	Subhumid	Marls	95
11	Istiea (Evia)	50	Subhumid	Marls	100
12	Kassandra (Chalkidiki)	100	Subhumid	Marls	90
13	Sithonia (Chalkidiki)	50	Semiarid	Phyllites	85
14	Gomati (Chalkidiki)	200	Subhumid	Gneisses	100

Table 1. Main environmental features of the 14 Aleppo pine populations.

Meteorological Station	Longitude	Latitude	Altitude (m)	Population
Pirgos	21 18′	37 40′	13	1 and 2
Observ. of Athens	23 43′	37 58′	107	3, 4, 5, 6, 7 and 8
Kimi	24 06′	38 38′	221	9, 10 and 11
Thessaloniki	22 56′	40 39′	39	12, 13 and 14

Table 2. Meteorological stations and Aleppo pine populations used for the response functions.

Population	Total number of elementary residual series	Variance of the series (mean value) %	Number of selected elementary residual series	Variance of the selected residual series (mean value) %
1	36	49	15	62
2	36	46	16	57
3	36	80	17	86
4	35	63	35	63
5	34	82	34	82
6	36	42	23	55
7	30	45	20	50
8	30	87	18	88
9	36	36	19	41
10	36	46	17	49
11	36	39	20	44
12	33	74	33	74
13	36	45	18	51
14	30	44	16	48

Table 3. Total number of elementary residual series and number of selected series according to the response functions results with the percentage (%) of explained variance, for each population of Aleppo pine.

For the fourth step, a response function is established upon this mean standardised chronology.

This response function expresses the tree-ring to climate relationship for each population. A detailed description of these steps is presented in the following sections.

Standardisation of ring-width series

An important task in dendroclimatology is the standardisation of tree-ring series in order to minimise the non-climatic signal (Fritts, 1976; Graybill, 1982; Cook, 1987; Cook *et al.*, 1990; Guiot, 1990a). Each elementary ring-width series used in the present study was previously modelled (Papadopoulos, 1992) by an Auto Regressive Moving Average (ARMA) process (Box & Jenkins, 1970; Guiot *et al.*, 1982; Guiot, 1986, 1990b) to create 30-36 elementary residual series for each population. Reduced to a white noise (Guiot, 1990b) the elementary residual series obtained, represent at best the inter-annual variability (Guiot *et al.*, 1982; Guiot, 1986). The choice of such a powerful standardisation is imposed by the human disturbances always present in Aleppo pine forests. Because low and medium frequency variability is more likely to be induced by human activities (grazing, resin harvest) than by climate fluctuations, it was decided to remove such variations, even if doing so some climatic information may be lost.

Calculation of response function

Calculation of response functions involves orthogonal regression (for more details see Guiot, 1990b). Each residual chronology (the dependent variable) is matched against 24 monthly climate parameters after principal component analysis applied on climate data. These climate regressors include monthly precipitation (P) in three combinations with minimum, maximum, and mean temperatures (respectively Tmin, Tmax, and Tm). The simultaneous use of precipitation and temperature was preferred because of the combined effect of these factors on tree-growth processes. The combination P with Tm was used only for calculating the preliminary response functions on elementary residual chronologies. Statistical significance of the relationship was tested

using the Bootstrap method (Guiot, 1990b) where regression is calculated on 50 sub-samples (ring-width and climatic data) randomly chosen among the 35 annual combinations. This number of simulations was chosen since the procedure was repeated 100 times and the correlation coefficients were stable over the 40th simulation. The statistical model is calculated on the randomly selected years and verified on the unselected years. The significance level of the response function was provided for the calibration years (Fc) and the verification years (Fv) by the ratio R/s, where R is the mean correlation coefficient between values predicted by the tree-ring to climate relationship model and actual values, s is the standard deviation of R for the 50 regressions simulated. The significance level of each regression coefficient was expressed by the ratio of each regression coefficient (r) and the corresponding standard deviation (s) for the 50 simulations. To make the comparison easier, the response functions were coded according to the significance of the regression coefficients (Student`s t test), as suggested by Tessier (1986) and Serre-Bachet & Tessier (1989):

code 1: $0.90 \leq P < 0.95$ for $1,65 \leq r/s < 1,96$,
code 2: $0.95 \leq P < 99\%$ for $1.96 \leq r/s < 2,57$,
code 3: $0.99 \leq P$ for $r/s \geq 2,57$.

Each of the above given codes is preceded by a positive (+) or negative (-) sign representing respectively, a positive or negative correlation between the variables. The mean R^2 obtained for the calibration years provided the variance explained by the 24 climate regressors.

Construction of the mean chronologies

The mean population chronology, used eventually as the dependent variable, is the mean of the elementary chronologies selected according to the response functions results among the 30 to 36 obtained within the population. The purpose of such a selection, as suggested by Guiot *et al.* (1982) and Tessier (1986), is to include in the mean chronologies, the series that provide the most homogeneous and most significant response functions. Comparison of results obtained for the different elementary chronologies of the same population showed a strong homogeneity of response function profiles. Only a few elementary chronologies were discarded for their heterogeneity (6 from population 1, 7 from population 2, and 6 from population 14). From the remaining ones, only those for which the significance level of response function reached 80% were selected. According to this procedure, 15 to 35 elementary residual chronologies were selected in order to construct the mean chronology and to represent each population. Using of selected chronologies raised the mean residual series' variance by approximately 10% (Table 3) without changing the response functions' profile.

RESULTS

Figures 2 and 3 summarize the response functions profiles obtained for P with Tmin and P with Tmax. The variance explained by the response functions (Table 4) is always high ($72<R^2<92$). For the calibration years, all response functions are found significant at the 99,9% level. On the contrary, on the verification years, only 50% of the populations show response functions significant at a level up to 90% (Table 4). Such results emphasise the temporal instability of the climate-growth model. The most significant response functions (Fv= 90-99%) are those of populations 3, 4, 5, 6, 7, and 8. Both types of response functions (P with Tmax and P with Tmin) of all the Aleppo pine populations are positively correlated with precipitation and, except for one case, negatively correlated with temperatures. Strong correlation with precipitation occurs in winter, mainly in December and January, and in spring, mainly in April for populations 1 to 10 and in May for populations 12, 13, and 14. Negative correlation with temperatures occurs in spring, mainly in April and May. The strongest correlation occurs in April for populations 4, 5, 6, 7, 8, and 9 and in May for populations 3, 4, and 5. Minor correlation with temperatures occurs in April for populations 12 and 13 and in May for populations 1 and 2. Populations 10, 11 and 14 are not correlated with temperatures. Results provided by both combinations (P with Tmin) and (P with Tmax) are similar as regard to precipitation, but not to temperature: populations 1 and 2 are more sensitive to minimum temperatures as compared to the maximum temperatures, whereas populations 6, 7, and 8 are sensitive in March only to maximum temperatures. No relationship appears both for precipitation and temperature in early summer (June-July). Some precipitation influence is observed in August and September.

Population	Meteorological Station	P with Tmin		P with Tmax	
		R^2	F_v	R^2	F_v
1	Pirgos	79	80	79	80
2	>>	81	80	83	80
3	Obser. of Athens	83	90	83	90
4	>>	88	95	88	95
5	>>	90	95	92	99
6	>>	85	90	90	95
7	>>	90	95	92	95
8	>>	86	90	86	95
9	Kimi	77	80	81	80
10	>>	72	80	76	80
11	>>	72	80	76	85
12	Thessaloniki	84	90	81	85
13	>>	81	85	81	90
14	>>	83	80	73	80

Table 4. Residual variance (R^2) and significance of response function (Fv) on verification years using the combination P with Tmin and P with Tmax

DISCUSSION

Based on these results, it appears that precipitation plays a more important role for *Pinus halepensis*, radial growth than temperature. However, the positive effect of precipitation does not involve the dry summer period, which is not surprising since diameter growth stops during the dry summer period as Nicault (1999) showed it by means of tree growth monitoring. Relatively abundant precipitation in spring seems crucial for a good radial growth and the amount of water stored in the soil during the winter period plays a major role. Moreover, negative relationships with spring temperature can be attributed to water stress. High temperature induces high rate of evapotranspiration when water fluxes can be limited by water availability in soil (Serre, 1976; Kozlowski *et al.*, 1991; Serre-Bachet, 1992; Nicault, 1999).

Similar relationships were observed in other Mediterranean areas mainly involving precipitation but less temperature. In Southern France, Serre (1976), Serre-Bachet (1982), found positive correlation with the precipitation of the winter dormant period and early growth period in spring. Negative correlation was found with spring and summer temperature. For the same area, Nicault (1999) found also positive correlations with March and April temperatures and negative from May to August. In Israel, Lev-Yadun *et al.* (1981) found positive correlation with precipitation of the end of winter and spring, and negative with March and November temperatures. Mokrim (1989) in Morocco and Safar (1994) in Algeria found similar positive response functions with precipitation before and during the growth period.

The most interesting result is that affinities between response functions (Figures 2 and 3) are closely linked to the geographical location of populations (Figure 1) as regard to latitude and ecological zonation (Table 1). According to these similarities, four groups are identified: southwestern populations (1, 2) south-eastern populations (3, 4, 5, 6, 7, 8), northern populations (12, 13, 14) and, between the two previous groups, a transition zone with the populations 9, 10, and 11. The most significant relationships (highest values of R^2 and Fv) occur for all the southeastern populations growing in semiarid bioclimate (Table 1).

Such results emphasise the strong role of water stress in *Pinus halepensis* growth. Positive effect of winter precipitation is greater for the populations of the southeastern group growing in semi-arid conditions (3, 4, 5, 6, 7, and 8).

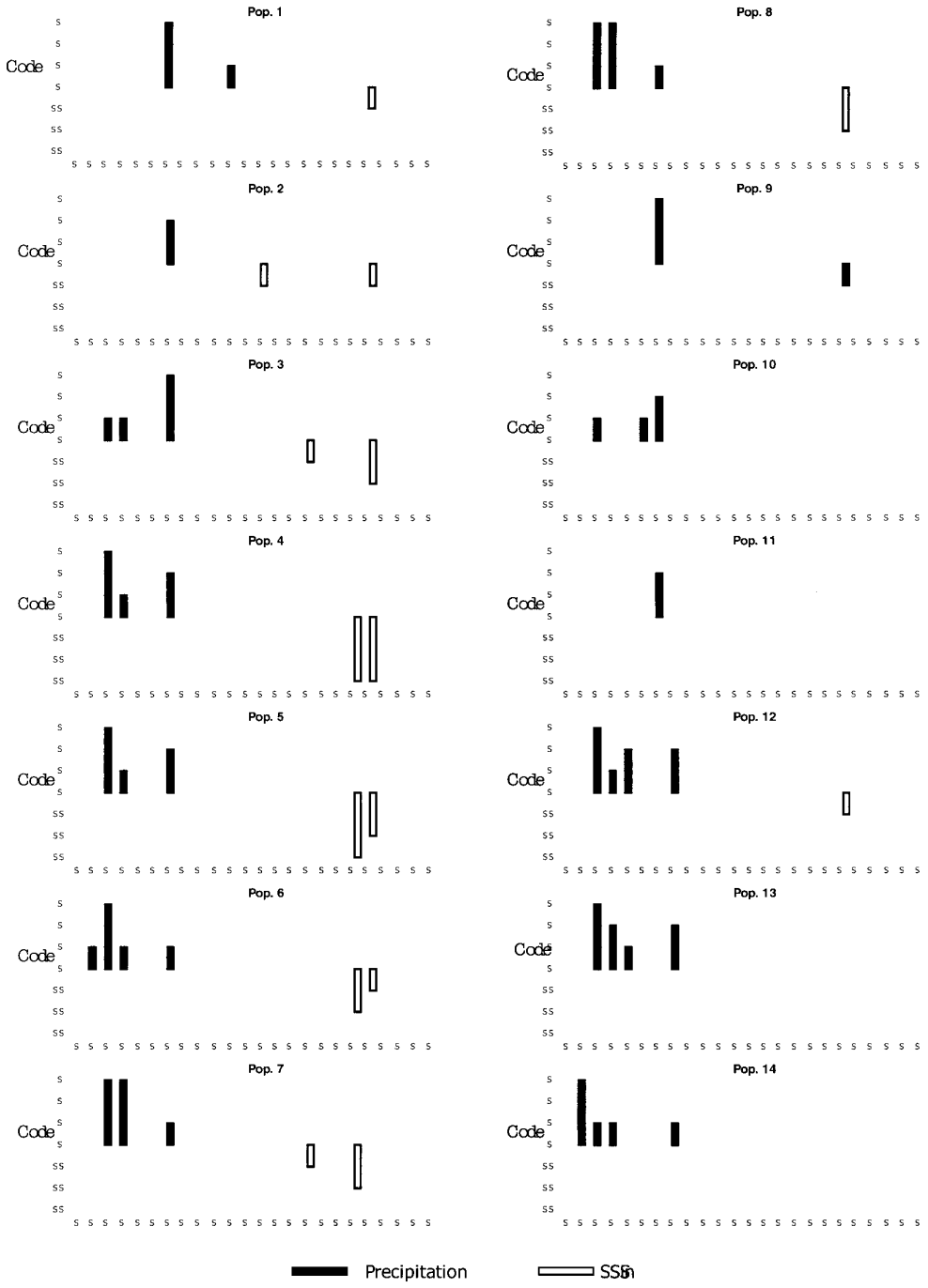

Figure 2. Response functions profiles with the 24 climate regressors (P with Tmin), code 1: 90% ≤ P < 95%, code 2: 95 % ≤ P < 99 %, code 3: P ≥ 99 %, +: positive correlation, -: negative correlation

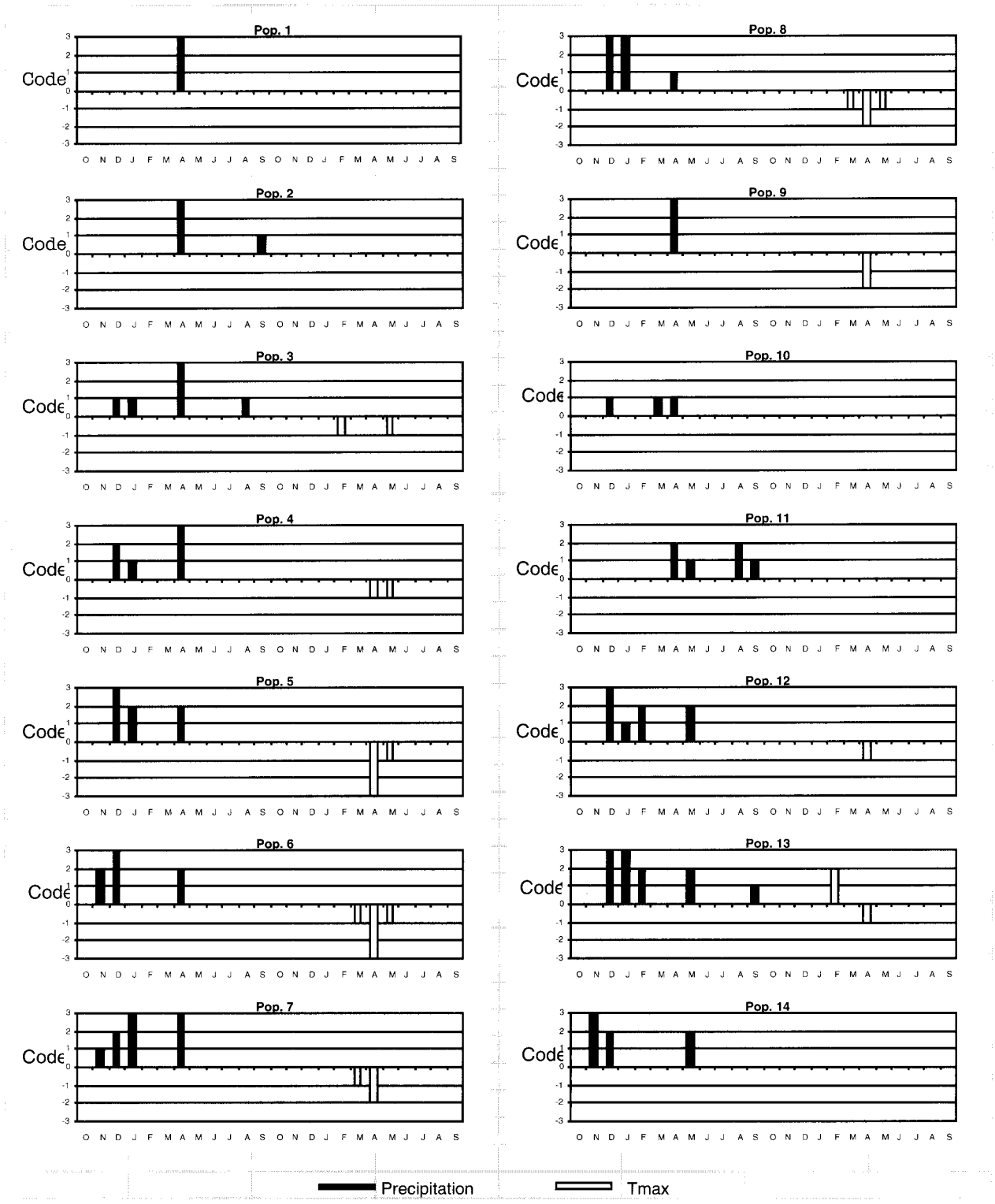

Figure 3. Response functions profiles with the 24 climate regressors (P with Tmax), code 1: 90% ≤ P < 95%, code 2: 95 % ≤ P < 99 %, code 3: P ≥ 99 %, +: positive correlation, -: negative correlation

The lack of significant relationships between ring widths and winter precipitation for the south-western populations 1 and 2 of west Peloponessos and for 9, 10 and 11 of Evia, can be attributed to their higher winter precipitation (approximately 75-100 mm) in these areas than in any other area of Aleppo pine's natural distribution. Northern populations (12, and 13) show an effect of winter precipitation with a secondary maximum in February (Papadopoulos 1992). The positive effect of spring precipitation evidenced for all populations may be attributed to the increased water demands for the various physiological processes such as intense cambium reactivation and growth release after winter dormancy. Tree growth monitoring shows that most of the earlywood is built during this early spring period (Nicault, 1999). All populations show this direct relationship in April with the exception of northern populations that show this relationship in May. This may be attributed to their geographical position that results to a later cambium reactivation. Such a delay is due also to a climate differentiation of Northern Greece characterised by increased continentality and a different spring precipitation regime (Papadopoulos, 1992, 1993). As regard to temperature, the strong inverse relationship observed in April involves only southeastern populations. Such a relation is interpreted in connection with the positive relation with precipitation and the evapotranspiration process (Serre-Bachet, 1992). It can be noticed that summer climate conditions do not influence significantly tree growth. This is common and obvious for many mediterranean species that even reduce or stop cambial activity in that period (Liphschitz & Lev-Yadun, 1986; Schweingruber, 1996; Nicault, 1999). Diamantoglou & Kull (1982), based on phenological observations in Athens over the period 1975-76, point out that Aleppo pine's growth occurred between February and June.

CONCLUSIONS

The relationships observed reflect the effect of climate differentiation on *Pinus halepensis* growth in Greece according to geographical location of the sites. It appears that the species growth is mainly influenced by conditions prevailing before and at the beginning of the growing season. No relation appears neither with precipitationnor temperatures for the dry summer period. Water storage in winter appears as the main limiting factor of tree radial growth. Combination of precipitation and temperature, at the beginning of the growing period (April-May), is, through evapotranspiration processes, another limiting factor for growth. Evidencing of these correlations cannot be immediately interpreted as causal effects due to the complexity of the physiological processes and their interaction with site factors. These correlations just show how tree growth is controlled by seasonal distribution of the main climate parameters. But the results obtained by *a posteriori* analysis of the relationships between tree radial growth and climate is coherent as regard the results obtained in growth monitoring. The dendroecological approach supplies the spatial dimension necessary to precise Aleppo pine autoecology in Greece. If such a characterisation brought valuable information for *Pinus* forest management, however, the large distribution area of *Pinus halepensis*, widespread from arid to mesic type of climate does not allow to define precisely the potentialities of the species on the whole Mediterranean basin. Several studies (see bibliography) have described these different climate situations but a thorough synthesis of the behaviour of this species is far from being achieved. Such knowledge would contribute to the assessment of the impact of climate change on forests and to a forest management adapted to such a climate change.

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Ecologie du genre *Hedysarum* en Tunisie : répartition des espèces en fonction des facteurs du milieu

Ecology of *Hedysarum* in Tunisia: distribution of species in relation with environmental factors

Aziza ZOGHLAMI [1], Hamadi HASSEN [1] & Larry David ROBERTSON [2]

[1] Laboratoire des Cultures Fourragères, Institut National de la Recherche Agronomique de Tunisie (INRAT), 2080 Ariana,Tunisie.

[2] International Center for Agriculture Research in Dry Areas (ICARDA), Aleppo, Syria.

RESUME

Afin de sauvegarder et de valoriser les légumineuses fourragères et pastorales en Tunisie, en particulier les espèces du genre *Hedysarum* ou sainfoin d'Espagne, dont les espèces sont abondamment pâturées par le bétail et dont certaines se trouvent menacées de disparition, sous l'action de différents facteurs, plusieurs prospections ont été réalisées dans le nord et le centre du pays. Au cours de ces prospections, 84 populations représentant 5 espèces de sulla ont été répertoriées, sur un total de 77 stations réparties dans 5 étages bioclimatiques de la Tunisie. *H. coronarium* est largement répandu, suivi par *H. spinosissimum* et *H. carnosum. H. pallidum et H. humile* sont rares. L'analyse de variance appliquée aux données climatiques et édaphiques a montré que la répartition naturelle des espèces de sulla est principalement déterminée par la pluviométrie et l'altitude du site d'origine et,à un moindre degré, par la température. Les teneurs en élements chimiques ainsi que la texture du sol s'avèrent avoir peu ou pas d'influence sur leur répartition de ces espèces.

Mots-clés: Sulla, répartition géographique, pluviométrie, altitude, Analyse Factorielle des Correspondances.

ABSTRACT

In order to preserve and valorise forage and pasture legumes in Tunisia, particularly the genus *Hedysarum* wich species are preferably eaten by animals and some of them are threatened because of many reasons, 3 collections missions were conducted in northern and central Tunisia. During these missions, 84 populations covering 5 species of *Hedysarum* were recorded over 77 sites distributed on 5 bioclimatic zones. *H coronarium* was the most widespread followed by *H spinosissimum* and by *H carnosum. H pallidum* and *H were* rare. The variance analysis applied to climatic and soil factors showed that natural distribution of *Hedysarum* species is mainly affected by rainfall and altitude and secondly by temperature. Chemical nutrients of soil and texture affected few or not the distribution of these species.

Key-words: Sulla, geographic distribution, pluviometry, altitude, Correspondence Analysis.

ABRIDGED ENGLISH VERSION

Forage legumes including the genus *Hedysarum* (sulla or "sainfoin d'Espagne") show many advantages wich make justified their utilisation for improving rangeland and forage production The genus *Hedysarum* (which includes annual and perennial species) is called to play an important role in forage and pastoral prouction Unfortunately, some of these species are threatened by rarefaction mainly due to overgrazing or crop intensification. In Tunisia, all species of *Hedysarum* are eated by animals even only the *coronarium* species is under cultivation. The other species still growing as weeds. In order to valorize this germoplasm of forage and pastoral interest in Tunisia, and as already done for *Medicago, Scorpiurus and Trifolium*, we propose in this paper to study the ecological distribution of spontaneaous species of *Hedysarum* in relation to environmental factors. Thus, a survey mission was conducted in 1995 in northern and central Tunisia jointly with ICARDA and CLIMA in addition to other previous data collected. During these surveys, 84 populations from 5 species of *Hedysarum* were recorded on 77 stations distributed over the following bioclimates: very humide (4 stations), humide (24 stations), sub-humide (14 stations), semi-arid (27 stations) and arid (8 stations). Environmental informations were also collected and soil samples were sampled for further analysis. Data were analysed using an Anova and a correspondence analysis. Among the 6 species of *Hedysarum* present in Tunisia, 5 were found but only 3 were frequent enough to be statistically analysed. *H. coronarium* was the most widespread, followed by *H. spinosissimum* and *H. carnosum*. *Hedysarum pallidum*, an endemic species from north Africa was particularly rare (only one station) as *H. humile* was. Anova analysis showed that rainfalls and altitude are the most discriminating factors of the natural distribution of *Hedysarum*, followed by minimal temperature. Soil parameters were proved to have weak or no effect on their distribution. Correspondence analysis showed that *H. carnosum* and *H. spinosissimum* have similar requirements for low rainfalls with the preference of *H. spinosissimum* for high elevations contrarely to *H. coronarium* wich prefers wet and heavy soils. In general, all the studied species prefered calcareous soils. The presence of *H. spinosissimum* and of *H. carnosum* was also depending on high soil silt contents. On the other hand, these species grow equally in relation to phosphorus and salt.

INTRODUCTION

Les légumineuses fourragères, dont fait partie le genre *Hedysarum* (sulla ou sainfoin d'Espagne), présentent de nombreux intérêts qui rendent leur utilisation justifiée dans l'amélioration des parcours et des productions fourragères (capacité de fixer l'azote, qualité fourragère et rôle important dans l'amélioration de la fertilité des sols en cas de rotations culturales) (Abdelguerfi *et al.*, 1991 ; Sulas *et al.*, 2000). Le genre *Hedysarum* (qui comprend des espèces annuelles et pérennes) est appelé à jouer un rôle fondamental dans la production fourragère et pastorale et dans d'autres domaines comme l'apiculture, la protection des sols contre l'érosion, la mise en valeur des terres. Malheureusement, certaines espèces de ce genre se trouvent menacées de rarefaction voire de disparition sous l'action de plusieurs facteurs dont principalement, le surpâturage, l'intensification des cultures et la réduction des terres de parcours au profit des cultures céréalières et arboricoles. Il est à noter que toutes les espèces présentes en Tunisie sont abondamment pâturées par le bétail. Ceci leur confère un intérêt supplémentaire, même si seule *H. coronarium* fait l'objet d'une culture (Baatout *et al.*, 1976 ; Louati *et al.*, 2000). L'introduction du sulla dans la rotation culturale se justifie particulièrement dans les terres lourdes où les céréales souffrent de l'excès d'humidité. Sur les versants, du fait de l'érosion, on a intérêt à maintenir le sulla en pâturage permanent. La plante du sulla (*H. coronarium*) est spontanée sur les marnes assez bien drainées partout où la pluviométrie dépasse 350 mm/an (Corriols, 1965).

Dans le souci de préserver et d'utiliser ces ressources végétales naturelles d'intérêt fourrager et pastoral en Tunisie et comme cela a été fait pour les *Medicago* annuelles, les *Trifolium* et les *Scorpiurus* et d'autres espèces spontanées locales, nous nous proposons d'étudier la répartition des espèces spontanées du genre *Hedysarum* en Tunisie en fonction de quelques facteurs du milieu.

MATERIEL ET METHODES

Le genre *Hedysarum* (sulla), fabacée pastorale, est représenté en Afrique du Nord par onze espèces spontanées (Quézel et Santa, 1962 ; Pottier-Alapetitte, 1979 ; Abdelguerfi *et al.*, 1991 ; Boussaîd *et al.*, 1995 ; Ben Fadhel et al., 1997). La majorité d'entre-elles est menacée d'érosion génétique voire de disparition. Les taxons annuels et pérennes, diploïdes (2n=16) et tétraploïdes (en=4x=32) sont très polymorphes et essentiellement allogames (Boussaîd *et al.*, 1995). Ils présentent une bonne valeur nutritive, une bonne croissance hivernale et sont bien adaptés aux irrégularités du climat en zones semi-arides et arides de l'Afrique du nord (Ben Fadhel *et al.*, 1997). Selon

Baatout *et al.* (1976), le genre *Hedysarum* regroupe lui-même 2 ensembles : l'un constitué d'espèces alpines, asiatiques et arctiques dont le nombre chromosomique de base est x=7 et l'autre constitué de plantes méditerrannéennes dont le nombre chromosomique de base, au moins pour les espèces tunisiennes est x=8. L'espèce *H.coronarium* est caractérisée par une variabilité morphologique considérable. Les plantes spontanées sont généralement prostrées et celles à port érigé sont rarement trouvées dans la nature (Louati-Namouchi *et al.*, 2000).

Matériel prospecté

Une prospection spécifique du genre *Hedysarum* a été menée en 1995 dans le Nord et le Centre de la Tunisie en collaboration avec l'ICARDA et le CLIMA. Cette prospection s'ajoute à d'autres prospections réalisées antérieurement en 1992 et en 1994 par la même équipe respectivement dans le centre (de part et d'autre de la dorsale tunisienne), le nord et nord-est du pays. Au cours de ces trois prospections, 84 écotypes du genre *Hedysarum* représentant 5 espèces (2 pérennes et 3 annuelles) ont été collectés sur un total de 77 sites répartis sur les étages bioclimatiques suivants : perhumide (4 sites), humide (24 sites), sub-humide (14 sites), semi-aride (27 sites) et aride (8 sites) (Tableaux 1 et 2). Afin de mieux expliquer l'écologie des sites et permettre des analyses ultérieures, nous avons établi pour chaque site visité une fiche où ont été relevés les paramètres suivants : topographie, structure des sols, vocation des terres et abondance des espèces. Un échantillon de sol a également systématiquement été prélevé pour analyse physico-chimique (pH, conductivité électrique, calcaire total, matière organique, phosphore assimilable, azote, carbone, potassium et granulométrie). Les données telles que l'altitude et les coordonnées géographiques (latitude et longitude) ont été mesurées à l'aide d'un GPS au cours de la prospection. Pour les paramètres climatiques (pluviométrie et température), nous nous sommes référés aux stations météorologiques les plus proches des sites de collecte. Ces données estimées sur de longues périodes, nous ont été fournies par le laboratoire de bioclimatologie de l'INRAT et l'Institut National de la Météorologie. L'échantillonage des sites a été réalisé de manière aléatoire et les populations ont été collectées à des intervalles de 10 à 20 km. En effet, nous ne savions pas au départ si dans la région explorée, il sera possible de découvrir et de rapporter des spécimens des plantes recherchées. C'est seulement sur place que nous avons été amenés à orienter nos parcours et nos prélèvements en fonction des renseignements obtenus. Les lieux de relevés ont été sélectionnés aléatoirement sur une carte routière de façon à couvrir la totalité de la zone programmée. Ainsi, les prospections ont porté sur des jachères, des parcours, des champs de céréales, des plantations d'oliviers et d'amandiers et même sur des bords de routes. Sur chaque site visité, a été prélevé un mélange de gousses représentatif de la population échantillonée sur une dizaine de plantes au minimum et ceci dans le but d'établir des essais d'évaluation ultérieurs. Les espèces ont été identifiées sur place en utilisant la flore de Tunisie (Pottier-Alapetite, 1979).

Traitement statistique des données

Les données ont d'abord été soumises à une analyse de variance, en vue de connaître la prépondérance des différents facteurs sur la distribution des espèces (seuls les sites contenant l'espèce ont été retenus), puis à une analyse factorielle des correspondances (AFC) afin d'extraire les variables les plus discriminantes pour la présence des espèces. Cette dernière analyse permet d'établir un diagramme de dispersion dans lequel aparaissent à la fois les individus observés et les variables considérées et de mettre en évidence des proximités naturelles existant entre les éléments des deux ensembles (Abdelguerfi *et al.*, 1991). L'intérêt de cette méthode n'est pas nouveau et elle a déjà été utilisée dans l'étude de la répartition des espèces de *Medicago* annuelles et autres légumineuses pastorales en Tunisie (Zoghlami *et al.*, 1996 ; Zoghlami et Hassen, 1999 ; Hasssen *et al.*, 1994), en Algérie (Abdelguerfi *et al.*, 1991) et au Maroc (Bounejemate, 1994). Pour homogéneiser variables qualitatives et quantitatives, ces dernières ont été divisées en classes. Les bornes des classes ont été choisies de façon à ce

que celles-ci contiennent toutes le même nombre d'individus (Tableau 3).

RESULTATS

Résultats de la prospection

D'après une première analyse des résultats (Tableau 4), il s'avère que *H. spinosissimum* est fréquente dans la zone aride et semi-aride (bien qu'elle soit également présente dans l'humide et le sub-humide). D'après Abdelguerfi (1991), c'est une espèce qui se localise dans les régions sablo-limoneuses arides et subdésertiques et elle est plus fréquente en Algérie et au Maroc qu'en Tunisie.

En outre, *H. carnosum* a été trouvée uniquement dans la zone aride. D'après Boussaîd *et al.* (1995), elle est endémique d'Afrique du nord et elle semble être particulièrement sensible au surpâturage, ce qui a provoqué une nette diminution de ses populations naturelles. C'est une espèce des régions difficiles qui se rencontre également dans le sud tunisien (Baatout, 1976). Selon Abdelguerfi (1991), cette espèce appartient à l'association des pelouses sablonneuses et argilo-sablonneuses de la Tunisie méridionale. En Lybie, Boussaid *et al.* (1995), l'indiquent comme espèce côtière dans les habitats calcaires. En Tunisie centrale, elle a été trouvée sur des sols sableux à des altitudes inférieures à 575 m en association avec *Trigonella monspeliaca, Hippocrepis bicontorta, Medicago littoralis* et *M. laciniata* (Hassen *et al.*, 1994). Selon Baatout (1976), *H spinosissimum* est présente sur l'ensemble du territoire tunisien avec toutefois quelques différences observées au niveau de l'appareil floral, entre les représentants nordiques et ceux récoltés dans le sud qui ont permis la distinction de 2 sous-espèces. En Algérie, Abdelguerfi *et al.* (1991) la signalent également dans le bioclimat aride et saharien.

En outre, *H. coronarium* occupe une large aire de répartition, s'étendant de l'humide au semi-aride. Au nord de la Tunisie, cette espèce est très commune sur les vertisols à pH élevé et constitue des peuplements spontanés parfois très importants formant à la période de floraison (avril-mai) d'immenses taches rouges. Ces peuplements naturels sont exploités par les éleveurs, soit en pâture, soit en fauche. Dans les secteurs les plus arrosés, nous l'avons trouvée en sympatrie avec *Medicago ciliaris.* Au centre et au sud de l'Italie, *H. coronarium* présente un développement important sur les sols calcaires des zones semi-arides (Bravi *et al.*, 2000). Les différentes espèces poussent rarement en mélange à l'exception de l'association d'*H. coronarium* avec *H. spinosissimum* (4 relevés uniquement).

Effet des facteurs sur la distribution des espèces

Données du milieu

Les données relatives à l'aspect du paysage, la roche mère, la texture du sol, l'habitat et la pente ont été brièvement analysées. *H.spinosissimum* et *H. carnosum* sont présentes dans les pâturages dégradés et les vergers d'oliviers, sur une roche mère calcaire de texture sableuse ou rocheuse et de pentes variables. *H.coronarium* pousse fréquemment dans les pâturages et les champs de blé sur des vertisols de faible pente. *H. pallidum*, espèce peu répandue en Tunisie, est fréquente dans les zones forestières de forte pente du centre tunisien. Elle compte parmi les espèces pastorales les menacées par l'érosion génétiques (Boussaîd *et al.*, 1998).

Espèces	Présence	Fréquence (%)
H. coronarium L.	46	60
H. spinosissimum L.	25	33
H. carnosum Desf.	4	5
H. pallidum Desf.	1	1
H. humile L.	1	1

Tableau 1. Fréquence relative des espèces d'*Hedysarum* collectées

Espèces	Etages bioclimatiques				
	PH	H	SH	SA	A
H. coronarium	4	30	11	5	-
H. spinosissimum	-	3	4	8	11
H. carnosum	-	-	-	-	6

PH : Perhumide (P>1200mm), H : Humide (800<P<1200mm) ; SH : Sub-Humide (600<P<800mm) ; SA : Semi-Aride (300<P<600mm) ; A : Aride (P<100mm), d'après Le Houérou (1969).

Tableau 2. Répartition des espèces d'*Hedysarum* en fonction des étages bioclimatiques

Variables	Code Classes	Limites supérieures 1	2	3
Pluviométrie (mm)	Plv1 à Plv3	477,9	626	1534
Altitude (m)	Alt1 à Alt 3	125	230	1005
tmin (°C)	m1 à m3	4,9	6,7	10,6
tmax (°C)	M1 à M3	31,8	33,4	37,7
pH	pH1 à PH3	7,8	8,1	9,5
Matière organique (%)	MO1 à MO3	1,51	2,98	7,39
Conductivité (mmhos/cm)	CE1 à CE3	0,29	0,51	5,81
Calcaire total (%)	Ca1 à Ca3	8,1	22,3	68,3
Phosphore (ppm)	P1 à P3	4,1	9,3	172,3
Azote (ppm)	N1 à N3	935	1511	4063
Sable (%)	Sb1 à Sb3	11,8	19,3	61,2
Argile (%)	Arg1 à Arg3	15,7	23,3	34,9
Limon (%)	Lim1 à Lim3	46,7	64,9	34,9
Carbone (%)	C1 à C3	0,9	1,36	3,21
Potassium (ppm)	K1 à K3	0,56	0,74	1,28

Tableau 3. Variables et classées utilisées dans l'Analyse Factorielle des Correspondances (AFC)

Espèces	Altitude (m)	Pluviométrie (mm)	T min. (°C)	T max. (°C)
H. spinosissimum	321***	355,4***	5,4***	33
H. coronarium	172,1+	749,6**	6,4	32,1+
H. carnosum	235,8	377,9	3,6	37,1
Moyenne (77 sites)	230,2	597	5,8	32,5

+, ***: seuil de signification: +: 10%, ***: 0,1%

Tableau 4. Moyenne des principales variables climatiques et de l'altitude pour les différents sites où l'espèce est présente

Variables climatiques

Les facteurs climatiques, essentiellement la pluviométrie, l'altitude et la température sont les variables les plus discriminantes (Tableau 4). *H. spinosissimum* préfère les altitudes relativement élevées (en comparaison avec l'altitude moyenne de l'ensemble des sites prospectés) et les endroits à faible pluviométrie contrairement à *H. coronarium,* qui se rencontre sur les sites de basses altitudes mais bien arrosés. *H carnosum* semble avoir une large adaptation à l'altitude et a tendance à se localiser dans les régions à faible pluviométrie et à hiver frais. En Algérie, elle se rencontre essentiellement dans les régions peu arrosées et de moyenne altitude (Abdelguerfi *et al.*, 1988).

Variables édaphiques

Les facteurs chimiques et physiques du sol ont peu ou pas d'influence sur la répartition des espèces étudiées (Tableau 5). Comme pour les facteurs climatiques, *H. carnosum* semble être indifférente aux facteurs édaphiques. Selon Boussaîd *et al.* (1995), il s'agit d'une espèce des terrains argileux gypseux et salés. *H. spinosissimum* est plus fréquente sur les sols à pH neutre, pauvres en azote et en MO mais riches en limon. La présence d'*H. coronarium* est liée aux sols pauvres en calcaire total et à pH neutre. D'après (Boussaîd *et al.*, 1995), cette espèce se développe sur les sols argilo-limoneux bien drainés sous des pluviométries supérieures à 350 mm/an. Certains facteurs tels que les teneurs en phosphore, carbone et potassium, ainsi que la conductivité électrique n'ont aucun effet sur la répartition naturelle de ces espèces.

Relation entre la présence des espèces et les variables du milieu

Interprétation par l'Analyse Factorielle des Correspondances (AFC)

Sur la figure 1, nous avons présenté les résultats de l'AFC. Les 2 premiers axes contribuent à expliquer 100% de l'inertie totale du nuage des points.

L'axe 1 absorbe 85,2% de cette inertie ; il est positivement correlé avec les classes moyennes de limon (lim2), d'argile (arg2) et de sable (sb1 et sb2) et les faibles classes de matière organique (MO1) et d'azote (N1) ainsi qu'à la classe de pluviométrie faible (plv1). Il est négativement correlé avec les pluviométries élevées (plv3).

L'axe 2 absorbe 14,8% de l'inertie totale du nuage des points ; il est positivement correlé avec les faibles classes d'argile et de limon (arg1 et lim1) et négativement correlé avec les classes de température élevée (tmax3). Dans le tableau 6 sont représentées les corrélations des variables avec les axes.

Dans le plan factoriel formé par les axes 1 et 2, l'axe 1 oppose le groupe formé par *H. coronarium* à celui formé par *H. spinosissimum et H. carnosum.* Le premier groupe apparait sous les pluviométries élevées, les faibles altitudes et les sols riches en MO, en P et en N et le second est lié aux altitudes plus élevées, aux sols sableux, pauvres en sel et peu fertiles (N1, P1, MO1). D'après Abdelguerfi *et al.* (1988), ces 2 espèces se rencontrent sur les sols caillouteux et bien pourvus en calcaire total. D'autre part, *H. carnosum* semble préférer les endroits chauds (tmax3) contrairement à *H. spinosissimum* qui se localise dans des endroits plus frais (tmin2) et sous de faibles pluviométries.

Espèce	pH	CE	P	Caco3	N	MO	Sb	Arg	lim
H. spinosissimum	7,5	0,5	5,2	44,8	939+	1,8+	21,2+	19+	60*
H. coronarium	*7,5**	*0,8*	*14*	*19**	*1610*	*3*	*46*	*29*	*25*
H. carnosum	*8,5*	*0,8*	*5*	*28*	*726*	*1,2*	*21*	*27*	*52*
Moyenne	7,6	0,7	11	28 (77sites)	1315	4	22	21	57

Tableau 5. Moyennes des principales variables de sol pour les différents sites où l'espèce est présente
+, *: seuils de signification: +: 10%, *: 5%

Variables	Axes 1	Axe 2
Plv1	1062	-49
Plv3	-829	-124
min3	-490	60
max3	628	-502
pH1	644	200
pH3	688	-94
CE1	644	200
P1	774	252
N1	819	-53
MO1	746	-93
sb1	1070	909
sb2	1240	-225
arg1	1070	909
arg2	1240	-225
arg3	969	-372
lim1	884	195
lim2	1325	-792
lim3	1070	909
C3	-558	23
K2	-702	-55

Tableau 6. Principales corrélations des variables étudiées avec les axes factoriels de l'AFC

a/ Pluviométrie		
H.coronarium	*H.carnosum*	*H.spinosissimum*
Cl1→ 4%	Cl1→ 100%	Cl1→ 77%
Cl2→ 62%	Cl2→ 0%	Cl2→ 23%
Cl3→ 34%	Cl3→ 0%	Cl3→ 0%
b/ Altitude		
H.coronarium	*H.carnosum*	*H.spinosissimum*
Cl1→ 47%	Cl1→ 17%	Cl1→ 23%
Cl2→ 32%	Cl2→ 50%	Cl2→ 27%
Cl3→ 21%	Cl3→ 33%	Cl3→ 50%
c/ Température minimale		
H.coronarium	*H.carnosum*	*H.spinosissimum*
Cl1→ 30%	Cl1→ 100%	Cl1→ 39%
Cl2→ 28%	Cl2→ 0%	Cl2→ 42%
Cl3→ 42%	Cl3→ 0%	Cl3→ 19%
d/ Température maximale		
H.coronarium	*H.carnosum*	*H.spinosissimum*
Cl1→ 48%	Cl1→ 0%	Cl1→ 38%
Cl2→ 42%	Cl2→ 0%	Cl2→ 31%
Cl3→ 10%	Cl3→ 100%	Cl3→ 31%

Tableau 7. Fréquence relative (%) des 3 espèces par classe de variable étudiée

Fréquence des espèces étudiées dans les différentes classes des variables les plus discriminantes

La fréquence relative de l'espèce dans les différentes classes des variables les plus discriminantes (pluviométrie, altitude et températures) permettent de visualiser les résultats obtenus (Tableau 7). *H. coronarium* est abondante dans la classe moyenne de pluviométrie (Plv2) contrairement à *H. carnosum* et à *H. spinosissimum* qui sont plus fréquentes dans la classe de pluviométrie faible (Plv1). Quant à l'altitude, elle se trouve correlée avec la température minimale pour les espèces telles que *H. carnosum* et *H. spinosissimum* qui, toutes les deux inféodées à des sites de moyenne à haute altitude, sont liées à des températures hivernales faibles (<4,9°C).

La température maximale de l'été semble affecter en premier lieu la présence d'*H. carnosum* et à moindre degré celle *d'H. spinosissimum*.

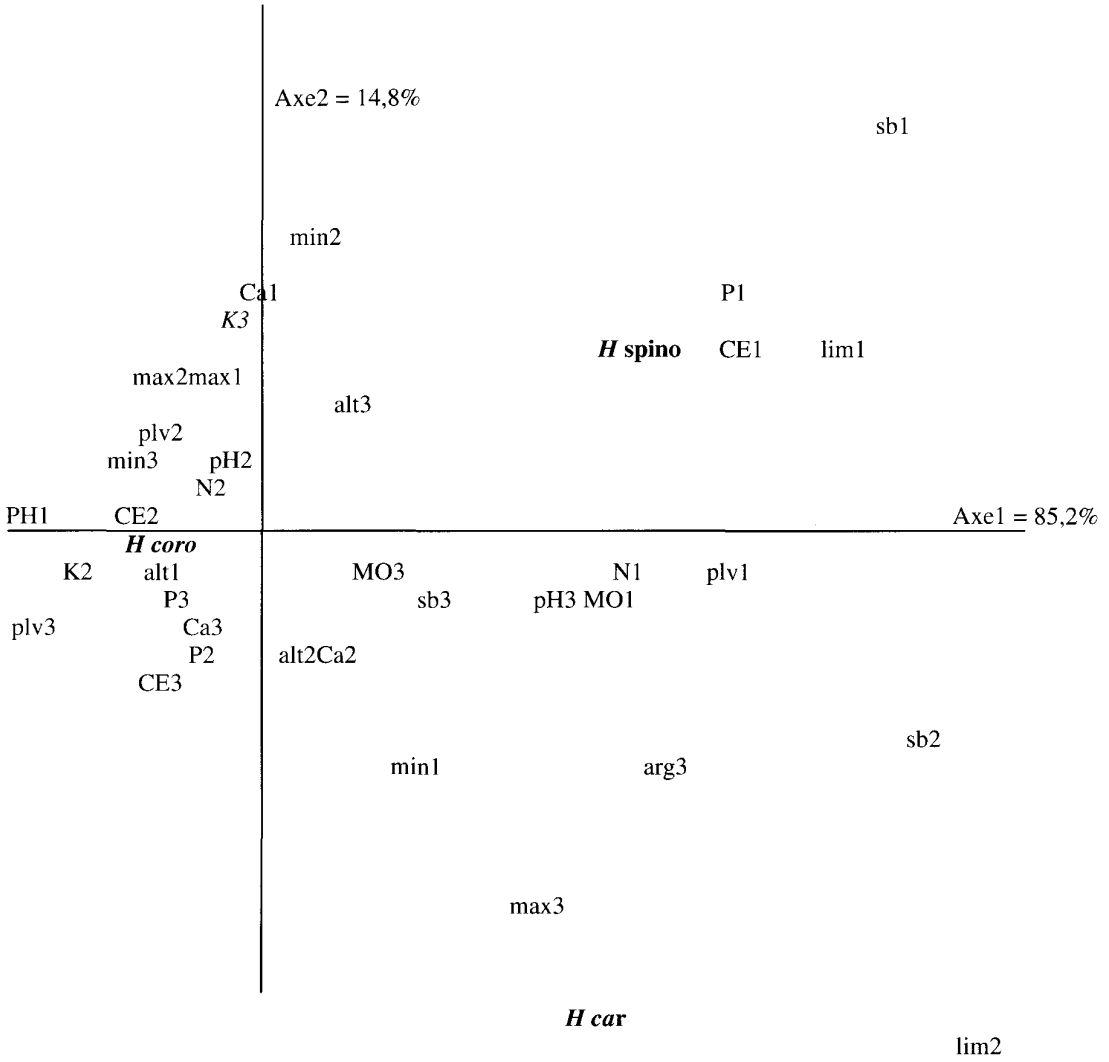

Figure 1. Plan factoriel 1-2 de l'AFC

Les points superposées sont: sb1 & arg1, sb1 & lim3, plv2 & C1, plv2 & C2, plv2 & K1, N2 & MO2, pH1 & C3, N3 & 2, sb2 & arg2.

DISCUSSION ET CONCLUSION

Cette première étude montre que la répartition écogéographique des espèces du genre *Hedysarum,* - dont la fréquence est supérieure ou égale à 6 %, en fonction des facteurs édaphiques (pH, CE, MO,...), climatiques (pluviométrie et température) et d'altitude - est principalement discriminée par la pluviométrie et l'altitude et secondairement par la température. Les élements chimiques du sol influencent peu ou pas leur distribution.

H. carnosum et *H. spinosissimum* présentent des exigences assez voisines et sont des espèces des zones arides. La première pousse sur des sols sableux d'altitude moyenne alors que la deuxième pousse sur des sols argilo-limoneux d'altitude élevée.

H. coronarium préfère les zones les plus arrosées (750 mm contre 597 mm comme moyenne de tous les sites) et les sols argileux. En Algérie, elle est fréquente sur les sols marneux du Tell (Abdelguerfi *et al.*, 1988).

D'une façon générale, les espèces étudiées croissent toutes sur des sols bien pourvus en calcaire total (à l'exception d'*H. coronarium*) à pH neutre. La présence d'*H. spinosissimum* et celle d'*H. carnosum* semble être influencée par la teneur élevée en limon. D'autre part, ces trois espèces se développent indifféremment par rapport au phosphore et au sel.

Les résultats obtenus montrent que ces espèces d'intérêt fourrager et pastoral présentent certaines adaptations qu'il serait intéressant de valoriser. Selon Corriols (1965), le sulla *(H. coronarium)* n'est pas une plante nouvelle pour la Tunisie et peut reprendre une place de choix mais dans des conditions assez différentes de celles du passé en répondant aux nouvelles exigences des agriculteurs pour son multiple usage (fourrage, ensilage, verdure, pâturage, grain) et son introduction dans des systèmes de cultures appropriés. De même, le sulla (*H. coronarium*) paraît être mieux adaptée à l'association avec l'avoine que la vesce velue (*Vicia villosa*) en zone sub-humide (Ben Tamallah, 1987). En Italie, bien que les superficies semées en sulla ont regressé depuis les années cinquantes jusqu'à nos jours (Lombardi *et al.*, 2000), un regain d'intérêt pour cette culture est apparu et de nouveaux rôles, différents de l'utilisation traditionnelle de production de fourrage peuvent être prévus.

H. carnosum est bien adaptée aux irrégularités du milieu aride et sa tolérance à la salinité peut constituer un atout majeur (Boussaîd *et al.*, 1995). Selon les critères de l'IUCN (Boussaîd *et al.*, 1998), l'espèce *H carnosum* est une espèce à protéger.

Ce travail apporte un nouvel acquis à la panoplie de connaissances dont dispose la Tunisie en cette matière. Il doit être cependant soutenu et amplifié durant les années à venir, en vue d'une part de limiter la perte des ressources génétiques spontanées locales et d'autre part de constituer une base génétique aussi large que possible, indispensable aux programmes d'amélioration fourragères et pastorales qui utiliseront ces espèces.

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Premiers essais de polyploïdisation chez *Vicia narbonensis* par l'utilisation de la colchicine

First polyploidisation trials in *Vicia narbonensis* using colchicine

H. HASSEN [1], D. COMBES [2] & M. BOUSSAID [3]

[1] Institut National de la Recherche Agronomique de Tunisie, Tunisie

[2] Université de Pau et des Pays de l'Adour (IBEAS), France

[3] Institut National des Sciences et de Technologie de Tunis, Tunisie

RESUME

En vue de produire des génotypes tétraploïdes de *Vicia narbonensis* (population locale), de nombreux tests ont été réalisés. Les meilleurs résultats sont obtenus avec des graines préalablement germées pendant 96 heures puis trempées dans une solution aqueuse de colchicine de concentration 5 x 10^{-4} (0,05 g de colchicine dans 100 cc d'eau) pendant deux heures à 25°C et en présence de lumière. La sélection des mixoploïdes est appréciée à l'aide de tests cytologiques incluant des observations microscopiques de certaines cellules (stomates, pollens) et morphologiques (déformation de la troisième feuille, nature des ramifications, croissance de l'axe principal,...). Ces tests sont appliqués à différentes périodes de la vie des plantes. Comparés aux diploïdes correspondants, les plantes polyploïdes sont caractérisées par des déformations morphologiques nettes et durables, des stomates de grande taille renfermant plus de chloroplastes et par des pollens volumineux, multicolporés de forme tétraédrique. Le pollen diploïde est typiquement ovale et triaperturé

Mots clés: *Vicia narbonensis*, colchicine, tétraploïdes, chloroplastes, densité stomatique, comptage chromosomique

ABSTRACT

In order to produce tetraploid genotypes of *Vicia narbonensis* (local population), seeds germinated during 96 hours were dropped in aqueous solution of colchicine at 5 x 10^{-4} concentration during 2 hours at 25°C in presence of permanent light. Selection of mixoploid plants was done using cytological tests including microscopic observations of some cellular organites (stomata, pollen) and morphological ones (third leaf and branch deformation, main apex growth...). These tests were used at different stages of plant growth; morphological observations was used on seedling in nursery in order to discard diploid forms and to simplify the transplantation into pots. Whereas, in order to determine polyploid genotypes, cytological tests were used during vegetative growth. Compared to diploid forms, polyploid ones were characterized by clear and persistent morphological deformation, large stomatic cells with more chloroplast and voluminous pollen grains with tetraedric shape. The diploid pollen was typically oval and tricolporate.

Key-words: *Vicia narbonensis*, colchicine, tetraploids, chloroplasts, stomatical density, chromosomical counting

ABREGED ENGLISH VERSION

The aim of this work is to set experimental techniques based on colchicine treatment in order to get tetraploid forms in a local population of *Vicia narbonensis* L. Many trials with various vegetative organs and different concentrations of colchicine were used. The review of several conclusions allowed as to note that:

- the stathmocinetic activity of colchicine is associated with a toxic effect which increase with high concentration.
- moderate concentration reduces the mortality of the plant as well as the production of mixoploid ones
-the stathmocinetic activity of the colchicine is induced by light and adequate temperature (25°C)
- germination seed seems allow the obtention of a good rate of polyploid forms

The experimental method adapted in this study consists of germinating seeds at constant temperature in the presence of light. After 96 hours of germination, the seeds were shelled and dipped in a solution of colchicine at 50 x 10^{-5} during 2 hours in the same condition that the previous germination. They are, then, washed with tap water (2 to 3 times), sowed in 'Giffy-pots' and kept at the laboratory in a illuminated and aerated room during a period of one month maximum before transplantation. The selection of mixoplid is appreciated using morphological tests (leaflet deformation, growth and axis formation...) and cytological observations of some cell (stomata, pollen...). These tests are applied at different periods of the plant morphogenesis: the morphological observations were used on seedling in nursery in order to eliminate the diploid forms and to simplify, at the same time, the transplantation. Meanwhile, the cytological tests are used during the vegetative growth for a final detection of the polyploid forms. The confirmation of the tetraploidy is obtained with a chromosomic counting on C1 and C2 generations. 12.5% of tetraploids were obtained based on seedling being survived the treatment The morphological traits wich caracterise the polyploids of *Vicia narbonenis* are represented by the stomatic size, chloroplast number, shape and number of aperture of seed pollen. In comparison with diploids, the polyploids have a low stomatic density by optical field. This is explained by the increase of the cell sizes. The mean rates are 116 and 75 stomata/mm^2 in diploids and polyploids, respectively. The stomata contain an increased number of chloroplats: 35 by stomata compared to a mean of 18 for the diploid. Pollen of diploid forms is oval and tricolporat, the polyploid has shape varying from oval to tetraedric form with intermediate shapes like spheric or rotund. In addition, polyploid pollen has many apertures: 3 to 6/seed of pollen.

INTRODUCTION

Les vesces constituent l'un des genres le plus cultivé pour ses qualités fourragères. Les principales espèces de ce genre, en l'occurrence *Vicia narbonensis L.*, (2n=14) largement utilisées en Tunisie, sont à l'origine de la mise en valeur de superficies fourragères importantes à travers le pays (Hassen, 1994). Mais depuis une dizaine d'années, les superficies réservées à ces espèces continuent à diminuer au profit d'autres spéculations. L'une des causes de cette perte d'importance est l'absence de variétés productives et bien adaptées à une utilisation intensive.

L'utilisation de la polyploïdie artificielle pour améliorer les plantes fourragères a été envisagée et expérimentée par divers auteurs et a permis dans certains cas la réalisation d'un progrès génétique appréciable. En effet, le passage 2n à 4n chromosomes touche un grand nombre de caractères et conduit à la création de génotypes nouveaux contribuant ainsi à l'amélioration de la variabilité existante. La présence de 4 emplacements alléliques pour un même locus permet celle d'un nombre plus important de combinaisons et ralenti les modifications de structure des populations (Mansat & Picard, 1966).

Les techniques de traitement sont nombreuses, et de cette diversité découle une difficulté de choix. Celui-ci est d'abord guidé par des critères pratiques de faisabilité, compte tenu de la biologie de l'espèce considérée, et ensuite par l'expérience qui a pu être accumulée chez cette espèce ou chez les taxons voisins. Quelques travaux de doublement chromosomique ont été réalisés sur des graines germées du genre *Vicia*, ce sont ceux de Bourgeois (1980) et de Alexy (1996). Ces travaux relatent tous les mêmes problèmes rencontrés par divers auteurs suite aux traitements: stérilité, diminution de la croissance, déformations morphologiques, mortalité élevée et production de plantes en chimères.

Dans le cadre de cette étude, nous avons élaboré une série de protocoles complémentaires, mais différents les uns des autres par la combinaison de facteurs physiologiques ou physiques en vue d'optimiser nos investigations. Notre objectif est : (i) d'apporter des réponses concernant la concentration optimale évaluée sur la base des réactions morphologiques et cytologiques des plantes, (ii) de déterminer les délais et les durées des traitements et enfin, (iii) de préciser l'âge des organes à traiter en vue d'obtenir un taux de polyploïdes le plus élevé possible avec une mortalité acceptable.

En matière de contrôle des génotypes polyploïdes, le problème majeur reste la connaissance d'une méthode simple et fiable qui permet de déterminer précocement le degré de ploïdie des plantes traitées. La forme et les dimensions des feuilles des diploïdes et des polyploïdes ont été comparées (Stebbins, 1950; Béji, 1980). Les polyploïdes se caractérisent par une augmentation des dimensions foliaires et par la couleur vert foncé du limbe, suite à une accumulation plus importante de substances synthétisées (vitamines, pigments...). D'autres critères ont été aussi utilisés, tels que le nombre total de feuilles, la présence ou l'absence de poils sur le limbe et son épaississement, le nombre de ramifications à un stade déterminé... L'ensemble de ces caractères traduisent, plus ou moins objectivement, la distinction entre les deux niveaux de ploïdie. Cependant, il a été indispensable de se fier à des caractères microscopiques beaucoup plus objectifs pour discerner entre les différentes races chromosomiques. Nous avons retenu, ici, le nombre des chloroplastes dans les stomates, la densité et la longueur des stomates, ainsi que l'étude du pollen (forme, pores germinatifs et viabilité). Ces caractères ont été utilisés par Combes (1972) sur *Panicum maximum*, Taylor *et al.* (1976) sur *Trifolium pratense* et Béji (1980) sur *Hedysarum coronarium.*

Cet article présente et discute les principaux protocoles employés pour l'induction de la tétraploïdie chez *Vicia narbonensis,* les tests de dépistage de la polyploïdie sur des plantules à différents moments de leur morphogenèse et leur relation avec le nombre de chromosomes.

MATERIELS ET METHODES

Matériel végétal

Nous avons utilisé une population locale de *Vicia narbonensis* var. *narbonensis* diploïde (2n=14), multipliée et stabilisée par autofécondation depuis 5 générations. Les semences de départ ont été récoltées dans la région d'Utique (Nord-est de la Tunisie) en 1994, dans l'étage bioclimatique semi-aride supérieur à hiver doux. Les individus de cette population poussent sur des terrains de faibles altitudes (< 300 m), sous une pluviométrie comprise entre 300 et 550 mm de pluie par an (Hassen & Zoghlami, 1996).

Technique de traitement

Afin d'optimiser la technique de tétraploïdisation, nous avons utilisé plusieurs protocoles de traitement colchicinique variables par la concentration en colchicine, la durée d'application et l'âge de la germination. Chaque protocole est évalué en se basant sur l'intensité des déformations morphologiques, le taux de plantes survivantes au traitement et le résultat de tests cellulaires englobant le comptage des chloroplastes sur les cellules de garde des stomates, la densité stomatique et le dénombrement chromosomique.

Premier protocole

Cet essai préliminaire porte sur 4 concentrations différentes: 20 (C1)-50 (C2)-80 (C3) et 100 (C4) x 10^{-5} et deux durées de trempage T1 (1 heure) et T2 (2 heures). Les expériences sont réalisées en conditions ambiantes du laboratoire.

Deuxième protocole

Dans ce protocole, nous avons tenté de déterminer l'influence de l'âge de la germination sur la réaction des plantules traitées à l'action mitoclasique de l'alcaloïde. Quatre durées de germination préalable: 24, 48, 72 et 96 heures, trois concentrations de colchicine: 0,05% (C2), 0,08% (C3) et 0,1% (C4) et deux durées d'immersion 1 heure (T1) et 2 heures (T2) ont été considérées.

Troisième protocole

Les protocoles précédents ont permis de déterminer la durée de prégermination idéale pour un effet optimum de la colchicine: 96 heures. Ils ont montré aussi que les traitements 50 x 10^{-5} et 2 heures de trempage (T2C2) et 100 x 10^{-5} et 1 heure de trempage (T1C4) assurent les meilleurs résultats. Le but des recherches suivantes est d'évaluer l'effet de la température et de la lumière. Ont été testées:

- trois températures: 18 (1)- 23 (2) et 25 (3)°C,
- deux concentrations: 0,05% (C2) et 0,1% (C4),
- deux durées de trempage de 1 et 2 heures respectivement pour C4 et C2,
- la présence de la lumière (L) ou de l'obscurité (OB) durant les expériences.

Tests de dépistage de la polyploïdie

Des tests morphologiques et cytologiques ont été utilisés dans cette étude pour caractériser les plantes traitées et opérer un tri à un stade précoce de développement entre plantes diploïdes et plantes polyploïdisées.

Mesure de la longueur (GA) et de la densité des stomates (DS)

La méthode consiste à étaler du vernis incolore sur une petite surface du limbe de la face inférieure de la 3ème feuille de l'axe principal des plantes. Après dessèchement du liquide, un ruban adhésif incolore est appliqué sur la surface traitée puis délicatement enlevé et collé sur une lame. Le nombre des stomates est évalué par champ optique (16 x 10^{-2} mm^2) et la longueur des stomates est mesurée avec un micromètre puis traduite en microns (µm).

Comptage des chloroplastes

Un fragment d'épiderme est prélevé sur la face inférieure de la $3^{ème}$ feuille de l'axe principal puis déposé sur une lame dans une goutte de solution aqueuse de nitrate d'argent à 1%. Le comptage des chloroplastes est fait sur les cellules de garde stomatiques. Nous avons réalisé 167 observations sur les plantes témoins et 984 sur les plantes déformées appartenant aux différents groupes morphologiques.

Etude du pollen

Forme du grain et pourcentage de viabilité

Le pollen est prélevé sur des anthères de fleurs en début d'épanouissement. L'anthère non déhiscente est écrasée sur une lame dans une goutte de la préparation d'Alexander (1969). Le pollen viable apparaît au microscope coloré en rouge alors que le pollen vide est coloré en vert.

L'évaluation de la viabilité a été faite sur un nombre important de grains prélevés sur 530 fleurs (110 fleurs appartenant au témoin diploïde et 420 fleurs appartenant aux plantes polyploïdisées). Nous avons noté en même temps les différentes formes des pollens.

Nombre de pores germinatifs

La technique consiste à écraser une ou deux anthères dans une goutte d'acide sulfurique concentré. Après un léger chauffage à l'aide d'une lampe à alcool (virement de la coloration au rouge orangé), les lames sont soigneusement épongées et observées au microscope. Pour déterminer le nombre d'apertures, nous avons utilisé environ 250 grains de pollen prélevés sur des fleurs épanouies appartenant aux différentes catégories de plantes testées.

Comptages chromosomiques

Sur mitoses radiculaires

Des extrémités de racines sont plongées dans une solution aqueuse de colchicine de concentration 0,5% pendant deux heures à température ambiante. Après rinçage à l'eau courante pendant 30 mn, puis à l'eau distillée, elles sont placées dans de l'alcool acétique (3 volumes d'alcool absolu et 1 volume d'acide acétique glacial) à 5°C pendant 24 heures. Les racines rincées à l'eau distillée sont ensuite hydrolysées dans l'acide chlorhydrique normal à 59°C pendant 15 mn, lavées et trempées dans du colorant de Fulgen (préparé d'après Jahier *et al.*, 1992). La coloration nécessite une trentaine de minutes après lesquelles les méristèmes sont écrasés entre lame et lamelle et observés au microscope.

Sur méiose

L'étude des appariements en méiose est faite en prophase I et en métaphase I dans les cellules mères des grains de pollen. Les boutons floraux récoltés sont trempés dans un premier fixateur constitué par le fluide de Carnoy (6 volumes d'éthanol + 3 volumes de chloroforme + 1 volume d'acide acétique) pendant 24 heures au réfrigérateur. Le lendemain, ces boutons sont transférés dans du Carnoy propre. pendant 24 heures supplémentaires. Au troisième jour, le Carnoy est remplacé par de l'alcool acétique et les flacons gardés au réfrigérateur. Si les inflorescences ne sont pas observées immédiatement, elles sont conservées alors dans l'éthanol à 70%.

Sur un bouton floral de 1 à 1.4 mm de longueur, deux anthères sont prélevées et dilacérées sur une lame contenant une goutte de carmin acétique. Les différents stades de la méiose sont alors observés au microscope photonique.

Test statistique

Les données morphologiques (nombre de chloroplastes, densité et dimensions stomatiques) et

celles relatives aux pollens (nombre de pores germinatifs et viabilité) ont été soumises à une comparaison de moyennes. Pour chaque variable étudiée, La comparaison se fait entre les moyennes des plantes polyploïdisées (ou déformées) et celle du témoin diploïde. Les calculs ont été réalisés sur ordinateur par le programme MSUSTAT (version 3.20) avec la procédure TSINGLE *(tests for single samples)*. La formule utilisée est de la forme:

$$t = |mt-mp| / S\ (1/nt-1/np)^{1/2}$$

où,
mt = moyenne du témoin
mp = moyenne des plantes polyploïdisées
s = écart-type commun
nt et np représentent le nombre d'observations.

RESULTATS ET DISCUSSION

Mise au point de la méthode de traitement

Choix des organes à traiter

La mise au point de la technique de traitement a nécessité la réalisation de plusieurs essais expérimentaux. Nous avons traité des graines et des organes végétatifs en utilisant des doses et des durées d'application variables.

L'immersion des graines sèches dans des solutions de colchicine ne produit une déformation persistante qu'avec des doses et des durées d'immersion importantes, atteignant respectivement 1% de colchicine et 24 heures de trempage. La germination des graines est alors considérablement réduite. Les plantules qui arrivent à développer un appareil végétatif, en conditions atmosphériques contrôlées (serre), se dessèchent très peu de temps après leur repiquage en pots.

Le traitement des bourgeons axillaires (des cinq premiers étages foliaires de la tige principale) par application d'un coton maintenu imbibé de colchicine pendant 3 jours, n'a pas été meilleur que l'immersion des graines sèches. Quelques jeunes ramifications jugées polyploïdes, par une augmentation de dimensions des cellules de garde, se sont desséchées avant la floraison.

L'application d'une solution de colchicine à différentes doses sur l'embryon de la graine au début de la germination ralentie considérablement la levée en inhibant la croissance du bourgeon terminal des plantules. Les concentrations en colchicine supérieures à 10^{-3} entraînent la destruction des radicules. Avec des doses plus faibles, nous observons une croissance normale des racines et du bourgeon terminal; les plantes obtenues présentent peu de déformations morphologiques et reviennent à l'état normal à partir de la 2ème feuille.

Le traitement du bourgeon apical a permis l'obtention d'un certain nombre de plantes présentant des déformations foliaires permanentes jusqu'à la floraison. Les gousses formées sont vides ou renferment des petites graines de couleur noire stériles (germination nulle).

Enfin, l'immersion des graines, germées et décortiquées, dans une solution de colchicine à 0.05% pendant 2 heures a donné les meilleurs résultats.

Les différentes techniques citées précédemment ont révélé des déformations morphologiques importantes très apparentes sur les 3 premières feuilles des plantules, une croissance ralentie du bourgeon terminal et un système de ramifications plus ou moins modifié selon les modalités de traitement. Dans nos expériences, nous pouvons observer que le limbe de la première feuille unifoliolée est toujours fortement déformé (petite taille, contour irrégulier, épaississement du limbe), la deuxième l'est à un degré moindre, mais le limbe de la troisième feuille multifoliolée présente une variation importante caractérisée par (Figure 1) :
- une asymétrie d'insertion des folioles sur le pétiole,
- une transformation de la vrille en foliole terminale,
- une soudure de deux folioles en un limbe entier,
- des folioles inégales,
- une perte de la vrille,
- le limbe foliaire plus ou moins lobé avec des dentitions au sommet.

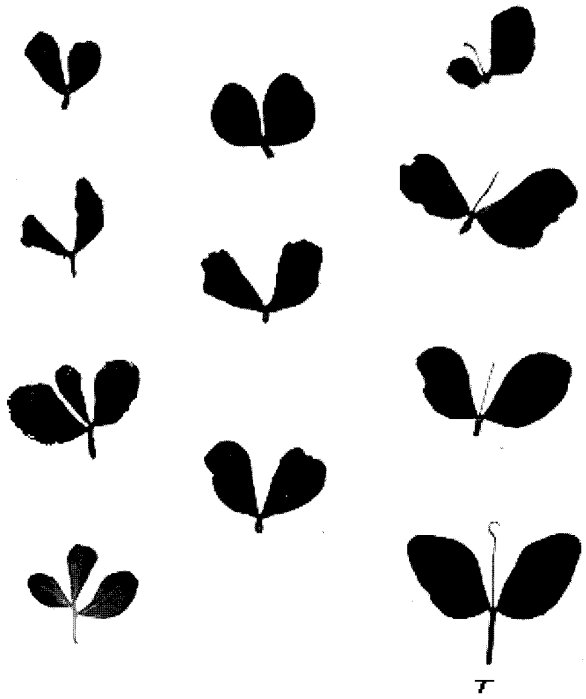

Figure 1. Différents types de déformations enregistrés sur la troisième feuille des plantes traitées à la colchicine. T = feuille témoin

Sur la base de l'intensité et de la nature de ces déformations, nous avons défini une structure morphologique témoin des plantes traitées dans le but d'objectiver la réaction des plantes à l'action mitoclasique de la colchicine et de faciliter le dépistage des formes polyploïdes. Cette structure comprend les 4 groupes morphologiques suivants :

GI= plantes indemnes n'ayant pas réagi au traitement: la troisième feuille ne présente pas d'anomalies ;

GII= plantes faiblement atteintes; la déformation, peu accusée ou fugace, est visible jusqu'à la 3ème feuille de l'axe principal. La croissance aussi bien des racines que de la tige principale reste normale ;

GIII= plantes déformées; la déformation s'étend au-delà de la 3ème feuille et peut affecter la 7ème feuille de l'axe principal. La croissance du bourgeon terminal est légèrement stoppée au début, mais elle redevient normale après le repiquage. De plus, les plantes de ce groupe se caractérisent par un port élancé, une bonne vigueur végétative et une ramification axillaire simple et ascendante ;

GIV= plantes très déformées; la déformation est très accusée et persistante plus longtemps. Les ramifications apparaissant dès les premiers jours de développement présentent aussi des déformations morphologiques prononcées. La croissance de l'axe principal est ralentie voire même stoppée pour certaines plantules. Cet axe disparaît après environ un mois de croissance et la plante sera constituée uniquement par les ramifications axillaires et collatérales à la base des plantes en leur donnant un aspect de "rosette".

Effets conjugués des concentrations et de la durée de trempage sur les réactions morphologiques des plantes traitées

La figure 2 donne le résultat d'un essai d'immersion des graines de *Vicia narbonensis* réalisé en conditions ambiantes de laboratoire selon le premier protocole de notre méthode expérimentale *Vicia narbonensis* présente une sensibilité croissante à l'action mutagène de la colchicine en fonction des doses et des durées de trempage. Cette sensibilité se matérialise par l'apparition de déformations morphologiques nettes et persistantes (GIII et GIV). La proportion de plantes normales ou peu modifiées (GI et GII) est élevée pour le traitement T1C1.

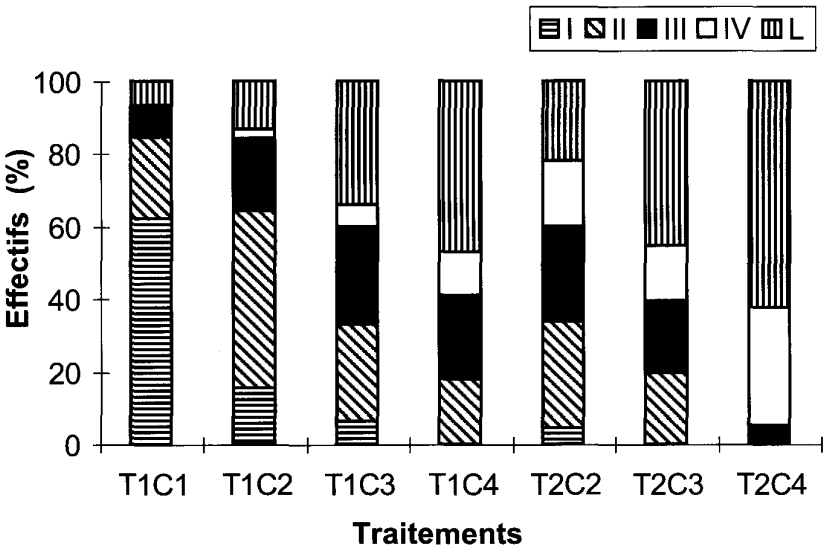

Figure 2. Effets de la concentration et de la durée du trempage sur la déformation morphologique des plantes traitées
TiCj= les combinaisons "durée x concentration" ; T1 = 1 heure ; T2 = 2 heures ; C1 = $20x10^{-5}$; C2 = $50x10^{-5}$; C3 = $80x10^{-5}$; C4 = $100x10^{-5}$; I = pourcentage des plantes appartenant au groupe I ; II = pourcentage des plantes appartenant au groupe II ; III = pourcentage des plantes appartenant au groupe III ; IV = pourcentage des plantes appartenant au groupe IV ; L = pourcentage de plantes mortes.

Mais dés que la durée de trempage et la concentration augmentent, nous assistons à l'apparition de déformations morphologiques nettes associées à l'augmentation du taux de mortalité. Néanmoins, la tendance vers les formes extrêmes (GIII et GIV) s'accroît plutôt avec la variation des concentrations qu'avec l'allongement de la durée du trempage des graines.

Nous pouvons constater, aussi, que l'augmentation des concentrations et des durées de trempage n'a pas empêché l'existence des formes presque normales (GI) et GII. La persistance de ces types de plantes dans les traitements T2C2 et T2C3 peut être justifiée soit par une application trop tardive de la colchicine alors qu'un certain nombre de massifs cellulaires diploïdes existent déjà; ces derniers dotés d'une vitesse de multiplication importante prennent alors le dessus sur les cellules tétraploïdes issues du traitement, soit à la lenteur du rythme des premières mitoses faisant que certains secteurs échappent à l'action de la colchicine.

Ceci laisse supposer que le présent protocole nécessite des améliorations pour pallier la persistance de ces formes peu modifiées et surtout de limiter la mortalité qui peut atteindre ici un peu plus de 60% des graines traitées (T2C4).

Guidés par les quelques tentatives d'amélioration de l'efficacité des traitements à la colchicine, citées dans la littérature (Von Rosen, 1949 ; Essad & Cachon, 1965 ; Berthaut, 1968), nous avons établi une série de protocoles dans laquelle nous avons essayé d'évaluer l'importance de la germination préalable sur la réaction morphologique des jeunes plantules au traitement ainsi que le rôle que peut jouer une température constante sur ces réactions. L'efficacité de ces protocoles est estimée par les proportions des plantes manifestant des déformations précoces et durables de type GIII et GIV, et par la diminution du taux de mortalité.

Effets conjugués des concentrations et de la durée de la germination

Les résultats obtenus montrent que la déformation enregistrée avec les faibles durées de prégermination, en particulier 24 et 48 heures, était peu diversifiée; il y a peu de plantes des groupes III et IV. En revanche, la mortalité était élevée montrant ainsi la grande sensibilité des jeunes germinations à l'action létale de la colchicine.

A 96 heures de germination préalable (Figure 3), la tolérance des plantules a été nettement améliorée. Nous assistons à une baisse notable de la mortalité et à l'apparition des groupes 'utiles' GIII et GIV en proportions importantes. Les meilleures configurations morphologiques ont été obtenues par les traitements qui utilisent les concentrations 50 x 10^{-5} et 100x10^{-5} pour des durées de trempage respectives de 2 et 1 heure (pas de formes normales GI et taux de mortalité enregistré acceptable).

Effets conjugués de la lumière et de la température

La mortalité est toujours plus importante dans l'obscurité et s'intensifie avec l'augmentation de la concentration (Figure 4). Pour la première température (18°C); le taux de mortalité passe de 30 à 55% respectivement pour les concentrations C2 et C4. Néanmoins, cette mortalité s'atténue notablement avec l'élévation de la température, en particulier, pour la concentration C2. D'autre part, les effectifs en plantes des groupes GI et GII sont plus importants à l'obscurité. Leur présence est favorisée par l'augmentation de la température et la diminution de la concentration en colchicine.

Les proportions en plantes GIII et GIV sont, au contraire, plus élevées en présence de la lumière. Leurs effectifs les plus forts ont été enregistrés avec la température de 25°C et la concentration C4. Il semble donc que les faibles températures (18°C) favorisent, en absence de la lumière, la formation de plantes GI et GII, conséquence d'une activité mitotique réduite, et provoque l'augmentation du taux de mortalité.

Nous pouvons constater, enfin, qu'avec la concentration C4 (Figure 4), le taux de mortalité reste élevé quelque soit le traitement utilisé. De plus, les plantes de type GIV montrent une déformation très accusée, accompagnée d'une diminution nette de la croissance et certaines d'entre elles n'atteignent pas le stade de la floraison. Ceci donne la préférence pour la concentration C2 qui, en dépit d'un effectif en GIII et GIV moins important, permet l'obtention d'un meilleur taux de survie.

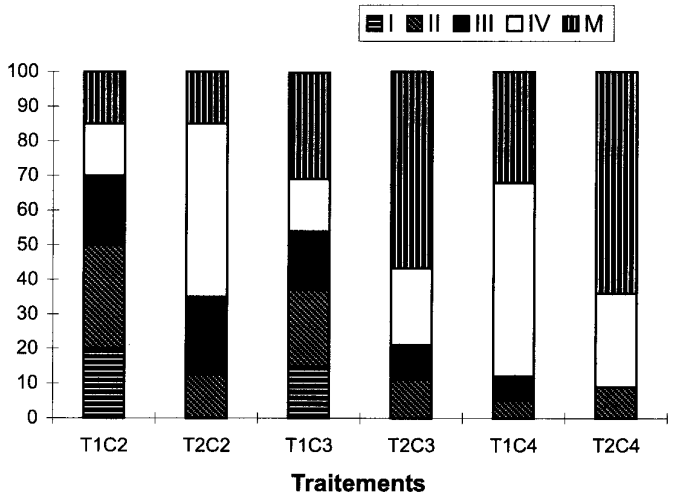

Figure 3. Effets de la colchicine sur la morphologie des plantes issues des graines préalablement germées pendant 96 heures. TiCj = les combinaisons "durée x concentration" ; T1 = 1 heure ; T2 = 2 heures ; C2 = 50x10^{-5}; C3 = 80x10^{-5}; C4 = 100 x 10^{-5}; I = pourcentage des plantes appartenant au groupe I ; II = pourcentage des plantes appartenant au groupe II ; III = pourcentage des plantes appartenant au groupe III ; IV = pourcentage des plantes appartenant au groupe IV ; L = pourcentage de plantes mortes.

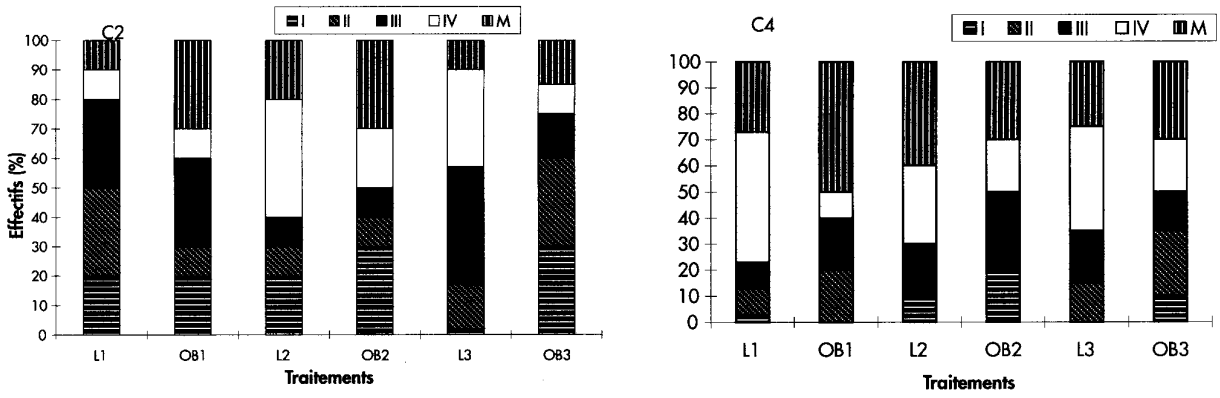

Figure 4. Effets de la lumière et de la température sur les déformations morphologiques en présence de deux concentrations de colchicine C2 et C4
C2 = $50x10^{-5}$; C4 = $100x10^{-5}$; L = lumière; OB = obscurité ; 1 = 18°C; 2 = 23°C; 3 = 25°C ; I = pourcentage des plantes appartenant au groupe I ; II = pourcentage des plantes appartenant au groupe II ; III = pourcentage des plantes appartenant au groupe III ; IV = pourcentage des plantes appartenant au groupe IV ; L = pourcentage de plantes mortes.

A l'issue de l'ensemble de ces protocoles, il nous a été possible de définir pour *Vicia narbonensis* une méthode optimale de traitement à la colchicine.

La méthode consiste à faire germer des graines dans des boites de pétri à une température constante de 25°C et en présence de la lumière. Après 96 heures de germination préalable, les graines sont décortiquées et trempées dans une solution de colchicine à 50 x 10^{-5} pendant 2 heures dans les mêmes conditions que la prégermination. Elles sont, ensuite, lavées à l'eau courante (2 à 3 fois) puis semées dans des 'Giffy-pot' et gardées au laboratoire dans une salle bien aérée et bien éclairée pendant une durée maximale de 1 mois avant le transfert en pots.

Action polyploïdisante des traitements: contrôle des résultats

Nombre des chloroplastes

Ce procédé est basé sur la corrélation existante entre le nombre de chloroplastes des cellules de garde des stomates et le degré de ploïdie. Cependant, l'existence d'une aire de chevauchement (Hassen, 1978 & Béji, 1980) rend assez délicat le dépistage des polyploïdes avec ce seul critère. Une étude réalisée par Bourgeois (1980) a montré que la polyploïdie de *Vicia narbonensis* s'accompagne d'un accroissement du nombre de chloroplastes. Nous avons alors essayé de vérifier s'il en est de même pour la population utilisée dans ce travail (Tableau 1)

Groupes	Nombre de mesures	Moyennes	Ecart-type	Prob>t
Témoin	167	18.12	1.51	-
GI	250	19.05	3.47	0.2486
GII	228	25.79*	3.50	0.0000
GIII	250	31.35*	2.13	0.0000
GIV	256	33.90*	2.23	0.0000

* signifie une différence significative entre la moyenne du groupe et celle du témoin.

Tableau 1. Nombres moyens de chloroplastes par cellule de garde des plantes traitées et des témoins

Le nombre moyen de chloroplastes des cellules des plantes diploïdes (18,12) est significativement inférieur à celui des plantes traitées (27,52). Ce résultat est comparable à celui observé par Bourgeois (1980) sur la même espèce. De plus, ce nombre varie dans le même sens que la déformation morphologique. Les plantes des groupes III et IV contiennent la densité la plus élevée en chloroplastes.

Cependant, on peut noter la présence de chevauchements entre les différentes classes morphologiques. Les plantes GI et GII, dont les valeurs moyennes sont significativement différentes entre elles possèdent une aire de chevauchement importante. Le même phénomène de chevauchement existe aussi chez les groupes GIII et GIV. Ceci est de nature à affaiblir le rôle discriminatoire de ce caractère pour distinguer entre les différents groupes de plantes traitées.

En pratique, le test des chloroplastes a été utilisé pour effectuer une première sélection sur des plantes âgées de 1 mois. Toutes les plantes ayant un nombre moyen de chloroplastes supérieur à 25 ont été repérées et gardées en pépinière d'observation.

Longueur et densité des stomates

Chez *Vicia narbonensis*, les plantes traitées manifestent une diminution du nombre de stomates par unité de surface par rapport aux témoins diploïdes. Ce résultat rappelle celui observé sur *Hedysarum coronarium* L., (Béji, 1980), *Trifolium pratense* L., (Berthaut, 1965) et *Trifolium subterraneum* L., (Hutton & Peak, 1954). Cependant, il nous a semblé utile d'entreprendre des mesures systématiques de détermination de la densité stomatique pour élucider les différences entre les 4 groupes que nous avons identifiés morphologiquement (Tableau 2). La densité stomatique diminue avec l'importance de la déformation morphologique ; l'épiderme des plantes GIV contiennent moins de stomates par unité de surface que les autres catégories de plantes. Les plantes témoins, au contraire, en contiennent plus que les plantes traitées. La moyenne des témoins est de l'ordre de 18,50 cellules par champ optique soit 116 cellules /mm^2 en moyenne, les plantes traitées ne contiennent que 74 cellules/mm^2. La diminution de la densité des stomates semble être compensée par une augmentation de la taille des cellules de garde. Nous avons mesuré le grand axe de ces cellules chez les témoins et les plantes traitées. Une augmentation de longueur caractérise les plantes déformées : 43,2 à 75,6 µm, contre 29,7 à 48,6 µm chez les témoins (Tableau 3). Les groupes III et IV se distinguent facilement des témoins, car l'intervalle de variation des longueurs de leurs stomates ne présente pas de chevauchement avec celui des plantes normales. Ce dernier varie de 47 à 73 µm. Le test de la longueur et de la densité des stomates a été appliqué sur la cinquième feuille de la tige principale et des ramifications latérales de plantes âgées de plus d'un mois. Les individus ayant une densité inférieure à 14 stomates par champ optique et une longueur supérieure à 47 µm ont été sélectionnés et soumis aux autres tests de dépistage.

Groupes	Nombre de mesures	Moyennes	Ecart-type	Prob>t
Témoin	50	18.52	2.42	-
GI	50	17.44	3.58	0.5383
GII	50	14.47*	3.36	0.0000
GIII	50	11.26*	2.97	0.0000
GIV	50	08.46*	2.58	0.0000

* signifie une différence significative entre la moyenne du groupe et celle du témoin.

Tableau 2. Densité stomatique évaluée sur des plantes appartenant aux différents groupes morphologiques

Etude du pollen

Chez *Trifolium pratense*, Laczinska & Mackiewics (1963) ont mis en évidence une nette différence de nombre de pores germinatifs entre diploïdes et polyploïdes. Gupta & Gupta (1978) signalent, sur des 'colchiploïdes' du genre *Crotalaria*.L., plusieurs types de variations touchant la forme et le nombre d'apertures. De même, Bourgeois (1980) a montré que la polyploïdisation de *Vicia narbonensis* L., s'accompagne d'une augmentation du nombre des pores germinatifs et d'un changement de la forme des grains de pollen; ceux-ci deviennent tétraédriques, elliptiques et parfois circulaires.

Morphologie

Sur *Vicia narbonensis*, nos observations microscopiques ont montré que les grains de pollen des plantes diploïdes (8 populations locales et 11 populations étrangères) ont toujours une forme typiquement ovale. Chez les plantes traitées, au contraire, nous avons observé un grand polymorphisme pollinique avec une dominance nette des formes tétraédriques ou arrondies. Cependant, le pourcentage du pollen déformé est extrêmement variable d'un individu à un autre, allant de 21,14 à 99,16% selon les groupes morphologiques.

Nombre de pores germinatifs

Le pollen de *Vicia narbonensis* diploïde non traitée comprend 3 pores. Par contre, celui des plantes déformées comporte de 3 à 6 apertures, 4 le plus souvent (Tableau 4). Les pollens de forme tétraédrique présentent un pore central identique à celui des diploïdes et 3 pores périphériques situés aux extrémités du tétraèdre. Le pollen du groupe GI ne renferme que des grains à 3 pores, s'identifiant ainsi à celui des plantes diploïdes non traitées (Tableau 4). Le pollen des plantes GII présente à peu près les mêmes proportions de grains triporés que de grains à plus de 3 pores. Les plantes des groupes GIII et GIV se distinguent clairement des groupes précédents par la réduction massive de la forme normale des grains ovales tricolporés au profil des autres classes à 4 -6 pores germinatifs. Seul le GIV (plantes à déformations morphologiques persistantes) renferme une majorité de pollen à 5 et 6 pores.

Groupes	Nombre de mesures	Moyennes	Ecart-type	Prob>t
Témoin	47	32.0	0.0011	-
GI	17	42.8*	0.0015	0.0000
GII	33	46.2*	0.0041	0.0000
GIII	26	54.6*	0.0073	0.0000
GIV	33	58.1*	0.009	0.0000

* signifie une différence hautement significative entre la moyenne du groupe et celle du témoin.

Tableau 3. Longueur des stomates (en µm) des plantes appartenant aux différents groupes morphologiques

	Nombre de mesures	% des grains de pollen 3 pores	4 pores	5 pores	6 pores
Témoin	88	100	-	-	-
GI	100	100	-	-	-
GII	52	49.75	33.00	11.00	6.25
GIII	49	31.02	34.20	23.46	11.32
GIV	46	11.67	26.36	33.85	28.12

Tableau 4. Nombre de pores germinatifs des grains de pollen en fonction des groupes morphologiques

Viabilité

La viabilité du pollen a été utilisée comme critère de discrimination, par exemple sur *Hedysarum coronarium*, Béji (1976) a démontré que les pollens des plantes polyploïdisées accusent une baisse de viabilité par rapport aux grains des diploïdes.

Chez *Vicia narbonensis*, le taux de viabilité pollinique, exprimé en pour-cent du nombre total de grains observés, varie de 48 à 98% selon les individus. Sa diminution va de pair avec l'augmentation des déformations morphologiques; les taux de viabilité les plus faibles ont été notés chez les plantes des groupes GIII et GIV, alors que ceux du groupe GI ne présentent pas de différence significative avec les populations témoins (Tableau 5).

D'autre part, nous avons remarqué que le taux de viabilité varie en sens inverse avec les proportions des grains de pollen de forme tétraédrique; le coefficient de corrélation linéaire (r = -0.3837) mesurée entre les deux facteurs est significatif au seuil de 5% (p = 0,1327 x 10^{-1}). Les plantes ayant un taux élevé de pollen déformé possèdent en général le taux de viabilité pollinique le plus faible. Ceci se vérifie aisément chez les plantes des types III et IV dont le pollen est riche en forme aberrante tétraédrique: 92.5%, avec une fréquence élevée d'anthères renfermant jusqu'à 100% de grains déformés.

Confirmation des résultats: Comptages chromosomiques

L'ensemble des caractères présentés plus haut ont été très utiles pour opérer une première sélection entre plantes normales (diploïdes) et individus morphologiquement modifiés (plantes polyploïdisées). Cependant, ces caractères ne peuvent renseigner sur le véritable niveau de ploïdie des divers individus. Celui-ci ne peut être obtenu que par un comptage du nombre de chromosomes des plantes appartenant aux différents groupes morphologiques identifiés.

En ce qui concerne les plantes témoins, les résultats ont été toujours identiques à ceux obtenus par de nombreux chercheurs et en particulier Maxted (1995). Ces résultats révèlent, pour *Vicia narbonensis* L., un nombre gamétique de n = 7 (Figure 5).

Sur les plantes mixoploïdes (C0) issues des graines traitées

Avant la récolte des semences, nous avons entrepris un premier contrôle chromosomique sur des boutons immatures prélevés sur les plantes mixoploïdes retenues (C0) au cours de la période florale. Plusieurs méioses ont montré un nombre haploïde supérieur à 7 et la présence d'univalents et de quadrivalents, associations chromosomiques caractéristiques des tétraploïdes (Figure 6A). Sur un total de 18 plantes (GII, GIII et GIV), un pied du groupe III (2C1) s'est révélé tétraploïde à n = 14 (Figure 6B) et 4 plantes du groupe II ont présenté une métaphase I diploïde. Le reste des plantes (5 du GIV, 7 du GIII et 1 du GII) sont des mixoploïdes avec un nombre variable de secteurs tétraploïdes.

Groupes	Nombre de mesures	Moyennes	Ecart-type	Prob>t
Témoin	110	90.26	2.16	-
GI	30	88.9	2.23	0.3331
GII	70	82.3*	4.16	0.0478
GIII	140	76.12*	5.42	0.0000
GIV	180	73.81*	6.08	0.0000

* signifie une différence significative entre la moyenne du groupe et celle du témoin.

Tableau 5. Viabilité pollinique évaluée sur des plantes appartenant aux différentes classes morphologiques

Un deuxième comptage a eu lieu sur les graines récoltées sur les plantes C0 et le pied 2C1 (GIII). Plus de 300 graines germées ont été examinées pour confirmer la tétraploïdie de la plante 2C1 et vérifier le nombre chromosomique de celles qui n'ont pas été confirmées par les comptages précédents (sur boutons floraux). Toutes les plantules issues des du pied 2C1 (12 au total) se sont révélées tétraploïdes (Figure 7).

Pour les autres plantes examinées, les différents comptages ont montré que les individus du groupe III ont permis l'obtention du meilleur rendement en tétraploïdes (Tableau 6). Ils ont montré aussi que les déformations excessives (GIV) n'entraînent pas forcément un taux de ploïdie élevé; plusieurs plantes de ce groupe se sont révélées diploïdes.

Plantes G	GGR	M	PDD	TET	% TET	
1C2	IV	20	4	14	2	12.50
B41	IV	24	8	15	1	6.25
B42	IV	27	7	18	2	10.00
B81	IV	16	3	11	2	15.38
D61	IV	19	6	11	2	15.38
		Moyenne	**11.90**			
1C6	III	19	2	14	3	17.65
2C6	III	10	2	7	1	12.50
B11	III	20	5	13	2	13.33
C63	III	22	3	16	3	15.79
F73	III	50	5	37	7	15.56
F72	III	25	2	20	3	13.04
K31	III	16	3	11	2	15.38
		Moyenne	**14.75**			
1C5	II	34	2	31	1	3.25

G = groupe ; GGR = graines germées repiquées ; M = mortalité ; PDD = plantes diploïdes ou douteuses ; TET = plantes tétraploïdes ; %TET = taux de tétraploïdie par rapport aux graines survivantes

Tableau 6. Dénombrements chromosomiques sur méristèmes radiculaires de *Vicia narbonensis* mixoploïde

Figure 5. Métaphase I de *Vicia narbonensis* diploïde (n = 7)

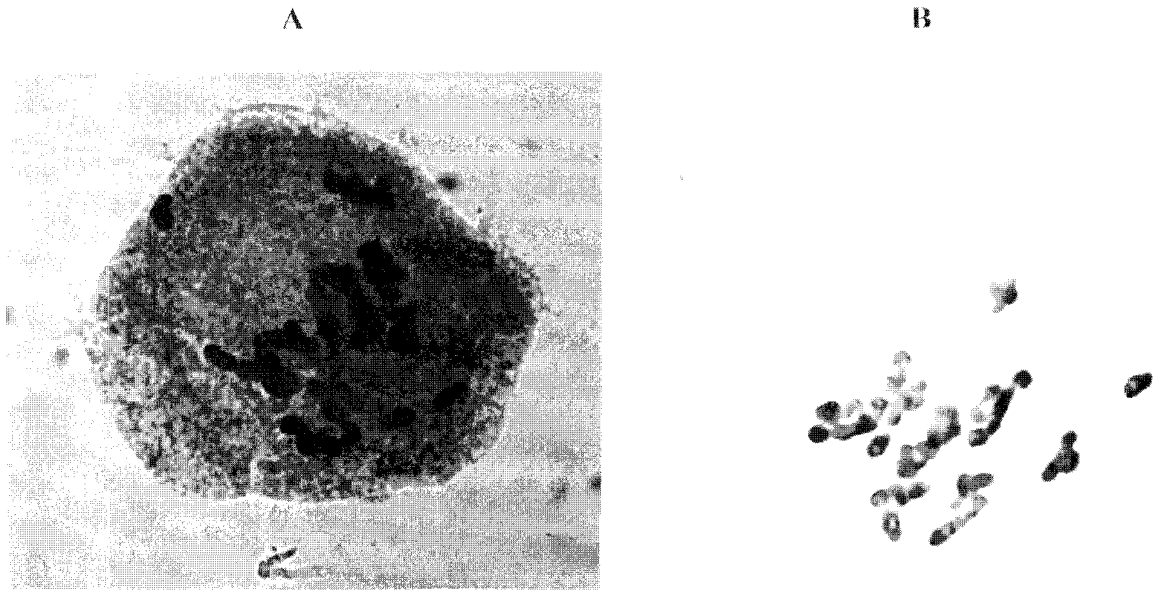

Figure 6. Métaphase I de *Vicia narbonensis* mixoploïde (A) montrant un nombre de chromosomes supérieur à n = 14, avec la présence d'univalents et de quadrivalents, et de *Vicia narbonensis* tétraploïde (B) avec 8 bivalents, 2 quadrivalents, un trivalent et un monovalent.

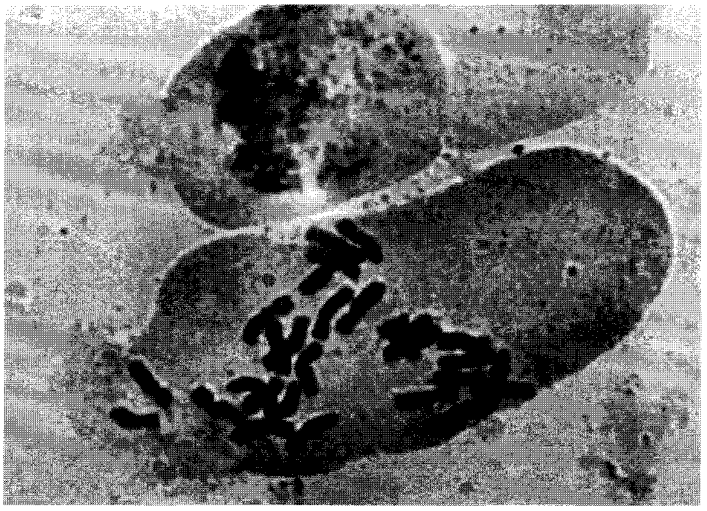

Figure 7. Métaphase de *Vicia narbonensis* tétraploïde (2n = 4x = 28).

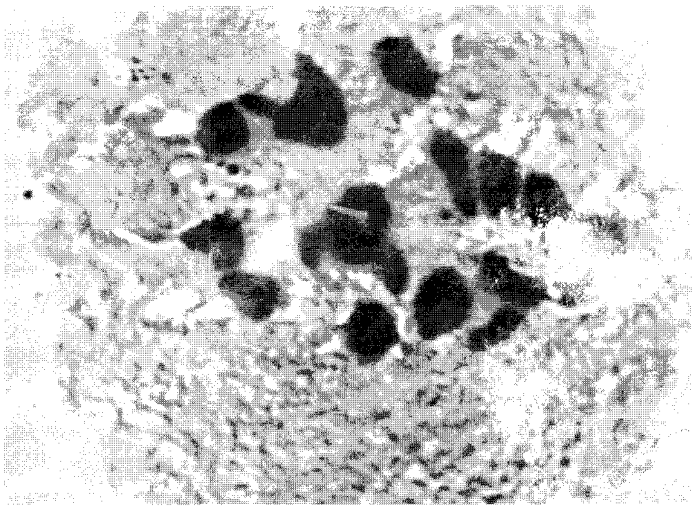

Figure 8. Métaphase I de *Vicia narbonensis* autotétraploïde (2 quadrivalents en anneau et 10 bivalents).

Sur les plantes C1 issues des C0

Les comptages chromosomiques des plantes C1, issues par autofécondation contrôlées des plantes C0, ont été réalisés sur la méiose des cellules mères des grains de pollen et sur des méristèmes radiculaires.

Ces deux dénombrements ont confirmé la tétraploïdie des plantes retenues par le premier examen (C0): 31 pieds au total (Figure 8). Ils ont permis aussi d'extraire parmi les 29 plantes douteuses, les génotypes tétraploïdes complets (8 individus) et, quelques plantes aneuploïdes, au nombre de 7, dont le nombre somatique varie de 26 à 29 chromosomes par cellule. Plusieurs caractéristiques observées chez les tétraploïdes se trouvent modifiées chez ces polyploïdes; dentelure foliaire peu accentuée, germination de graines plus faible et stérilité importante.

Au total, 39 plantes tétraploïdes sur 302 plantules repiquées, ont été créées par notre méthode expérimentale. Ceci permet d'estimer un rendement global de l'ordre de 13%. Ce niveau d'efficacité est comparable aux meilleurs taux obtenus et révélé par quelques auteurs qui ont, d'ailleurs, utilisé des protocoles plus compliqués que le nôtre, incluant l'utilisation de substances stimulatrices de l'action de la colchicine (Deysson, 1964) et d'un vide partiel (Essad & Cachon, 1965).

Grâce à la technique adoptée et aux tests de dépistage de la polyploïdie élaborés, en particulier la densité stomatique, il est possible d'améliorer la réussite des traitements à la colchicine chez *Vicia narbonensis*. Il suffit désormais de choisir, sur des plantules C0 de 1 mois, des individus du groupe III (plantes déformées) pour élever le taux de réussite à 14,75% (Tableau 6).

CONCLUSION

L'augmentation du niveau de ploïdie a joué un rôle important dans l'amélioration de nombreuses plantes agronomiques telles que la betterave, le ray grass, le sorgho fourrager. Sur *Vicia narbonensis* nous sommes au début de nos investigations, mais l'on peut d'ores et déjà apprécier le gain de vigueur enregistré sur des plantes mixoploïdes appartenant au groupe morphologique III. Ces plantes, en dépit d'une croissance ralentie par l'effet toxique de la colchicine, ont manifesté au cours de leur développement une vigueur importante, un cycle végétatif plus étendu que le témoin diploïde et l'émission en fin de cycle de nouvelles formations végétatives donnant à ces plantes une valeur pastorale importante.

Ces premiers essais d'amélioration des traitements du *Vicia narbonensis* à la colchicine ont permis de tester les méthodes de détection des polyploïdes par un diagnostic précoce basé sur les premières réactions morphologiques des plantules et la mise au point d'un protocole pratique de traitement. Compte tenu des résultats obtenus, les concentrations utiles se situent entre 5×10^{-4} et 10^{-3} pour un traitement par immersion de 2 heures à 25°C, en présence de lumière, de graines préalablement germées pendant 96 heures.

Les concentrations utilisées ici sont plus importantes que celles signalées dans la littérature, mais l'analyse cytologique effectuée sur les plantes mixoploïdes obtenues (comptages chromosomiques sur des méristèmes radiculaires) a révélé leur efficacité pour la production d'une proportion non négligeable de plantes tétraploïdes. Cependant, le taux de plantes déformées GIII et GIV obtenu dans nos expériences n'est pas meilleur que ceux rencontrés dans la littérature. Peut-être pourra-t-on améliorer les résultats en modifiant certains paramètres expérimentaux (température, éclairement) ou en incluant le vide, au vu des résultats relatés par certains chercheurs.

A ce niveau de nos recherches, nous pensons que le problème le plus important dans la production de polyploïdes demeure le taux de division du matériel traité. L'amélioration de la réaction polyploïde des plantes aux traitements mitoclasiques doit passer obligatoirement par une étude approfondie du mécanisme des divisions. Celle-ci doit préciser les délais et la durée des divisions, l'apparition des premières mitoses et surtout leur fréquence en stathmocinèses et en divisions normales.

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Mycocoenological studies in some Mediterranean forest ecosystems (province of Siena, Italy)

Etudes mycocoenologiques de plusieurs forêts méditerranéennes (province de Siena, Italie)

Angela LAGANÀ, Elena SALERNI, Carla BARLUZZI & Claudia PERINI

Dip. Scienze Ambientali, Università degli Studi, Via P.A. Mattioli 4, I-53100 Siena (Italy)
Corresponding author: Angela Laganà, Dip. Scienze Ambientali, Univ. degli Studi di Siena, Via P.A. Mattioli 4, I-53100 Siena (Italy), e-mail: lagana@unisi.it

ABSTRACT :

In the last 20 years, the scientific community has shown increasing interest in questions related to biodiversity. Knowledge of biodiversity is a prerequisite for mapping the distribution of species and for the conservation of the organisms populating ecosystems. Here we report the results of mycocoenological research in various types of forest ecosystems (evergreen oak woods of the hill and coastal belts, hill and montane chestnut woods, natural and artificial fir woods, acidophilous and basophilous deciduous oak woods) in central-southern Tuscany, Italy. This research provides a fairly complete picture of the fungal communities of these ecosystems, as well as the similarities and differences between them. The identification of exclusive differential species of each type of forest community provides information about the ecology of the different fungal species.

Key-words: biodiversity, macrofungi, mycocoenology, cluster analysis, Tuscany

RÉSUMÉ. :

Durant ces vingt dernières années, la communauté scientifique a montré un intérêt croissant au sujet des études concernant la biodiversité. La connaissance de la biodiversité est un préalable indispensable pour dresser une carte de la distribution des espèces et pour la conservation des organismes qui peuplent les écosystèmes. Les auteurs reportent les résultats de recherches mycocoenologiques dans plusieurs écosystèmes forestiers (chênaies sempervirentes de collines ou en situation côtière, châtaigneraies de colline et de montagne, sapinières naturelles et artificielles, chênaies caduques acidophiles et basiphiles) en Toscane centrale et du sud. Ce travail décrit de manière assez exhaustive les communautés fongiques des écosystèmes considérés ainsi que leurs ressemblances et différences. L'identification d'espèces différentielles exclusives de chaque type de communauté forestière permet de documenter l'écologie des diverses espèces de champignons.

Mots-clés: Biodiversité, macrofungi, mycocoénologie, analyse cladistique, Toscane

INTRODUCTION

In the last 20 years, the scientific community has shown increasing interest in questions related to biodiversity, in response to a growing demand for conservation of the biological heritage. Biodiversity reflects the quantity of biological information in a system. Biodiversity can be measured at different levels of organization, from genetic to that of ecosystem. Species diversity is a practical level for research, being simple to analyse and well correlated with other levels. It also provides useful additional information for environmental impact studies and management of natural resources in protected and anthropized areas. The main parameters of species diversity are the number (and identity) of species, and their abundance. A good taxonomic-systematic foundation is therefore required for correct study of species diversity. Methods have also been developed for studying biodiversity at ecosystem level; by quantitative study of biocoenoses, these methods make it possible to evaluate, manage and monitor the biological heritage of a given area. Knowledge of biodiversity is a prerequisite for mapping the distribution of species and for the conservation of the various organisms populating ecosystems (Ebenhard, 1998). These questions, which are routine for zoologists and botanists, have also become important for mycologists (Lawrynowicz & Perini, 1997; Arnolds, 1998). In central and northern Europe, there have been a good number of studies on fungal communities, and their distribution and variations over the years (e.g. Arnolds, 1987; Fellner & Soukup, 1991; Arnolds & Jansen, 1992; Lizon, 1993; Boujon, 1997). The same is not true for the Mediterranean area, where relatively little is known about the ecology and distribution of fungal species. The lack of data prompted mycologists at the Department of Environmental Science, Siena University, to begin mycocoenological research in various Mediterranean forest ecosystems at the end of the 1970s (De Dominicis & Barluzzi, 1983; Perini *et al.*, 1989; 1995; Barluzzi *et al.*, 1992; Salerni *et al.*, 1995; Laganà *et al.*, 1996). This research is still underway. Here we report the results obtained in the various forest ecosystems examined (evergreen oak woods of the hill and coastal belts, hill and montane chestnut woods, natural and artificial fir woods, acidophilous and basophilous deciduous oak woods). The aim of this paper is to give as complete a picture as possible of the fungal communities of the main forest ecosystems of central-southern Tuscany and to note similarities and differences between them. The information obtained also provides insights into the ecology of individual fungal species.

MATERIALS AND METHODS

Since fungal fruit body production is a seasonal event, mycocoenological studies must be long enough not to miss any important species. However, evolution of the vegetation places an upper limit on the length of research. The curve of the annual increment of mycoflora can be used to check the validity of the duration of observations (Perini & Barluzzi, 1987); a mycocoenological study can be regarded as concluded when the curve is parallel or almost parallel to the abscissa, or when very few species are added to the list each year. The data reported here is from studies of different duration (2 to 4 years) in the different ecosystems. The study areas ranged in size from 400 to 2000 m^2, depending on the type of forest community (how easy it was to find homogeneous areas). When the first investigations began, expertise in this type of research was in an early stage in Italy, and to some extent also abroad, and the main reference text for method (Arnolds, 1981) had not yet been published. Relevés were carried out once a month throughout the year and once every 2 weeks in the seasons of major fruit body production. During each excursion, all fruit bodies of macrofungi in the study area were identified and counted. According to the definition of Arnolds (1981), macrofungi are fungi which produce fruit bodies visible to the naked eye, greater than 1 mm in size. The species found in the study areas are listed in Appendix 1 and 2. Sporadic taxa (i.e. fungi present in only one station with mDCv < 2) were not included, nor were those that could not be determined with certainty. Species nomenclature was according to Arnolds *et al.* (1995). Species not included in this text are marked with an asterisk in Appendix 1, and the nomenclature was from various texts and monographs (Romagnesi, 1967; Moser, 1983; Alessio, 1985; Jülich, 1989; Stangl, 1991; Antonin & Noordeloos, 1993; Courtecuisse & Duhem, 1994; Candusso, 1997). Abbreviations of names of authors of species were according to Brummitt & Powell (1992). The exsiccata are in the

Herbarium Universitatis Senensis (SIENA). The mDCv of Arnolds (1981) was used as index of abundance. Relevés of vegetation were carried out according to the method of Braun-Blanquet (1965); plant nomenclature was according to Pignatti (1982). Multivariate analysis of the data was carried out with the programme PC SYNTAX, using: d = 1 - s, where s is the Jaccard (1901) index, as dissimilarity index, and the mean link as clustering function. Relevés were ordered by Principal Components Analysis (PCA) using the programme CANOCO for Windows (Ter Braak & Smilauer, 1998).

Study areas

The ecosystems investigated are situated in a large, orographically variable area (Figure 1) that extends from sandy and rocky soils of the coast, through alluvial plains and the hills of the provinces of Grosseto and Siena, to the central Apennine. Climate is typically Mediterranean on the coast, becoming sub-Mediterranean and continental in more inland and higher altitude stations. Climatic conditions on the coast are optimal for the development of *Quercetum ilicis*; those of the hinterland favour deciduous oak woods (*Quercus spp.*). Above an altitude of 1000 m, beech and fir are the most common trees. Table 1 shows the main characteristics of the various forest ecosystems considered.

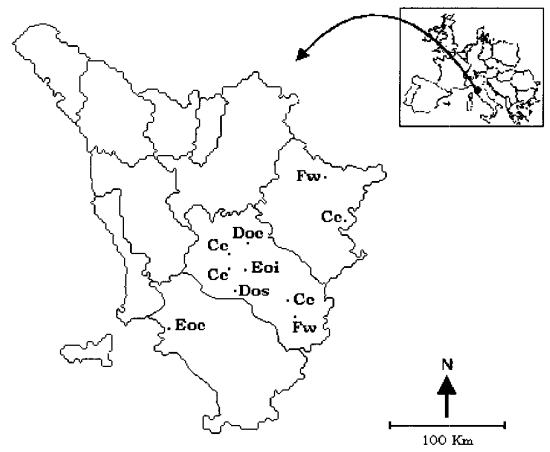

Figure 1. Map of the study area (Dos = silicicolous deciduous oak woods; Doc = calcicolous deciduous oak woods; Cc = chestnut coppices; Eoi = inland evergreen oak woods; Eoc = coastal evergreen oak woods; Fw = fir woods).

RESULTS AND DISCUSSION

A total of 468 species of fungi were found (Appendix 1 and 2a-f). A first comment regards the floristic diversity of the different ecosystems. In line with Arnolds (1981), the number of entities found in each station was taken as a measure of fungal biodiversity, even when the studied stations were of different dimensions. Figure 2 shows the number of species found in each forest ecosystem; 188 were recorded in basophilous deciduous oak woods, 174 in acidophilous deciduous oak woods, 215 in chestnut woods, 251 in evergreen oak woods of the Maremma coast, 140 in evergreen oak woods of the Siena hills and 192 in fir woods. The greatest fungal biodiversity was therefore found in coastal evergreen oak woods and the least in those of the Siena hills, particularly since the total of 140 species is for five stations, each of 2000 m^2. The graph of Figure 3 was plotted to show the relationships between the fungal communities of the various forest communities. Each of the principal clusters of mycocoenoses correspond to a forest community. Greatest similarity was found between basophilous and acidophilous deciduous oak woods, which resemble each other in terms of vegetation. Group V of Appendix 1 contains the 18 species common to these two types of forest. No indications were found in the literature that any of them prefer deciduous oaks to other broadleafs. The next link was with evergreen oak woods of the Grosseto coast, and is explained mainly by the similarity between evergreen oak woods and basophilous deciduous oak woods. In fact as many as 18 fungal species were common to these two types of forest community (group VII, Appendix 1). The vegetation of these areas is similar, since both have species such as *Asparagus acutifolius* L., *Crataegus monogyna* Jacq., *Erica arborea* L., *Fraxinus ornus* L., *Phillyrea latifolia* L., *Quercus cerris* L., *Q. ilex L.*, *Q. pubescens* Willd., *Rosa sempervirens* L., *Ruscus aculeatus* L., *Tamus communis* L., albeit with different abundances. The next link was with chestnut woods which are most similar to acidophilous deciduous oak woods, with which they share 10 fungal species (group VI, Appendix 1). This can be explained by the fact that both forest communities develop on acid substrates, and that all acidophilous deciduous oak woods have a large contingent of vascular species in common with chestnut woods. Besides *Castanea sativa* Miller, these

include *Cytisus scoparius* (L.) Link, *Festuca heterophylla* Lam., *Lathyrus montanus* Bernh., *Physospermum cornubiense* (L.) DC., *Pteridium aquilinum* (L.) Kuhn, *Serratula tinctoria* L., *Solidago virga-aurea* L., *Sorbus torminalis* (L.) Crantz, *Stachys officinalis* (L.) Trevisan and *Teucrium scorodonia* L. Unexpectedly, forest communities with *Castanea sativa* occupied a position between evergreen oak woods of the coastal and hill belts, which have as many as 10 fungal species in common (group VIII, Appendix 1). Nine of them are regarded as linked to forests of *Quercus ilex*; in the literature (Malençon & Llimona, 1980; Bertault, 1982; Termorshuizen, 1990), *Tricholoma equestre* is reported as a mycorrhiza of pines, which were in fact present in some of the evergreen oak woods investigated.

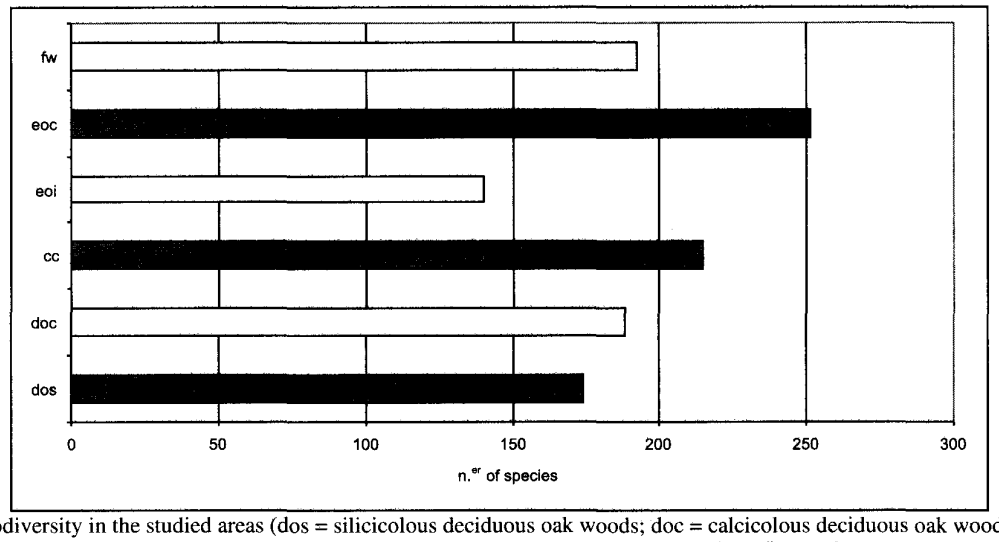

Figure 2. Biodiversity in the studied areas (dos = silicicolous deciduous oak woods; doc = calcicolous deciduous oak woods; cc = chestnut coppices; eoi = inland evergreen oak woods; eoc = costal evergreen oak woods; fw = fir woods).

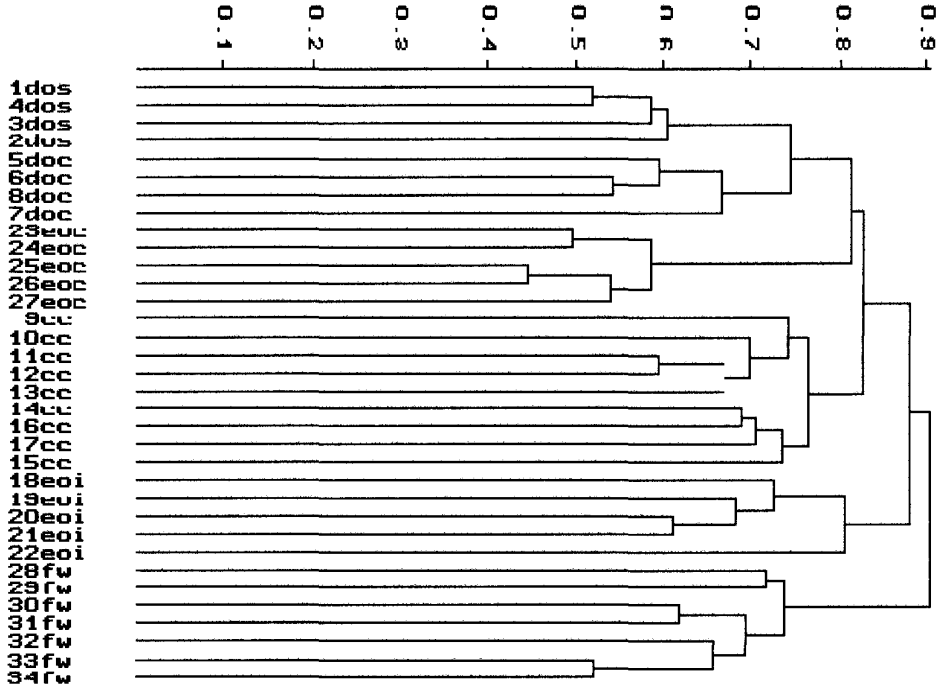

Figure 3. Dendrogram of the the fungal communities of the various forest communities clustered using the mean link algorithm.

St. n°	plot surface	altitude	slope	exposure	pH	lithological substrate	res. period	tc%	sc%	hc%	vegetational association	alliance	class
1dos	1000	380	15	S	5,06	"Verrucano"	1992-93	65	50	10	Erico-Quercetum cerridis	Lonicero-Quercion pubescentis	Quercetea ilicis
2dos	1000	260	17	NE	4,52	"Verrucano"	1992-93	75	30	50	Erico-Quercetum cerridis	Lonicero-Quercion pubescentis	Quercetea ilicis
3dos	1000	390	-	-	4,72	"Verrucano"	1992-93	80	50	40	Erico-Quercetum cerridis	Lonicero-Quercion pubescentis	Quercetea ilicis
4dos	1000	265	17	NW	5,1	"Verrucano"	1992-93	78	35	40	Erico-Quercetum cerridis	Lonicero-Quercion pubescentis	Quercetea ilicis
5doc	1000	240	15	WNW	7,03	limestone	1992-93	85	65	50	Cytiso-Quercetum pubescentis	Lonicero-Quercion pubescentis	Quercetea ilicis
6doc	1000	490	12	SE	6,83	limestone	1992-93	70	50	20	Cytiso-Quercetum pubescentis	Lonicero-Quercion pubescentis	Quercetea ilicis
7doc	1000	470	2	SE	6,83	limestone	1992-93	75	50	15	Cytiso-Quercetum pubescentis	Lonicero-Quercion pubescentis	Quercetea ilicis
8doc	1000	280	8	NNW	6,83	limestone	1992-93	70	60	15	Cytiso-Quercetum pubescentis	Lonicero-Quercion pubescentis	Quercetea ilicis
9cc	2000	470	7	NE	-	rhyolitic lava-flows	1979-82	95	40	30	Rubia peregrina-Quercus cerris	Quercion robori-petraeae	Quercetalia robori-petraeae
10cc	2000	470	7	NW	-	sandstone	1979-82	95	40	30	Rubia peregrina-Quercus cerris	Quercion robori-petraeae	Quercetalia robori-petraeae
11cc	2000	475	5	NE	-	pebbles and red soils	1979-82	90	60	20	Rubia peregrina-Quercus cerris	Quercion robori-petraeae	Quercetalia robori-petraeae
12cc	2000	525	5	NNE	-	polychromes sericitic scists	1979-82	90	30	40	Rubia peregrina-Quercus cerris	Quercion robori-petraeae	Quercetalia robori-petraeae
13cc	2000	550	15	NE	-	sandstone	1979-82	85	15	30	Physospermo-Quercetum petraeae	Carpinion betuli	Querco-Fagetea
14cc	2000	660	7	NE	-	rhyolitic lava-flows	1979-82	90	50	40	Physospermo-Quercetum petraeae	Carpinion betuli	Querco-Fagetea
15cc	2000	780	3	NE	-	sandstone	1979-82	90	50	20	Physospermo-Quercetum petraeae	Carpinion betuli	Querco-Fagetea
16cc	2000	830	10	NW	-	sandstone	1979-82	90	30	50	Physospermo-Quercetum petraeae	Carpinion betuli	Querco-Fagetea
17cc	2000	870	5	W	-	"Verrucano"	1979-82	95	50	50	Physospermo-Quercetum petraeae	Carpinion betuli	Querco-Fagetea
18eoi	2000	410	35	E	-	clastic quarzitic & phyllitic rocks	1977-79	40	80	25	-	Quercion ilicis	Quercetea ilicis
19eoi	2000	320	10	SW	-	gabbro	1977-79	100	50	15	-	Quercion ilicis	Quercetea ilicis
20eoi	2000	275	5	N	-	polygenic conglomerates	1977-79	95	40	40	-	Quercion ilicis	Quercetea ilicis
21eoi	2000	210	15	NE	-	limestone	1977-79	30	90	15	-	Quercion ilicis	Quercetea ilicis
22eoi	2000	450	15	E	-	periostite & serpentinite	1977-79	-	90	20	-	Quercion ilicis	Quercetea ilicis
23eoc	2000	20	5	W	6,67	sandstone	1981-84	95	60	10	Viburno-Quercetum ilicis subass. ornetosum	Quercion ilicis	Quercetea ilicis
24eoc	2000	50	5	N	5,65	sandstone	1981-84	95	60	10	Viburno-Quercetum ilicis subass. ornetosum	Quercion ilicis	Quercetea ilicis
25eoc	2000	125	7	W	6,9	sandstone	1981-84	80	60	20	Viburno-Quercetum ilicis subass. ornetosum	Quercion ilicis	Quercetea ilicis
26eoc	2000	150	10	S	5,65	sandstone	1981-84	70	40	10	Viburno-Quercetum ilicis subass. ornetosum	Quercion ilicis	Quercetea ilicis
27eoc	2000	250	4	S	7,1	limestone	1981-84	70	50	10	Viburno-Quercetum ilicis subass. ornetosum	Quercion ilicis	Quercetea ilicis
28fw	360	770	15	N	6,5	Pietraforte sandstone	1986-89	90	70	20	Polysticho setiferi-Fagetum	Laburno-Ostryon	Querco-Fagetea
29fw	400	730	10	W	5,15	Pietraforte sandstone	1986-89	80	60	10	Polysticho setiferi-Fagetum	Laburno-Ostryon	Querco-Fagetea
30fw	900	860	2	N	4,59	Pietraforte sandstone	1986-89	70	70	10	Polysticho setiferi-Fagetum	Laburno-Ostryon	Querco-Fagetea
31fw	800	880	3	N	4,77	Pietraforte sandstone	1986-89	80	60	2	Polysticho setiferi-Fagetum	Laburno-Ostryon	Querco-Fagetea
32fw	800	1115	3	S	5,82	Marnoso-arenacea formation	1986-89	70	50	70	Aceri-Fagetum subass. abietetosum	Fagion	Querco-Fagetea
33fw	400	1190	20	N	4,51	Marnoso-arenacea formation	1986-89	60	50	40	Aceri-Fagetum subass. abietetosum	Fagion	Querco-Fagetea
34fw	500	1210	12	N	4,65	Marnoso-arenacea formation	1986-89	60	40	60	Aceri-Fagetum subass. abietetosum	Fagion	Querco-Fagetea

Table 1. Stational parameters of the studied areas (dos = silicicolous deciduous oak woods; doc = calcicolous deciduous oak wood; cc = chestnut coppices; eoi = inland evergreen oak woods; eoc = coastal evergreen oak woods; fw = fir wo

The last link was with fir woods. The separation between broadleaf and conifer forests is therefore evident. Fifteen species were common to all broadleaf forests (group II, Appendix 1); only three of them (*Cortinarius callochrous, Entoloma rhodopolium fm. nidorosum* and *Tricholoma ustaloides*) are reported in the literature (Bon & Gehu, 1964; 1973; Brandrud *et al.*, 1990-94; Marchand, 1971-86; Noordeloos, 1992; Riva, 1988) as foreign to conifer forests, despite the fact that beech, present in all the fir forests investigated, is a possible symbiont for these species.

Nineteen species (group I, Appendix 1) were found in all study areas. Most of them have a wide ecological range, for example *Amanita rubescens, Laccaria laccata, Lactarius chrysorrheus, Mycena galopus* and *M. pura*.

Cortinarius obtusus, C. semisanguineus, Tricholoma acerbum and *T. atrosquamosum* (group III) seem linked to broadleaf woods in the hill and submontane belts, being totally absent from coastal evergreen oak woods and fir forests.

Finally, the typically montane character (in the studied area) of *Calocybe ionides, Cantharellus cibarius var. amethysteus, Exidia truncata, Lycoperdon umbrinum* and *Marasmius wynnei* emerges with their finding in high altitude fir and chestnut woods.

In a previous study, Perini *et al.* (1993) identified a number of exclusive differential species of various types of vegetation in southern Tuscany. Only some of those species (see Appendix 2) are confirmed as exclusive differentials by the present study. The greatest number of exclusive differential species (67) was recorded in fir woods, followed by coastal evergreen oak woods (36), basophilous deciduous oak woods (16), chestnut woods (12), hill belt evergreen oak woods (8) and acidophilous deciduous oak woods (7). The high number of exclusive species in fir woods is explained by the fact that they were the only conifer woods investigated, although some of the hill belt evergreen oak woods included pines. It is also worth considering that fir woods and coastal evergreen oak woods (i.e. environments with the highest numbers of exclusive differential fungal species) are vegetational extremes for Tuscany. Evergreen oak woods are the most thermoxerophilous forest community, as indicated by the presence of fungi such as *Lactarius rugatus, Mycena algeriensis* and *Volvariella murinella*, whereas fir woods are the most mesophilous.

In the ordering of relevés by PCA (Figure 4), three principal groups emerged: the first consisted of fir woods, the second of hill and submontane forest communities and the third of more thermoxerophilous forests, namely coastal evergreen oak woods. In the second group, a gradient can be discerned from cooler-moister environments (chestnut and deciduous oak woods on acid substrates) to warmer ones (inland

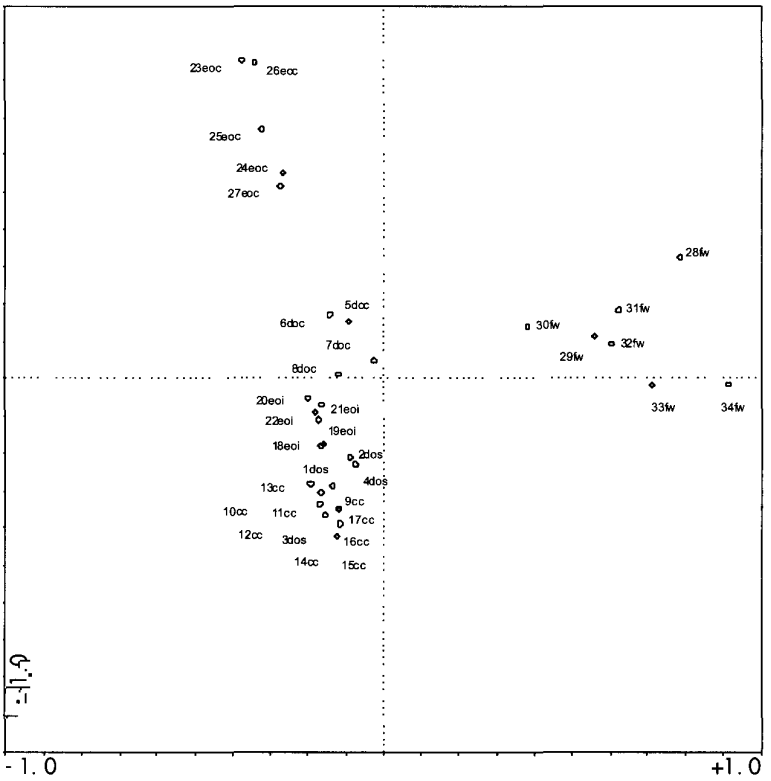

Figure 4. Ordination of samples by mean of PCA (dos = silicicolous deciduous oak woods; doc = calcicolous deciduous oak woods; cc = chestnut coppices; eoi = inland evergreen oak woods; eoc = costal evergreen oak woods; fw = fir woods)

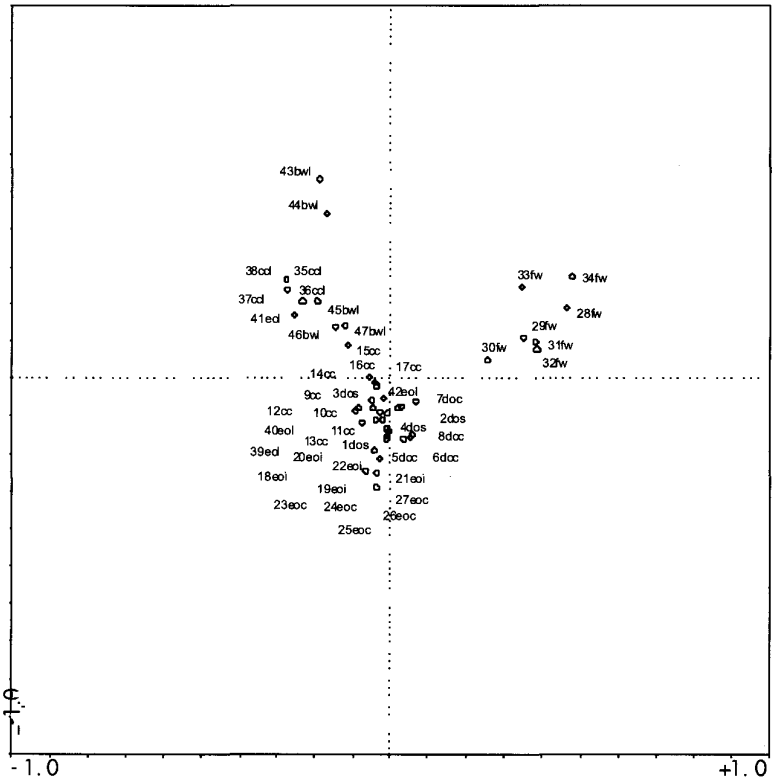

Figure 5. Ordination (PCA) of stations studied in central-southern Tuscany (Italy) together with stations studied in a different mediterranean region (dos = silicicolous deciduous oak woods; doc = calcicolous deciduous oak woods; cc = chestnut coppices; eoi = inland evergreen oak woods; eoc = costal evergreen oak woods; fw = fir woods; bwl = beech woods in Liguria; ccl = chestnut coppices in Liguria; eol = evergreen oak woods in Liguria)

evergreen oak woods and basophilous deciduous oak woods), with basophilous deciduous oak woods reaching towards coastal evergreen oak woods.

Figure 5 shows the ordering of relevés obtained pooling our data with that of other mycocoenological research carried out in the Mediterranean area (Orsino & Traverso, 1986; Orsino & Dameri, 1989, 1991; Orsino, 1991, 1993; Orsino *et al.*, 1999). Again the separation between broadleaf and conifer forests is observed, despite the fact that one of the studies regarded Ligurian beech woods which may be expected to bridge the gap between Tuscan broadleaf forests and fir woods, in which *Fagus sylvatica* L. is abundant.

CONCLUSIONS

These results demonstrate the influence of climate and vegetation on fungal communities, as reported in other studies (e.g. Dighton *et al.*, 1986; Loppi *et al.*, 1989; Barluzzi *et al.*, 1991; Laganà *et al.*, 1999). The picture of fungal communities in central-southern Tuscany, taken as an example of the Mediterranean area, is now relatively complete. Only the results of research in beech woods are lacking, but inclusion of Ligurian beech woods in the ordering of Figure 5 showed that this gap is marginal, at least at the general level of fungal community. However, future results for Tuscan beech woods will provide useful data on the fungal biodiversity of the region.

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APPENDIX 1. Syntesis of mycocoenological survey (dos = silicicolous deciduous oak woods; doc = calcicolous deciduous oak wood; cc = chestnut coppices; eoi = inland evergreen oak woods; eoc = coastal evergreen oak woods; fw = fir woods)

	1dos	2dos	3dos	4dos	5doc	6doc	7doc	8doc	9cc	10	11	12	13	14	15	16	17	18eo	19eo	20eo	21eo	22eo	23eo	24eo	25eo	26eo	27eo	28f	29f	30f	31f	32f	33f	34f
Amanita rubescens Pers.: Fr.	2	1	2	3			1		2	2	1	+	1	1	+	1	1							3		2		2			2		1	
Boletus chrysenteron (Bull.) ss. str.	1					1	2																2	2	1		2						2	
Cantharellus cibarius Fr.: Fr.	1		1				1			5	1	3	3	2	3	1	3	1	1				2		1	3	2							4
Collybia dryophila (Bull.: Fr.) P. Kumm.		2			3		1										2									3	3		3	3	2			
Cortinarius lividocchraceus (Berk.) Berk.	4	3	3	3	1		1			1	4	2	1					2				+		2	2	2	1	3	1	2	2			
Cortinarius trivialis J.E. Lange	2	3	2	2	3		3	2	2	4			2			1	1	1	1	2	2	1		2	+	2	1	1	1	1				
Craterellus cornucopioides (L.: Fr.) Pers.	4						3		5	4				2	5	4	2	3	3		1			3		5	5				2			5
Hydnum repandum L.: Fr.	4		2	2	2	2	1		4	1	4	3	3			4	2		2	3	1					1	2							1
Hygrophorus discoxanthus (Fr.) Rea	1	1			3	2			1		1						1	2	3		+	2	3		1	2	2	3				1	1	
Laccaria laccata s.l.	3	3	2	3		1	3		+	2	+		+	2	4	5	+	3	3		1	+	4	2	4	5	2	5		4	3	4	6	4
Lactarius chrysorrheus Fr.	3	4	4	3	2	4	3	1	3	2	1	+							3		2	1	2	4	3	1	2	+	1					
Lycoperdon perlatum Pers.: Pers.										1	1		2	3	2		4				1			1	2	3	2	2	4		4	4		2	3
Lyophyllum deliberatum (Britzelm.) Kreisel	1	2	1		1		1			2		+	+	1			1			+		1				+		2	1					
Mycena galopus (Pers.: Fr.) P. Kumm.	2	4	4	3	4	3	4	6	3	2	3	3	1	5	4	5	+	+			1	+		3	3	2	3	3	6	2	2	1		
Mycena pelianthina (Fr.: Fr.) Quél.				1	1		1	2						1	3							1					4		3	3	1	3			
Mycena polygramma (Bull.: Fr.) Gray	1			1	1	3	1	1	1	+	1	+	+	1	3					1					1				4	6	4	4		2	1
Mycena pura (Pers.: Fr.) P. Kumm.		1	2	2	3	4	3	3		4		1		1	4	4	2			2	1		4	4	3	3	4	7	7	6	5	3	3	4
Russula albonigra (Krombh.) Fr.		1	3	1	1	2				2	1							1						1	+	+								
Tricholoma saponaceum (Fr.: Fr.) P. Kumm.	3	2	1	1	1	2	1			3		+			3	1		4		1			1		1	+	3	2	1	2			4	3
Amanita vaginata (Bull.: Fr.) Lam. ss. str.	1	1		1			1			1	+	1		2	1	+	+		1		+			2	+	1	2	+						
Cortinarius calochrous (Pers.: Fr.) Fr.		1					2										+				+	2	2	2	1		+	1					
Crepidotus variabilis (Pers.: Fr.) P. Kumm. ss. str			3	4		4		4	2	2	4	1			1	2			1								2	3					
Entoloma rhodopolium (Fr.: Fr.) P. Kumm. f. nidorosum				1		1			1	1					1	4	2					2	1	1			2	+					
Hebeloma crustuliniforme (Bull.) Quél. ss. str.	1	1	2		2	2	2	1								3	1			+	+		2		1		2	3					
Hydnellum concrescens (Pers.) Banker ss. str.	4	4	4	5	1	4				4	4							4	2	2		2		2	4	3								
Hydnum rufescens Fr.: Fr.			1		2	2	2	1	+			+				4	4		1	+	3			2	2	2	4							
Lactarius vellereus (Fr.: Fr.) Fr.	4			1			4			1	2							1	1	+	1			1		3								
Marasmiellus ramealis (Bull.: Fr.) Singer	2	3		5	3		3			2	2		1		4				1		1					1								
Mycena galericulata (Scop.: Fr.) Gray	2	1				1	1					3	+		2				1	2	+					+								
Mycena rosea (Bull.-->) Gramberg	1	1	2	1	4	3	1	1	+	2		1			2	1	1	+		2	2	+	5	5	4	4	+							
Phellodon niger (Fr.: Fr.) P. Karst.		2							2	2			2						3	2	2		3		2	4	2							
Russula fragilis (Pers.: Fr.) Fr. ss. str.	3	2	2	2	1	2	3	2	2	1	+		+	+	1	1			1	+			2	2	1	2	1							
Russula risigallina (Batsch) Sacc.	1	1		1			1		1	1	1	1	1	1		1	+					1	+	2	1	2	1							
Tricholoma ustaloides Romagn.	2	2					1		1			1	3			2	3	2	2	2	3	1	+		2	+	+								
Marasmius androsaceus (L.: Fr.) Fr.	1		1	1	2			1		1		2									+							4	4	3		1	5	5
Clavulina coralloides (L.: Fr.) J. Schröt. ss. str.	2	3	3	4		1	1		3		2		1		4	2	1						2	2	2	1	1	6	2	5	7	3	6	6
Clitocybe phaeophthalma (Pers.) Kuyper				2								2				+											1	3						
Collybia butyracea (Bull.: Fr.) P. Kumm.	1		1	2	1	1	1								2								4	4	4	2	1		2	4		3	2
Cortinarius torvus (Bull.: Fr.) Fr.	1	1	2	1			1			1	4	+	1	3	+		+						+		2	1		5			1		1	
Marasmius rotula (Scop.: Fr.) Fr.		1		1		3	2	4	1	3				1	3	2									1						4			
Mycena epipterygia (Scop.: Fr.) Gray		3	2	2		2	2				1	+				3	+						+				4	4	4	2	3	3	5
Mycena sanguinolenta (Alb. & Schwein.: Fr.) P. Kumm.	4	5	5	3		2	2	2	+	1	+	1	1	+		1								2		4	1	1			1		2	
Mycena vitilis (Fr.) Quél.	3	3	2	3	1	3	4	2				1	+	+		+			1				1			2	1	2	1					
Russula cyanoxantha Schaeff.: Fr.	1	2	1	2				1	1	1	1	1	2	+	+	1	1		1				1	2					3	2		2	2
Russula delica Fr. ss. str.	1			3	1								3		2	+			1				3	2	3	3	2					2	3	3
Xylaria hypoxylon (L.: Fr.) Grev.	4	4	2	4	3	2	4	2	1				1	3	2				3				3	2	3	2	2	2	6	5			3	3
Tricholoma squamulosum Bres.*			1		1	1													3				2			2		6		4	4	5	6
Amanita pantherina (DC.: Fr.) Krombh.	2	1		1						+	1						1	1		1	+	1	2	1	1	3	1	1						
Clitocybe nebularis (Batsch:Fr.) P.Kumm.			2																2				2	1	1	1	+					2	
Inocybe geophylla (Fr.: Fr.) P. Kumm.	1										+							2	+						3	3			3				
Cortinarius infractus (Pers.: Fr.) Fr.					1		1													2	+		2	1	+	2	1			1	4	3	1
Lepiota clypeolaria (Bull.: Fr.) P. Kumm.					2	1		1	+							3	+		1	2	+		1	3	2						5	3	3
Cortinarius obtusus (Fr.: Fr.) Fr. ss. str.	3		1		1						1	1	1		1				2	2										2				
Cortinarius semisanguineus (Fr.: Fr.) Gillet		1					2		+							2			+														
Tricholoma acerbum (Bull.: Fr.) Quél.	1			1		2																											
Tricholoma atrosquamosum (Chev.) Sacc.*	1		3	1	1		1	1	+	2	+	2	1	+		3	2	1	2	1	3	3											
Amanita citrina (Schaeff. -->) Pers.	3	1	3	2			1		2	+	+	1	+		1	+																		

Aureoboletus gentilis (Quél.) Pouzar	1						1								+								1	1											
Clitopilus prunulus (Scop.: Fr.) P. Kumm.	1		1	1	1	1	2				+	1	+		1	+	1										+								
Cortinarius aprinus Melot*	4				3	2	2	1	1							1									2	1									
Cortinarius duracinus Fr.	2	3	2	2	2	1	3	1	1	2				1	2	1	1						2	2	3	3	3								
Hygrocybe virginea (Wulfen: Fr.) P.D. Orton & Watling		1		1	1	1	2	1	+					+									4		5	4	1								
Mycena maculata P. Karst.	1	1		1	1	1	2			2					1	4									+	2									
Russula vesca Fr.	4	1	1	2		1	1			2	+	1	2	1		+							2	2	2	2	2								
Tricholoma sulphureum (Bull.: Fr.) P. Kumm.			1	2	2		3		1		+			1	3	4	1							1	1	1									
Hygrophorus penarius Fr.	2				1			3												+						1									
Hygrophorus persoonii Arnolds var. fuscovinosus (Bon) Bon*	1	1	1		1		2											1	2	2	+		+	1	2	1									IV
Lyophyllum paelochroum Clemençon		1			1	2		1										1	+	1	+						1								
Russula foetens Pers.: Fr.				1			1															+	1	1	2										
Boletus aereus Bull.: Fr.	2								1				1						2				1	1		1									
Lepista nuda (Fr.: Fr.) Cooke				3					2		2			+	1			+	3	+			2	2	3	2	2								
Ramaria flava (Schaeff.: Fr.) Quél.*	2	3	2										+							+						2									
Russula heterophylla (Fr.: Fr.) Fr.		1													1				+					+											
Sarcodon cyrneus Maas Geest.*	2								2									2	2	3						1									
Tricholoma album (Schaeff.: Fr.) P. Kumm.		1													+	4			2	+	1	1				3									
Boletus luridus Schaeff.: Fr.					1		1	1									+		+			2	1	1	+	1	2								
Cortinarius sodagnitus Rob. Henry					2		1		+									+		1	2	+	1		2	2	2								
Entoloma sinuatum (Bull. ex Pers.: Fr.) P. Kumm.							2				+					1	2	1		1			+		1	4									
Ganoderma lucidum (M.A. Curtis: Fr.) P. Karst.					1								+							+	+		1	1			1								
Hebeloma sinapizans (Fr.) Gillet						1	2		+			1		+		1			2	3	3	4	1	1	2	4	3								
Hygrocybe conica (Schaeff.: Fr.) P. Kumm. f. pseudoconica (J.E. Lange)						2										+					+	1	2	1	3	3	1								
Phellinus torulosus (Pers.) Bourd. & Galzin						1						+		+				2	2	2	+		4	4	4	3	2								
Russula olivacea (Schaeff.) Pers.						2		1							+							1	+	+											
Tricholoma sejunctum (J. Sowerby: Fr.) Quél.							1						+							+			+			1									
Clitocybe fragrans (With.: Fr.) P. Kumm.				2		4	3								+															3	2	1			
Cortinarius paleaceus Fr. ss. str.	2	4	3	3	2	2	3	1								1												4							
Mycena leptocephala (Pers.: Fr.) Gillet	2	3	3	2		2	3	1	2	1		3	2			1												4	2	2	3	4	1	4	
Rickenella fibula (Bull.: Fr.) Raithelh.		4	3	4			4		2	1	2	2	+				2											3						2	
Lactarius piperatus (L.: Fr.) Pers.	2	1							+	1	1	2	+	1		1		+	2	1	1	+							1				1	3	
Psilocybe fascicularis (Huds.: Fr.) Noordel.			2										1	3	4	5		3												3					
Mycena xantholeuca Kühner								1			4	2			3							+												1	
Micromphale foetidum (J. Sowerby: Fr.) Singer		1			1																			2				4							
Mycena metata (Fr.: Fr.) P. Kumm.	2	3	1	1		2																	1	2	1	2	2			5		4	2	4	
Mycena stylobates (Pers.: Fr.) P. Kumm.	1	4	4	4	3	3	2	4																	1	1	1	4	2	2					
Cantharellus tubaeformis Fr.: Fr.	3	4	5	4					5	4	2	3	2			3	+									3					4				
Clitocybe odora (Bull.: Fr.) P. Kumm.				1					+	2	4	2			4	1	3										1		1						
Inocybe sindonia (Fr.) P. Karst.	1															2									1	1			2	3					
Laccaria amethystina (Huds.-->) Cooke	2	3	4	3					1	2					3	+										3		4		2	3	4	4	4	
Leotia lubrica (Scop.: Fr.) Pers.		1	1	2						2	1	1	1	2		2	1								2	2	2	4							
Mycena filopes (Bull.: Fr.) P. Kumm. ss. str.	1			1					1					1			+								+							3	1	3	
Amanita phalloides (Fr.: Fr.) Link					1		1		1						2	1							2	3	1	2		3	2		1				
Collybia peronata (Bolton: Fr.) P. Kumm.							1			5				+			1									2	2	3							
Cystolepiota seminuda (Lasch) Bon						2	1				1	+											1		1		2	3	3						
Collybia erythropus (Pers.: Fr.) P. Kumm.		3																1						1	3	2			4	2	1				
Tremella mesenterica Retz.: Fr.	1																		1	+			2	2	2	3	2					1		1	
Cortinarius trivialis J.E. Lange var squamosipes Rob. Henry										+											+				+	1	+	1		1					
Cortinarius uraceus Fr. ss. J.E. Lange											1	1	1						1	2	2				1	1			2		1	2			
Lactarius subdulcis (Bull.: Fr.) Gray										+		1							+						1	1	1	3				3		2	
Sarcoscypha coccinea s.l.																1	+			+				+	3	+	1		1						
Tricholoma argyraceum (Bull.: Fr.) Sacc.*												+								+		2				3	2	1							
Boletus ferrugineus Schaeff.	3		1	1			1			1			1		+																				
Cortinarius venetus (Fr.: Fr.) Fr.	1	1	2	1	1					1																									
Marasmius quercophilus Pouzar	4	5	4	5	6	4	6	4	2	5	4	4					2																		
Mycena pura (Pers.: Fr.) P. Kumm. f. alba (Gillet) Kühner				1					1						2		+				+														
Panellus stipticus (Bull.: Fr.) P. Karst.	2		4	2								2		3		1	2	1																	
Cortinarius cristallinus Fr. ss. str.								1			+	2	+					1		+															
Tricholoma scalpturatum (Fr.) Quél.*					1	1			1											2	3														
Tricholoma ustale (Fr.: Fr.) P. Kumm.							1		1		1	2					2	2		1															
Cantharellus cinereus (Pers.: Fr.) Fr.	3	1	2	5			4																		2	4									
Cortinarius cotoneus Fr.*	1				1		1																		1		1								
Cortinarius safranopes Rob. Henry	3	2	1	1	2	2	3	3																	3	4	1								
Hapalopilus rutilans (Pers.: Fr.) P. Karst.	2					3	2																			2									
Hygrocybe pratensis (Pers.: Fr.) Murrill			1	2			1																	1	2	3	2								
Inocybe asterospora Quél.	1						1																		+	1									
Pluteus romellii (Britzelm.) Sacc.	1		1		1	2	1	1															+		+		+								
Russula maculata Quél.	2	1		1	2	2	1	1															2	2	3	4	4								
Armillaria tabescens (Scop.: Fr.) Dennis & al.*	5		1							2					3								4		4	5									

Boletus edulis Bull.: Fr. ss. str.	2			2						+	1		+	+												1	+							
Lactarius atlanticus Bon*			2	3						1						1							2		1		3							
Omphalotus olearius (DC.: Fr.) Singer*	3										3		1												+	1	2							
Psathyrella piluliformis (Bull.: Fr.) P.D. Orton ss. str.			4	1						1		1	2	1	3	3	2						1											
Pseudocraterellus undulatus (Pers.: Fr.) Rauschert	3	3		1						1		+											2		3	3								
Russula aurata (With.) Fr.*	2									+	1		1	+									+	+										
Russula minutula Velen.		1														1							+											
Clavaria fragilis Holmsk.: Fr.					3	1	2	1					1										5		2	4	+							
Coprinus picaceus (Bull.: Fr.) Gray							2		1														2	+		1								
Lactarius insulsus (Fr.: Fr.) Fr.					1	1	1	1	3			2				+							1		1	1	+							
Lepista flaccida (J. Sowerby: Fr.) Pat.					1										2								4	4		1	1							
Marasmius epiphyllus (Pers.: Fr.) Fr.								1		3							2								2									
Tricholoma bresadolianum Clemençon*							2						+			1										3	1							
Xerula pudens (Pers.) Singer					1	1	1			+	+	+	+	+	1	1	+										1							
Hygrophorus arbustivus Fr.*	2	2	2	1															1	2	2						3							
Inocybe lacera (Fr.: Fr.) P. Kumm.			1																+						1		+							
Boletus satanas Lenz					1													2					+			1	1							
Cortinarius bulliardi (Pers.: Fr.) Fr.					2		2	1												1	+					3								
Hygrocybe acutoconica (Clemençon) Singer						1													+			2			1									
Hygrophorus russula (Fr.: Fr.) Quél.						3		2										4	2	5	3		2	3	3	3	1							
Lyophyllum transforme (Britzelm.) Singer*					2														1								1							
Armillaria mellea (Vahl.: Fr.) P. Kumm.										3										2			4	2	2									
Astraeus hygrometricus (Pers.: Pers.) Morgan														+		2			2						1	1								
Boletus calopus Pers.: Fr.									2				+									+				+								
Bovista plumbea Pers.: Pers.											+									+				+										
Coprinus plicatilis (M.A. Curtis: Fr.) Fr. ss. str.										1	1	+	1	1	+		1			1	+		+		1	+	1							
Cortinarius anserinus (Velen.) Rob. Henry												+				+			+		1		+		1	+								
Cortinarius cinnamomeus L.: Fr. var. cinnamomofulvus Rob. Henry*									1						+	1	1				+	1				+								
Cortinarius pseudosulphureus P.D. Orton																+					2		1											
Entoloma rhodopolium (Fr.: Fr.) P. Kumm. ss. str.									+		3			1	+	1						2			1	2								
Hygrophorus nemoreus (Pers.: Fr.) Fr.									1						+			2			1			+	1	2	1							
Lactarius uvidus (Fr.: Fr.) Fr.									2	+						1			1				+											
Macrolepiota mastoidea (Fr.: Fr.) Singer									1	+	+	+										+	1	1	1	1	2							
Ramaria botrytis (Pers.: Fr.) Ricken													2						+							1								
Russula undulata Velen.									+							1		1	2	1			+											
Bisporella citrina (Batsch: Fr.) Korf & Carpenter				4			5																						6		5			5
Collybia cookei (Bres.) J.D. Arnold		2	1				4																									1	4	
Collybia tuberosa (Bull.: Fr.) P. Kumm.		4	1				1																							3				
Crepidotus cesatii (Rabenh.) Sacc.	4			3	3			4																				5	3					2
Mycena erubescens Höhn.	4	1	3	3	2	2	1	2																				5	3	3	2	1		3
Mycena flavescens Velen.	2	1	1	4	1	3	5	2																				6	3	4	1			
Coprinus micaceus (Bull.: Fr.) Fr. ss. str.	1									+																							3	6
Cyathus striatus (Huds.: Pers.) Willd.		1								3																			3					
Galerina marginata (Batsch) Kühner ss. str.	1													1	2													3		3	4	4	2	3
Marasmius bulliardii Quél.			2	1					1					5	4	6	5											3					4	4
Russula laurocerasi Melzer var. fragrans (Romagn.) Kuyper & Vuure		1							3	+			+	1	+	2																	2	1
Russula nigricans (Bull.-->) Fr.	2	3	3	2					3																					3	2		4	
Psilocybe aeruginosa (M.A. Curtis: Fr.) Noordel ss. str.							1							+	2																		1	4
Xerula radicata (Relhan: Fr.) Dörfelt					1	1	2		+																			2	2				3	3
Hemimycena cephalotricha (Joss.) Singer*					4	3		4															3	4		4		1						
Boletus fechtneri Velen.													1				1								+				1					
Crepidotus pubescens Bres.									3														3		2		3	1						
Helvella crispa (Scop.: Fr.) Fr.												+															1					3		
Inocybe cervicolor (Pers.) Quél.															1										1		1					4		
Lycoperdon atropurpureum Vittad.*										1						+	1						2	+	1	2	2	2	4					3
Lycoperdon pyriforme Schaeff.: Pers.										3	3	2			2	1	4						1	2	3	2	1		1		2			
Marasmius torquescens Quél.															1		1								1				3			2		
Mycena sepia J.E. Lange																	1								+			4	2				1	3
Ramaria formosa (Pers.: Fr.) Quél.									4			1	4													1			1					
Cortinarius anomalus (Fr.: Fr.) Fr. ss. str.																		1		+					+			2			1		1	
Macrolepiota procera (Scop.: Fr.) Singer																			2				3	2	1	1	+				2			1

Cortinarius hinnuleus Fr. ss. str.	2			1	1		1																				
Crepidotus lundellii Pilat	4	2		1	2																						
Hydropus floccipes (Fr.) Singer*	2	2		2	2	1	2	1																			
Hydropus scabripes (Murrill) Singer		1				1	1																				
Hygrocybe conica (Schaeff.: Fr.) P. Kumm.	2			1		1																					
Inocybe flocculosa (Berk-->) Sacc.	1		1	1	1	2		1																			
Inocybe tenebrosa Quél.	1				3	1																					
Lactarius pterosporus Romagn.			1				1																				
Lactarius subumbonatus Lindgr.*	3	1		2			2																				
Mycena abramsii (Murrill) Murrill	1			2		2		1																			V
Mycena meliigena (Berk.: Cooke) Sacc.	3			1				2																			
Otidea alutacea (Pers.) Massee			1		1		1	1																			
Phellodon confluens (Pers.: Fr.) P. Kumm.	3	1	2			2		1																			
Pluteus plautus (Weinm.) Gillet	1	1			2	1	1	1																			
Pluteus thomsonii (Berk. & Broome) Dennis			1		1																						
Psathyrella spadiceogrisea (Schaeff.) Maire				1	3																						
Rhodocybe popinalis (Fr.: Fr.) Singer		1						2																			
Russula persicina Krombh.	1		1		2	3	2	1																			
Cantharellus friesii Quél.*	1								1							1											
Cortinarius orellanus (Fr.: Fr.) Fr. ss. str.		1	2	2					1																		
Entoloma sericellum (Fr.: Fr.) P. Kumm.			1						1																		
Fistulina epatica Bull.: Fr.				2					1	+	1	1	1	1		+	1										
Hygrocybe cantharellus (Schwein: Fr.) Murrill				1					+																		
Leccinum rufum s.l.			1								2																
Poculum firmum (Pers.: Fr.) Dumont	4		3	3							+		1	1													
Psilocybe sublateritia Fr.		3								+				3	4	4	1										VI
Ramaria fennica (P. Karst.) Ricken		1							1	+		2															
Schizophyllum commune Fr.: Fr.			4										2		2												
Collybia fusipes (Bull.: Fr.) Quél.							2			1							1										
Cortinarius claroflavus Rob. Henry*					1											+											
Mycena alba (Bres.) Kühner						4					1																
Psilocybe inquilina (Fr.: Fr.) Bres.							1			1	+	2															
Cantharellus aurora (Batsch) Kuyper		1																	2								
Ramaria aurea (Schaeff.: Fr.) Quél.		2	3																3	3							
Russula adusta (Pers.: Fr.) Fr.		1																	2								
Boletus radicans Pers.: Fr.								1														1					
Pseudoclitocybe expallens (Pers.: Fr.) Singer					1															+							
Tubaria furfuracea (Pers.: Fr.) Gillet*						2														1	2						
Boletus appendiculatus Schaeff.									+				1									1					
Cortinarius castaneus (Bull.: Fr.) Fr.													3							+							
Cortinarius coerulescens (Schaeff.) Fr.																+					1						
Cortinarius delibutus Fr.										+									+								
Cortinarius dibaphus Fr. var. nemoreus Rob. Henry*													+								1	2					
Cortinarius rufoolivaceus (Pers.: Fr.) Fr.*										+				+		1			+		2	+					
Entoloma incanum (Fr.: Fr.) Hesler												+						5									
Russula emetica (Schaeff.: Fr.) Pers. var. silvestris Singer									1									+	1								
Amanita excelsa (Fr.: Fr.) Bertillon f. spissa (Fr.) P. Kumm.		1																								+	
Auricularia mesenterica (J. Dicks.: Fr.) Pers.			3																						3		
Lactarius violascens (Otto: Fr.) Fr.	1	1	1	1																			1		+	1	
Macrolepiota konradii (P.D. Orton) M.M. Moser				1																					1		
Phellodon melaleucus (Sw.: Fr.) P. Karst.				1																					2	2	
Russula cyanoxantha Schaeff.: Fr. f. peltereaui Singer		1		2																					+	+	
Boletus rubellus Krombh. ss. str.					1																		+	2			
Cortinarius decipiens (Pers.: Fr.) Fr.*					2																					+	2
Cortinarius purpurascens (Fr.: Fr.) Fr.							1																+				
Entoloma mougeotii (Fr.) Hesler						1		1															2				
Flammulaster carpophilus (Fr.) Earle						5	1																3	3	1	2	+
Gyroporus castaneus (Bull.: Fr.) Quél.						1	1																+	+	1	1	+
Hohenbuehelia petaloides (Bull.: Fr.) S. Schulz.					1																						1
Humaria hemisphaerica (Wiggers: Fr.) Fuckel					1		2	1																			1
Hygrocybe psittacina (Schaeff.: Fr.) P. Kumm.								1																		1		VII
Hygrocybe reai (Maire) J.E. Lange								1															+	+	1	1	+
Hymenoscyphus fructigenus (Bull.: Fr.) Gray						2		1															2		2		3
Inocybe bongardii (Weinm.) Quél.					3	1	1	1															2				3
Inocybe cincinnata (Fr.: Fr.) Quél. var. major (S. Petersen) Kuyper					1																				2		
Micromphale brassicolens (Romagn.) P.D. Orton*							1																		1	3	+
Mutinus caninus (Huds.: Pers.) Fr.					1	1		2																1	+	+	
Russula acrifolia Romagn.						3																		1	2	2	
Russula decipiens (Singer) Svrcek					1																						2
Russula vinosobrunnea (Bres.) Romagn.						1																	+	1	2		2

Agaricus silvicola (Vittad.) Sacc. ss. str.										1					+		1								+										
Amanita caesarea (Scop.: Fr.) Pers.*													2										2												
Amanita crocea (Quél.) Singer														+		+										+	1								
Clavulina cinerea (Fr.) J. Schröt.										1						2							3			1	1								
Cortinarius croceo-coeruleus (Pers.: Fr.) Fr.									+	2		+	1												1										
Cortinarius trivialis J.E. Lange var. subolivascens Rob. Henry									1							2	1										1								
Entoloma hirtipes (Schumach.: Fr.) M.M. Moser														1			1						+		1	2	1								
Lactarius camphoratus (Bull.: Fr.) Fr.									2							1										1									
Lactarius controversus (Pers.: Fr.) Fr.									1			2	+										1												
Otidea cochleata (L.: Fr.) Fuckel													3			1										+									
Ramaria decurrens (Pers.) R.H. Petersen															2	2	2						3	3	2	3	2								
Russula alutacea (Pers.: Fr.) Fr.									1	1			+										1	+	2	+									
Russula amoenicolor Romagn.														+									2	2	1	2	2								
Russula densifolia Gillet													2			+									3	3	+								
Russula romellii Maire									1					3	1		+								1										
Russula rosea Pers.									2	1		+	4		1		+						2	1	+	1	2								
Scleroderma verrucosum (Bull.: Pers.) Pers. ss. str.														1		1	1						1		2										
Boletus impolitus Fr.																						2					1								
Boletus queletii Schulzer																			1			+	1	+	2		2								
Cortinarius cinnamomeoluteus P.D. Orton																			2						1										
Cortinarius multiformis Fr. ss. str.																					2	1	+		+	2	+								
Leccinum crocipodium (Letell.) Watling*																			2				+	+											
Leccinum lepidum (Bouchet ex Essette) Quadraccia*																		1	1	1	+	1	1	2	1	+	+								VIII
Leucopaxillus gentianeus (Quél.) Kotl.*																				3			5	5	3	4									
Lyophyllum tenebrosum Clemenç																				+							1								
Russula luteotacta Rea																				+			1	2		2									
Sarcosphaera crassa (Santi ex Steud.) Pouzar*																				1	+					+									
Tricholoma equestre (L.: Fr.) P. Kumm.																				+					+	+									
Cortinarius bicolor Cooke	2		1																												2				
Entoloma occultopigmentatum Arnolds & Noordel.	1																											1							
Inocybe petiginosa (Fr.: Fr.) Gillet	2	3	2	1																								1							
Mycena aurantiomarginata (Fr.: Fr.) Quél.		1	1	1																										1		1		4	
Mycena crocata (Schrad.: Fr.) P. Kumm.				1																														2	
Entoloma juncinum (Kühner & Romagn.) Noordel.							1																					3							
Hemimycena cucullata (Pers.: Fr.) Singer					2	3	1	1																				4							
Hemimycena lactea (Pers.: Fr.) Singer							1																											2	
Inocybe leiocephala D.E. Stuntz					2	2																						3							
Megacollybia platyphylla (Pers.: Fr.) Kotl. & Pouzar							1																					3							
Mycena acicula (Schaeff.: Fr.) P. Kumm.					1	1		1																				3							
Mycena flavoalba (Fr.) Quél.					4	1	3	2																				5	1	6	5	2	2	3	
Mycena polyadelpha (Lasch) Kühner					4	1																						4	4		3	3	5	6	
Boletus subtomentosus L.:Fr.													+																				2		
Calocybe ionides (Bull.: Fr.) Donk															1														1						
Cantharellus cibarius Fr.: Fr. var. amethysteus Quél.																2															4				
Exidia truncata Fr.: Fr.																+													7						
Lycoperdon umbrinum Pers.: Pers.															2															2					
Marasmius cohaerens (Pers.: Fr.) Cooke & Quél.									2	2		+		2	4		1															1			
Marasmius wynnei Berk. & Broome															2		2												5					2	
Mycena arcangeliana Bres.										1																			2						
Pluteus cervinus (Schaeff.) P. Kumm.															+														1	1	1	2	1	2	
Tricholoma fulvum (DC.: Fr.) Sacc.									+																			1							
Clitocybe clavipes (Pers.: Fr.) P. Kumm.																			+														1		
Clitocybe rivulosa (Pers.: Fr.) P. Kumm. ss. str.																			1															1	
Cortinarius dionysae Rob. Henry*																					+							3				4			IX
Hygrophorus chrysodon (Batsch: Fr.) Fr.*																			2										1		1	5			
Tricholoma stans (Fr.) Sacc.																			1									3							
Agaricus silvaticus Schaeff.: Fr.																							2	2			2				2				
Clavulinopsis corniculata (Schaeff.: Fr.) Corner																							1		+	2	2	2							
Coprinus atramentarius (Bull.: Fr.) Fr. ss. str.																							+									2			
Helvella elastica Bull.: Fr.																									1							3			
Hygrophorus discoideus (Pers.: Fr.) Fr.																											3		2						
Lepiota castanea Quél.																							2		1	+	1	2							
Marasmius alliaceus (Jacq.: Fr.) Fr.*																									1									2	
Mycena haematopus (Pers.: Fr.) P. Kumm.																										1		3				4			

APPENDIX 2. Exclusive species of each studied vegetational type; a = silicicolous deciduous oak woods, b = calcicolous deciduous oak woods, c = chesnut coppices, d = inland evergreen oak woods, e = coastal evergreen oak woods, e = coastal evergreen oak woods, f= fir woods

2a	1 dos	2 dos	3 dos	4 dos
Clitocybe harmajae Lam.*		2	1	1
Clitocybe metachroa (Fr.: Fr.) P. Kumm.			2	2
Coprinus insignis Peck	3	1		1
Cortinarius evernius (Fr.: Fr.) Fr.			1	1
Entoloma nitens (Velen.) Noordel.	1	1		
Resupinatus applicatus (Batsch: Fr.) Gray	4			
Rozites caperatus (Pers.: Fr.) P. Karst.		1	4	1

2b	5 doc	6 doc	7 doc	8 doc
Ciboria batschiana (Zopf.) N.F. Buchw.			3	1
Coprinus stercoreus Fr.	4			
Cortinarius olivaceofuscus Kuhner	3		2	1
Crepidotus epibryus (Fr.: Fr.) Quél.	3			3
Crepidotus mollis			3	
Entoloma byssisedum (Pers.: Fr.) Donk	1			2
Hemimycena hirsuta (Tode: Fr.) Singer		3		3
Hygrophorus lindtneri M.M. Moser*		2	1	
Hygrophorus roseodiscoideus Bon & Chevass.*	3		1	
Inocybe pusio P. Karst.			1	1
Inocybe splendens R. Heim	2	1		1
Macrotyphula juncea (Alb. & Schwein.: Fr.) Berthier	4			7
Mycena acicula (Schaeff.: Fr.) P. Kumm.	1	1		1
Phaeomarasmius erinaceus (Fr.: Fr.) Singer		1		1
Psathyrella ocellata (Romagn.) M.M. Moser	1		1	
Scenidium nitidum (Durant & Mont.) Kuntze*		2	3	

2c	9 cc	10 cc	11 cc	12 cc	13 cc	14 cc	15 cc	16 cc	17 cc
Boletus erythropus Pers.: Fr.	+								+
Clitocybe costata Kühner & Romagn.		+	+					2	2
Cortinarius acutus (Pers.: Fr.) Fr.	1	2	1	2	+			1	+
Cortinarius alboviolaceus (Pers.: Fr.) Fr.								1	+
Cortinarius pumilus (Fr.) J.E. Lange*	1							1	
Dasyscyphella nivea (Hedw.: Fr.) Raitv.	4								
Flammulina velutipes (M.A. Curtis: Fr.) Singer ss. str.						2	2		
Mycena galopus (Pers.: Fr.) P. Kumm. var. nigra Rea		1					1		
Mycena inclinata (Fr.) Quél.	2	5	3	4	4	4	5	4	3
Pseudoclitocybe cyathiformis (Bull.: Fr.) Singer							3		
Psilocybe coronilla (Bull.: Fr.) Noordel.				1			+		
Rutstroemia echinophila (Bull.: Fr.) Höhn.		1						2	

2d	18 eoi	19 eoi	20 eoi	21 eoi	22 eoi
Agaricus xanthoderma Genev.	1	1			
Cortinarius fulmineus Fr.*		2	1		
Gomphidius glutinosus (Schaeff.: Fr.) Fr.		1			1
Hebeloma hiemale Bres.		2	1	1	
Inocybe similis Bres.		1	1	1	+
Lactarius deliciosus (L.: Fr.) Gray		1	3		
Lactarius sanguifluus (Paulet: Fr.) Fr.*			4		
Mycena vulgaris (Pers.: Fr.) P. Kumm.				2	2

2e	23 eoc	24 eoc	25 eoc	26 eoc	27 eoc
Agaricus praeclaresquamosus A.E. Freeman	4	4	4	1	+
Agaricus xanthoderma Genev. var. griseus (A. Pearson)		2	2	2	
Bovista aestivalis (Bonord.) Demoulin	1				2
Clathrus ruber Pers.: Pers.	1			+	
Clavariadelphus flavoimmaturus R.H. Petersen*	4		4	4	
Clavulinopsis laeticolor (Berk. & M.A. Curtis) R.H.	4	3	2		2
Clavulinopsis luteoalba (Rea) Corner var. latispora		1	2	4	
Conocybe brunnea Watling	2		+		
Coprinus silvaticus Peck	+	+			
Cortinarius ionochlorus Maire*	2				+
Cortinarius rigens (Pers.: Fr.) Fr. ss. str.	1		2		
Entoloma undatum (Fr.--> Gillet) M.M. Moser				1	2
Helvella lacunosa Afzel: Fr.			+	2	3
Hygrocybe konradii R. Haller			+	2	1
Hygrocybe obrussea (Fr.: Fr.) Wünsche	3	1	2	2	3
Hygrocybe russocoriacea (Berk & Miller) P.D. Orton				1	2
Inocybe fraudans (Britzelm.) Sacc.	2			+	
Lactarius decipiens Quél.	4	2	2	1	+
Lactarius rugatus Kühner & Romagn.*	1	2	1	2	
Lepiota echinella Quél. & C. Bernard	2		1		
Leucoagaricus serenus (Fr.) Bon & Boiffard	3	2	1		2
Marasmiellus candidus (Bolton) Singer	4		4		4
Mycena algeriensis Maire ap. Kühner*			1		2
Mycena lenta Maire*	1			2	2
Peziza badia Pers.: Fr.	+		+	2	
Peziza badioconfusa Korf			1	1	
Peziza repanda Pers. ss. str.	1				+
Rhodocybe gemina (Fr.) Kuyper & Noordel.	1	2			
Russula lilacea Quél.			+	1	
Russula maculata Quél. var. bresadoliana (Singer)		2	3	2	
Russula pectinatoides Peck.	1	2	1	1	+
Russula seperina Dupain*	1				3
Scleroderma polyrhizum J.F. Gmel.:Pers.*	2		1	1	
Tubaria minutalis Romagn.	1		1		
Volvariella murinella (Quél.) M.M. Moser*	+		+		
Volvariella plumulosa (Lausch ex Oudem.) Singer ss.		+		1	

2f	28 fw	29 fw	30 fw	31 fw	32 fw	33 fw	34 fw
Agaricus luteomaculatus (F.H. Möller) F.H. Möller			1	1			2
Ascocoryne cylichnium (C. Tul.) Korf.					2		4
Bertia moriformis (Tode: Fr.) De Not.					4		6
Bisporella subpallida (Rehm) Dennis							4
Calocera viscosa (Pers.: Fr.) Fr.	5	2			3	4	5
Caloscypha fulgens (Pers.) Boud.		2			2		
Clitocybe foetens Melot	4	2		1			
Clitocybe pseudoobbata (J.E. Lange) M.M. Moser*	4						
Clitocybe sinopica (Fr.: Fr.) P. Kumm.					2		3
Clitocybe trullaeformis (Fr.: Fr.) Quél.	3		3	4	1		3
Clitocybe vermicularis (Fr.) Quél.	4						
Clitocybe vibecina (Fr.) Quél.	2		2				
Collybia alkalivirens Singer*	3						
Collybia confluens (Pers.: Fr.) P. Kumm.	4	4	4	4			
Conocybe pilosella (Pers.: Fr.) Kühner	3	2			2		
Conocybe tenera (Schaeff.: Fr.) Fayod							4
Cortinarius croceus (Schaeff.) Fr.	4					2	
Cortinarius erythrinus (Fr.) Fr.	5			2		4	4
Cortinarius flexipes (Pers.: Fr.) Fr. ss. Kühner 1961	5	2	3	5			
Cortinarius malicorius Fr.*						3	
Crucibulum crucibuliforme (Scop.) V.S. White	4						
Cystoderma amianthinum (Scop.) Fayod ss. str.						3	2
Cystoderma carcharias (Pers.) Fayod						2	4
Dacrymyces stillatus Nees: Fr. ss. str.	4	4		5	6	6	6

Entoloma sericeum (Bull. -->) Quél.	1		1				
Exidia thuretiana (Lév.) Fr.							5
Galerina stylifera (G.F. Atk.) A.H. Sm. & Singer	4	3	3	4	4	4	5
Gerronema strombodes (Berk. & Mont.) Singer*					1		3
Gymnopilus sapineus (Fr.: Fr.) Maire						3	3
Hemimycena gracilis (Quél.) Singer	6	4	2	4	4		1
Hygrophorus pudorinus (Fr.: Fr.) Fr.	3	2		3		1	5
Hymenoscyphus scutula (Pers.: Fr.) W. Phillips							4
Hymenoscyphus serotinus (Pers.: Fr.) W. Phillips	5				4	6	6
Hypoxylon fuscum (Pers.: Fr.) Fr.					5		7
Inocybe cookei Bres.				5		3	
Inocybe fuscidula Velen.	3	2	3	6	5	1	
Inocybe praetervisa Quél.				4			
Inocybe rimosa (Bull.: Fr.) P. Kumm.				4	2	3	
Inocybe whitei (Berk. & Broome) Sacc.				3	1	1	
Lachnellula subtilissima (Cooke) Dennis		4		4	9	9	9
Lachnum bicolor (Bull.: Fr.) P. Karst.						4	7
Lacrymaria lacrymabunda (Bull.: Fr.) Pat.	4						
Lactarius salmonicolor R. Heim & Leclair*	2	3	1	3	4		
Macrotyphula fistulosa (Holmsk.: Fr.) R.H. Petersen	3						
Micromphale perforans (Hofm.: Fr.) Gray	5						
Mycena amicta (Fr.: Fr.) Quél.	2		2		2	2	2
Mycena epipterygia (Scop.: Fr.) Gray var. viscosa							5
Mycena zephirus (Fr.: Fr.) P. Kumm.	6	6	4	4		2	1
Panellus mitis (Pers.: Fr.) Singer		3			4	5	6
Panellus violaceofulvus (Batch: Fr.) Singer*					5	5	5
Pholiota lenta (Pers.: Fr.) Singer						3	3
Pleurotus ostreatus (Jacq.: Fr.) P. Kumm.							3
Pseudohydnum gelatinosum (Scop.: Fr.) P.Karst.*	3	4	3	2		6	4
Ramaria flaccida (Fr.: Fr.) Bourdot	1			3			
Rhodocybe nitellina (Fr.) Sing.	5		2				
Russula cavipes Britzelm.	2			2			
Russula laurocerasi Melzer	2		1				
Russula puellaris Fr.	1		1				
Russula queletii Fr. ss. str.				1	3		
Russula violeipes Quél.	1		2	1		3	
Russula violeipes Quél. f. citrina Quél.			2	1		2	
Russula viscida Kudrna	2	3	1	2		1	3
Rutstroemia luteovirescens (Roberge) White*	4						
Tephrocybe coracina (Fr.) M.M. Moser	1			1			
Tremella simplex Jackson & Martin*				3		3	
Tricholomopsis rutilans (Schaeff.: Fr.) Singer		2	1	2	3	3	4
Xerula melanotricha Dörfelt*		2	1	2	3		

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Use of microhabitat and substratum types by sympatric snakes in a Mediterranean area of central Italy

Utilisation du micro-habitat et des différents types de substrats par des espèces de serpents sympatriques dans une zone méditerranéenne d'Italie centrale

Ernesto FILIPPI [1] & Luca LUISELLI [2]

[1] Via Gabrio Casati 43, I-00139 Rome, Italy. [E-mail: ernesto.filippi@tin.it]

[2] F.I.Z.V., via Olona 7, I-00198 Rome, Italy, *and* Institute of Environmental Studies DEMETRA, Via dei Cochi 48/B, I-00133 Rome, Italy, *and* Museo Civico di Storia Naturale, piazza Aristide Frezza 6, I-00030 Capranica Prenestina (Rome), Italy, *and* T.S.K.J. Nigeria ltd., Environmental Department, 142A Aba Road, Port Harcourt, Rivers State, Nigeria. [E-mails: lucalui@iol.it; lucamlu@tin.it]

ABSTRACT

The ecological distribution of three snake species (*Vipera aspis, Coluber viridiflavus, Elaphe longissima*), in relation to microhabitat and substratum type, was studied in a coastal Mediterranean area of central Italy (Castel Fusano Forest, province of Rome), characterized by sandy dunes facing the sea and internal pinewoods. Snake densities varied considerably from spot to spot, but averaged 0.2 specimens per ha for *Vipera aspis,* 3.5 specimens per ha for *Coluber viridiflavus,* and 1.5 specimens per ha for *Elaphe longissima.* Frequency of observations varied significantly among species in the various microhabitats: in general, *Vipera aspis* and *Coluber viridiflavus* appeared relatively similar in terms of microhabitat types preference. However, important seasonal variations in the frequency of utilization of the various microhabitats were recorded. All the three species basked primarily upon leaf litter substratum, despite there were some minor interspecific and interseasonal differences. In general, *Coluber viridiflavus* and *Elaphe longissima* appeared relatively similar in terms of substratum types preference. However, the three species tended to bask on given substratum types in a way independent from the availability of the given substratum types in the environment. Both in terms of micro-habitat and substratum types utilization, *Coluber viridiflavus* was the most generalist species, whereas *Elaphe longissima* was the most specialized species. The ecological reasons for the interspecific differences in the patterns of utilization of the substratum and microhabitat types are discussed in the light of other studies published to date.

Key-Words: *Vipera aspis, Coluber viridiflavus, Elaphe longissima,* microhabitat, substratum for thermoregulation, population density, central Italy, Mediterranean environment

RESUME

La distribution écologique de trois espèces de serpents (*Vipera aspis, Coluber viridiflavus, Elaphe longissima*) en relation avec les caractéristiques du micro-habitat et du substrat a été étudiée dans une situation méditerranéenne côtière d'Italie centrale (forêt de Castel Fusano, province de Rome), composée de dunes sableuses face à la mer et de pinèdes internes. Les densités de serpents varient considérablement d'une station à l'autre et présentent des valeurs moyennes de 0,2 individus par ha pour *Vipera aspis*, 3,5 individus par ha *pour Coluber viridiflavus* et 1,5 individu par ha pour *Elaphe longissima.* Les fréquences d'observation de chaque espèce varient significativement en fonction du micro-habitat. En général, *Vipera aspis* et *Coluber viridiflavus* présentent des préférences similaires en terme de micro-habitat. Cependant, d'importantes variation saisonnières dans la fréquence d'utilisation des différents micro-habitats ont pu être mises en évidence. Les trois espèces se réchauffent préférentiellement sur des litières de feuilles, bien que de légères différences interspécifiques et saisonnières aient pu être relevées. *Coluber viridiflavus* et *Elaphe longissima* s'avèrent relativement proches quant au choix préférentiel du substrat. Cependant, les trois espèces ont tendance à thermoréguler sur un type de substrat donné, de façon indépendante de sa disponibilité dans l'environnement. *Coluber viridiflavus* s'est avérée l'espèce la plus généraliste à la fois du point de vue de l'utilisation de chaque type de substrat et de micro-habitat, tandis que *Elaphe longissima* est apparue comme l'espèce la plus spécialisée. Les raisons écologiques impliquées dans ces différences interspécifiques sont discutées à la lueur des autres travaux disponibles sur ce thème.

Mots-clés : *Vipera aspis, Coluber viridiflavus, Elaphe longissima,* micro-habitat, substrat pour la thermorégulation, densité de population, Italie centrale, milieu méditerranéen.

INTRODUCTION

The snakes of Mediterranean Italy have been intensively studied during the last decade (for reviews, cf. Angelici & Luiselli, 1998a, 1998b). From the synecological perspective, issues such as trophic niche partitioning among coexisting species in relation to prey availability (Capizzi *et al.*, 1995; Luiselli & Angelici, 1996), competitive interactions between snakes and other types of predators (e.g. owls, cf. Capizzi & Luiselli, 1996), and the effects of habitat loss and forest fragmentation on the ecological distribution and the abundance of coexisting snake species (Luiselli & Capizzi, 1997), have been investigated. Moreover, anecdotal observations on the ecological distribution of the various Mediterranean snake species in relation to the types of macro-habitat are available (Bruno & Maugeri, 1990; Luiselli & Rugiero, 1990; Scali & Zuffi, 1994).

The distribution of coexisting species of snakes in Mediterranean Italy in relation to availability of both micro-habitat types and substratum types for thermoregulation have never been studied in detail till now. However, these factors are no doubt very important in determining temporal changes in several ecological traits of snakes, including population density, home ranges, social structure, etc. (Gregory *et al.*, 1987; Reinert, 1993).

In the present paper we address the results of a detailed field study on the ecological distribution of three sympatric species of snakes (*Vipera aspis, Coluber [Hierophis] viridiflavus, Elaphe longissima*) in relation to micro-habitat and substratum types availability in a coastal area of central Italy. Our aim is to understand (i) whether there is any significant interspecific difference among these species in terms of micro-habitat and substratum types preference, and (ii) whether any eventual interspecific difference could be interpreted in the light of factors such as species-specific ecological requirements, seasonality, etc.

MATERIALS AND METHODS

Study area

The field study was carried out in a forest coastal locality of central Italy (Foresta di Castel Fusano, about 20 km west of Rome, Latium). The study area, about 120 ha, is characterized by two wide zones with different vegetation (Mantero, 1992): a internal zone of *Pinus pinea* forest (approximately 90 ha surface in our surveyed area), with underbrush of *Quercus ilex, Erica arborea, Laurus nobilis, Smilax aspera, Ruscus aculeatus, Cytisus scoparius,* and *Spartium junceum,* and an external zone of sandy dunes facing the Thyrrenian Sea with evergreen "chaparral" vegetation (*Juniperus oxycedrus, Pistacia lentiscus, Rosmarinus officinalis, Arbutus unedo, Erica arborea, Myrtus communis, Cistus* sp., *Phillyrea* ssp.), 30 ha surface. In this latter zone also bushy formations of *Quercus ilex*, to 5 or 6 m height, are found.

In the study area the following six species of snakes were found: *Vipera aspis, Coluber (Hierophis) viridiflavus, Elaphe longissima, Elaphe quatuorlineata, Natrix natrix,* and *Coronella austriaca.* The three latter species proved to be very rare and/or extremely elusive, and thus we were unable to record a number of sightings enough to make any statistical study. Thus, we limited our analyses to *Vipera aspis, Coluber viridiflavus*, and *Elaphe longissima*

Methods employed to classify the various microhabitat and substratum types

Given the aims of the present research, it was necessary to classify the various types of microhabitat and of substratum available to snakes in the study area.

The following microhabitat types were catalogued (their order corresponding exactly to their spatial order, which means that α was contiguous to β, which was contiguous to γ, etc):

α = area with high and thick vegetation (> 3 m of height), in the sandy dune facing the sea. Canopy: 80-90%, dominant species: *Quercus ilex.*

β = area with low vegetation (< 0.5 m) interspersed into wide sandy zones, in the sandy dune facing the sea. Canopy: 10%, dominant species: *Cystus* sp., *Phillyrea* sp.

γ = area with extremely thick and high vegetation (> 5 m), in the sandy dune facing the sea. Canopy: 100%, dominant species: *Quercus ilex, Arbutus unedo.*

δ = area with thick vegetation of average height (about 1.5 - 2 m), in the sandy dune facing the sea. Canopy: 70-80%, dominant species: *Quercus ilex, Erica arborea, Arbutus unedo, Phillyrea* sp.

ε = area with sparse and low vegetation (0.8 to 1.2 m), in the sandy dune facing the sea. Canopy: 20%, dominant species: *Phillyrea* sp., *Cystus* sp.

ζ = area with arboreal vegetation (trees > 6-7 m in height), with dense and high underbrush (3-4 m), in the sandy dune facing the sea. Canopy: 70-80%, dominant species: *Quercus ilex.*

η = area with no arboreal vegetation but with thick underbrush of 1.5 to 3 m in height, in the sandy dune facing the sea. Canopy: 40-50%, dominant species: *Phyllirea* sp., *Arbutus unedo.*

θ = area with very high trees (7 to over 10 m in height), with dense underbrush, in the sandy dune facing the sea. Canopy: 80-90%, dominant species: *Quercus ilex, Pinus pinea.*

ω = area with *Pinus pinea* forest (with trees of over 20 m in height), with thick but low underbrush (0.8 to 2 m of height). Canopy: 60-70%, dominant species: *Pinus pinea, Cytisus scoparius, Rubus* sp., *Quercus ilex.*.

Plots of every micro-habitat types were surveyed on every field day. The surface of each study plot is presented in Table 1.

The following types of substratum were catalogued:

a = tree-branches or piles of wood cumulated on the ground, to an height of approximately two meters from the soil.

b = sand and leaf litter.

c = sand.

d = leaf litter.

To evaluate the quantitative availability of the various substratum types in each microhabitat we used the following methodology: within each microhabitat, we randomly selected 10 sample squares of territory, each 9 m^2 surface. Random selection of the various plots was done according to standard phytoecological procedures, that is by throwing an object on the ground, and choosing the surface surrounding the site where the object has felt. Then, we evaluated by eye the approximate percent composition of each of these sample squares in terms of the various substratum types. This procedure was repeated in three different days, and the arithmetic mean of the three samplings was assumed to be representative for the true substratum percent composition of each sample square of territory. Then, the arithmetic mean of the various percentages obtained from the ten randomly selected sample squares was assumed to be representative for the percent occurrence of the various substratum types in each microhabitat type (Table 1).

Snake census

The field study was conducted, primarily by one author (E.F.), between October 1995 and September 1997. In total, 124 field days were spent in the field, for a total of 474 hours of field-work. The sampling effort was maintained as constant as possible among the four seasons: 30 field days were done in spring (5 in March, 11 in April, 14 in May), 28 in summer (12 in June, 8 in July, 8 in August), 32 in autumn (5 in September, 9 in October, 18 in November), and 34 in winter (7 in December, 17 in January, 10 in February). Random routes across every microhabitat type present in the study area were done. "Ventral scale-clipping" was used as individual permanent marking method for snakes. In addition, each captured specimen was painted with a white number on the back to permit identification at distance without any further recapture (at least in the short term, i.e. between two sloughling cycles). Snakes were measured to Snout-Vent-Length (SVL, in cm) by chord, and sexed by analysing tail shape. The sexing method was accurate to 100% with adults of all the three studied species (Filippi, 1995). Whether a given snake was adult or subadult was decided on the basis of the following criteria: for *Coluber viridiflavus* and *Elaphe longissima* by their dorsal colouration (as adults have diverging livery from subadults, see Naulleau, 1984; Bruno & Maugeri, 1990); for *Vipera aspis* by assigning to the adult age all the specimens longer than 41 cm SVL (Naulleau & Bonnet, 1996; Naulleau *et al.*, 1999). Place, time, type of activity, microhabitat type, and substratum type were systematically recorded.

Population size of the three studied snake species was estimated by cumulating data from two study years and by using two different indexes to obtain a better approximation (Seber, 1982):

[1] $N = A \times n / a$ (Lincoln-Petersen index);

[2] $N = A (n + 1) / (a + 1)$;

where N is the population size, A is the total number of marked specimens, n is the total number of observed specimens, and a is the total number of recaptured specimens. However, these indexes can

	Surface of the surveyed plot	Substratum a (%)	Substratum b (%)	Substratum c (%)	Substratum d (%)
Micro-habitat α	1.6 ha	20 ± 7.5	30 ± 3.2	20 ± 5.1	30 ± 8.5
Micro-habitat β	1.6 ha	25 ± 11	30 ± 3.8	45 ± 7.8	0 ± 0
Micro-habitat γ	1.6 ha	25 ± 7	30 ± 2.9	5 ± 0.6	40 ± 20
Micro-habitat δ	1.6 ha	20 ± 4.5	30 ± 2.5	15 ± 1.5	35 ± 11.2
Micro-habitat ε	1.6 ha	15 ± 2.5	50 ± 7.5	15 ± 3.2	20 ± 3.7
Micro-habitat ζ	1.6 ha	20 ± 4.8	10 ± 3	5 ± 0.4	65 ± 21.6
Micro-habitat η	1.6 ha	50 ± 8.8	5 ± 0.8	5 ± 0.5	40 ± 8.8
Micro-habitat θ	1.6 ha	15 ± 6.2	55 ± 6.7	5 ± 0.9	25 ± 7.1
Micro-habitat ω	8.0 ha	30 ± 2.4	10 ± 2.1	5 ± 0.5	55 ± 8.8

Table 1. Percent availability of each substratum type in each microhabitat available to snakes in the study area. A detailed description of the methods employed to calculate this substratum availability is presented in the text. Symbols for the substratum types: a = tree-branches or piles of wood cumulated on the ground (to 2 m in height); b = sand and leaf litter; c = sand; d = leaf litter. Standard deviations are included.

produce some bias because of the open population characteristics of snakes at our study area (for more details, see discussion).

All data were processed with a STATISTICA (version for Windows 4.5) PC package, with $\alpha = 5\%$, and using two-tailed tests in all cases. Tree-clustering was done by UPGMA method, standardized to 100%. Micro-habitat and substratum use niche breadth for each species were assessed by Simpson's (1949) diversity index.

RESULTS

Density, population size and sex-ratio

Numbers of snake specimens observed, marked, and recaptured are presented in Table 2. Population size for the three species was estimated to be 30 to 32 individuals for *Vipera aspis,* 504 to 551 individuals for *Coluber viridiflavus,* and 180 to 260 individuals for *Elaphe longissima.* For both these latter species, the large population sizes are due to the high numbers of specimens that were just sighted and remained unidentified (Table 2). The density, which was very variable from zone to zone within the study area, averaged 0.2 specimens × ha^{-1} in *Vipera aspis,* 3.5 specimens × ha^{-1} in *Coluber viridiflavus,* and 1.5 specimens × ha^{-1} in *Elaphe longissima..*

Summarized data on observed adult sex-ratio and adult body sizes of the three studied species are presented in Table 3. There was not any significant sexual size dimorphism both in *Vipera aspis* ($t = 0.09$, $df = 12$, $P > 0.9$) and in *Elaphe longissima* ($t = 1.93$, $df = 20$, $P > 0.06$), whereas males attained significantly longer SVL than females in *Coluber viridiflavus* ($t = 2.48$, $df = 36$, $P < 0.02$). The lack of significant sexual size dimorphism in *Elaphe longissima* is likely attributable to the small sample size, as male length is known to exceed female length in many conspecific populations studied to date (e.g. see Naulleau, 1984; Filippi, 1995; Capula *et al.,* 1997). Concerning *Vipera aspis,* there is much literature stating that females exceeded males in body lengths (e.g. see Saint Girons, 1952; Naulleau, 1984; etc), but in Italian populations the males averaged at least as similar sizes as females, the same being true also for Swiss specimens (Monney *et al.,* 1996; Luiselli *et al.,* unpublished data).

SPECIES	N° MARKED	N° RECAPTURED	N° OBSERVED
Vipera aspis	11	9	26
Coluber viridiflavus	34	10	162
Elaphe longissima	20	2	26

Table 2. Number of observed, marked and recaptured specimens of the three snake species studied in Castel Fusano (Rome). Specimens recaptured more than once are included under "N° Recaptured" as well those recaptured just once, whereas under "N° observed" only the specimens that were sighted (but not identified) are included.

SPECIES	OBSERVED SEX-RATIO	MALE LENGTH (cm)	FEMALE LENGTH (cm)
Vipera aspis	1.8 : 1	56.3 ± 6.1 (n = 9)	56.0 ± 4.9 (n = 5)
Coluber viridiflavus	1.4 : 1	84.7 ± 6.4 (n = 22)	79.9 ± 5.1 (n = 16)
Elaphe longissima	2.1 : 1	98.5 ± 9.5 (n = 15)	90.6 ± 7.6 (n = 7)

Table 3. Adult sex-ratio (males : females) and body size (SVL, in cm) of the three species of snakes studied in Castel Fusano (Rome). Standard Deviation is indicated.

Snake ecological distribution in relation to microhabitat type

The distribution of sightings of the three snake species in relation to micro-habitat is presented in Figure 1. The distribution of the sightings was not equal in the various microhabitats for any of the studied species (*Coluber viridiflavus:* χ^2 = 159.57, df = 17, $P < 0.00001$; *Elaphe longissima:* χ^2 = 430.47, df = 17, $P < 0.00001$; *Vipera aspis:* χ^2 = 396.92, df = 17, $P < 0.00001$): *Coluber viridiflavus* was found mainly in the micro-habitats γ and ω, *Elaphe longissima* in the micro-habitats ω, and *Vipera aspis* in the micro-habitat γ. *Coluber viridiflavus* differed significantly in terms of micro-habitat use from both *Elaphe longissima* (χ^2 = 290.05, df = 17, $P < 0.00001$) and *Vipera aspis* (χ^2 = 353.80, df = 17, $P < 0.00001$), and *Elaphe longissima* also differed significantly from *Vipera aspis* (χ^2 = 295.40, df = 17, $P < 0.00001$). In general, estimates of niche breadth (Table 4) showed that the three species differed significantly in terms of micro-habitat specialization (Kruskal-Wallis ANOVA, $P < 0.0001$), and a Tukey honest significance *post-hoc* test indicated that *Coluber viridiflavus* was significantly more generalist than the other two species, whereas *Elaphe longissima* was extremely specialized. The seasonal variations in the frequency of observation of the three snake species in the various microhabitats are presented in Figure 2. *Coluber viridiflavus* showed important seasonal variations (χ^2 test, $P < 0.0005$) in that it was rarely observed in the micro-habitat ω during the winter months, but ω was the most utilized micro-habitat type during the summer. *Elaphe longissima* did not show any remarkable seasonal pattern in micro-habitat utilization (χ^2 test, $P > 0.65$; winter was removed from this analysis due to lack of records). *Vipera aspis* was also characterized by important seasonal variations (χ^2 test, $P < 0.00001$), being found mainly in the micro-habitat γ from autumn to spring, and mainly in the micro-habitat ω during summertime. The interseasonal comparisons may however have been partially biased in the case of *Coluber viridiflavus* by the relative scarcity of snake sightings during the winter months (just 19 records versus 85 in spring, 51 in summer, and 66 in autumn), and in the case of *Vipera aspis* by the scarcity of records during the summer months. Indeed, the above-ground activity of *Vipera aspis* is much reduced during the hottest months in coastal Mediterranean Italy, and is often even suspended ("aestivation phase", see Saviozzi, 1994; Luiselli *et al.*, unpublished data).

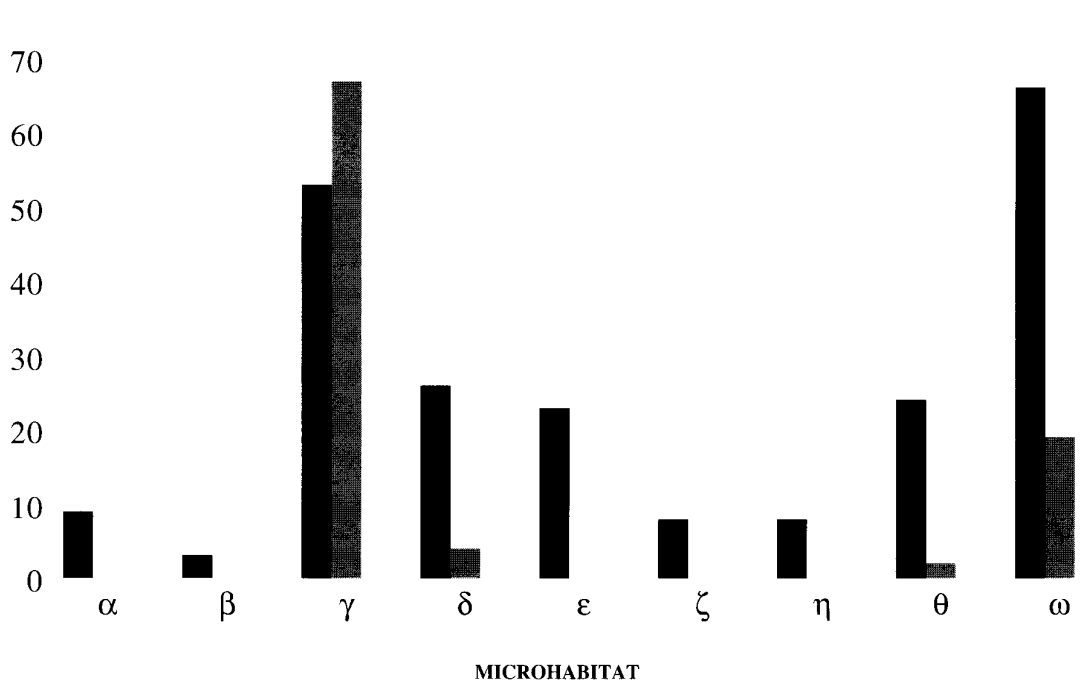

Figure 1. Distribution of the records of snakes in relation to the microhabitat type available in the study area. The numbers of observations are the numbers of specimens captured, recaptured (even on multiple times in several cases), and observed. For symbols relative to the various microhabitat types, see text. Black bars: *Coluber viridiflavus*; white bars: *Elaphe longissima*; grey bars: *Vipera aspis*.

	Coluber viridiflavus	*Elaphe longissima*	*Vipera aspis*
Microhabitat	5.299	1.036	1.678
Substratum	3.106	1.770	2.597

Table 4. Values of niche breadth (Simpson's, 1949, diversity index) applied to percent utilization of micro-habitat and substratum types, in the three study species at Castel Fusano (Rome).

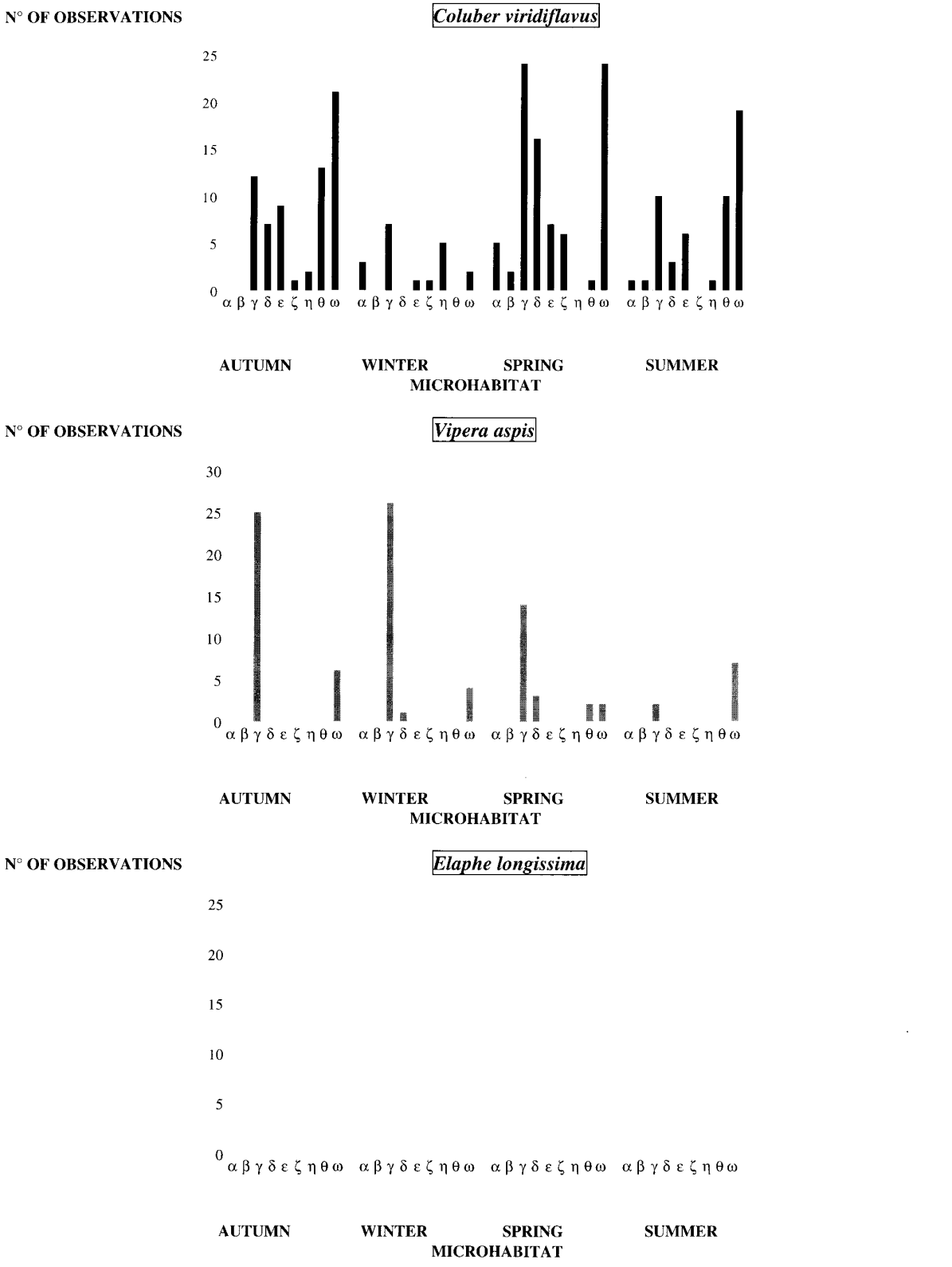

Figure 2. Seasonal variations of the frequency of observations of snakes in the various microhabitats available in the study area. For symbols relative to the various microhabitat types, see the text.

Snake ecological distribution in relation to substratum type

All the three snake species were observed on the substratum "d" much more frequently than on any other type of substratum (Figure 3). However, *Coluber viridiflavus* was also frequently found while basking on substratum "b". *Vipera aspis* and *Elaphe longissima* were relatively similar in terms of use of substratum types (χ^2 test with df =1, $P > 0.4$). Estimates of niche breadth (Table 4) showed that the three species differed significantly in terms of substratum specialization (Kruskal-Wallis ANOVA, $P < 0.005$), and a Tukey honest significance *post-hoc* test indicated that *Coluber viridiflavus* was significantly more generalist than the other two species, whereas *Elaphe longissima* was the most specialized species.

If we consider the seasonal variations in terms of substratum types utilization, there were diverging patterns among species (Figure 4). *Vipera aspis* and *Coluber viridiflavus* did not show any significant seasonal variations (for both species, χ^2 test, at least $P > 0.1$), but *Elaphe longissima* exhibited some important seasonal variations (χ^2 test, $P < 0.05$), as it was observed mainly on substratum "d" either in spring or in summer, and mainly on substratum "b" in autumn. Even in this case, however, a potential bias could be caused by the much smaller sample recorded in autumn than in spring and summer (see Figure 4b).

If we take in mind the frequency of occurrence of the various substratum types in the available microhabitats (cfr. Table 1), it appeared that all the snake species studied here did not use the various substratum types in relation to their availability in the field (multiple regression analysis: $r_{MULTIPLE} = 0.488$, $r^2 = 23.9\%$, $n = 36$, $P > 0.153$).

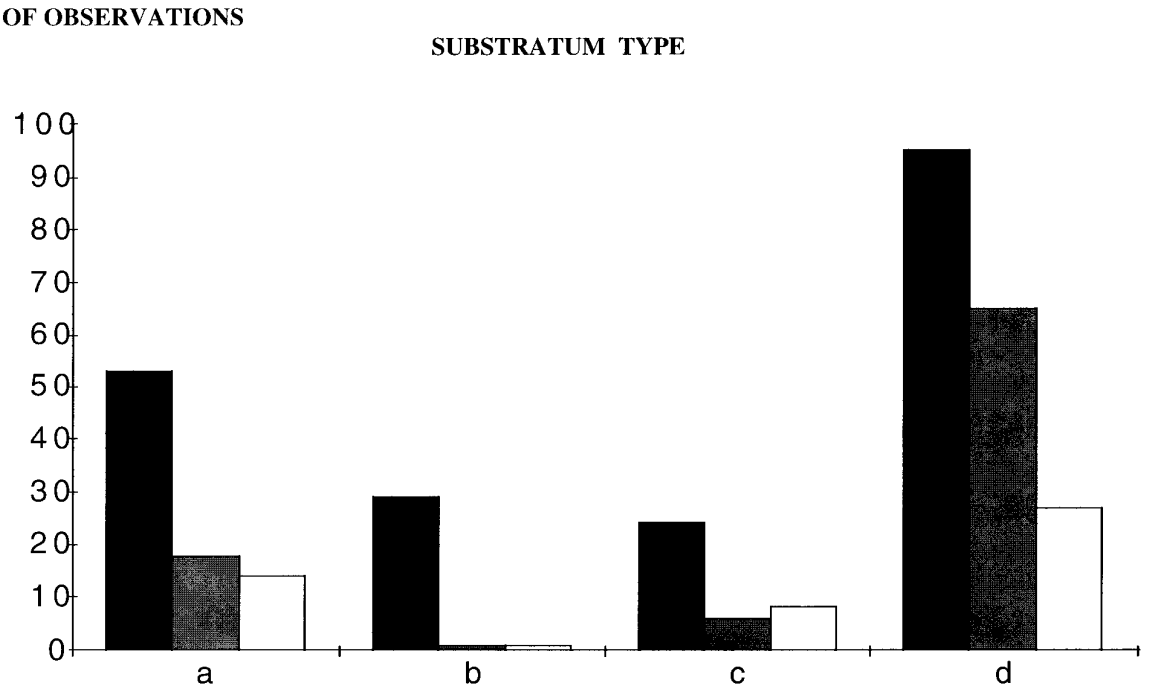

Figure 3. Distribution of the records of snakes in relation to the substratum type available in the study area.
For symbols relative to the various substratum types, see the text. Black bars: *Coluber viridiflavus*; white bars: *Elaphe longissima*; grey bars: *Vipera aspis*

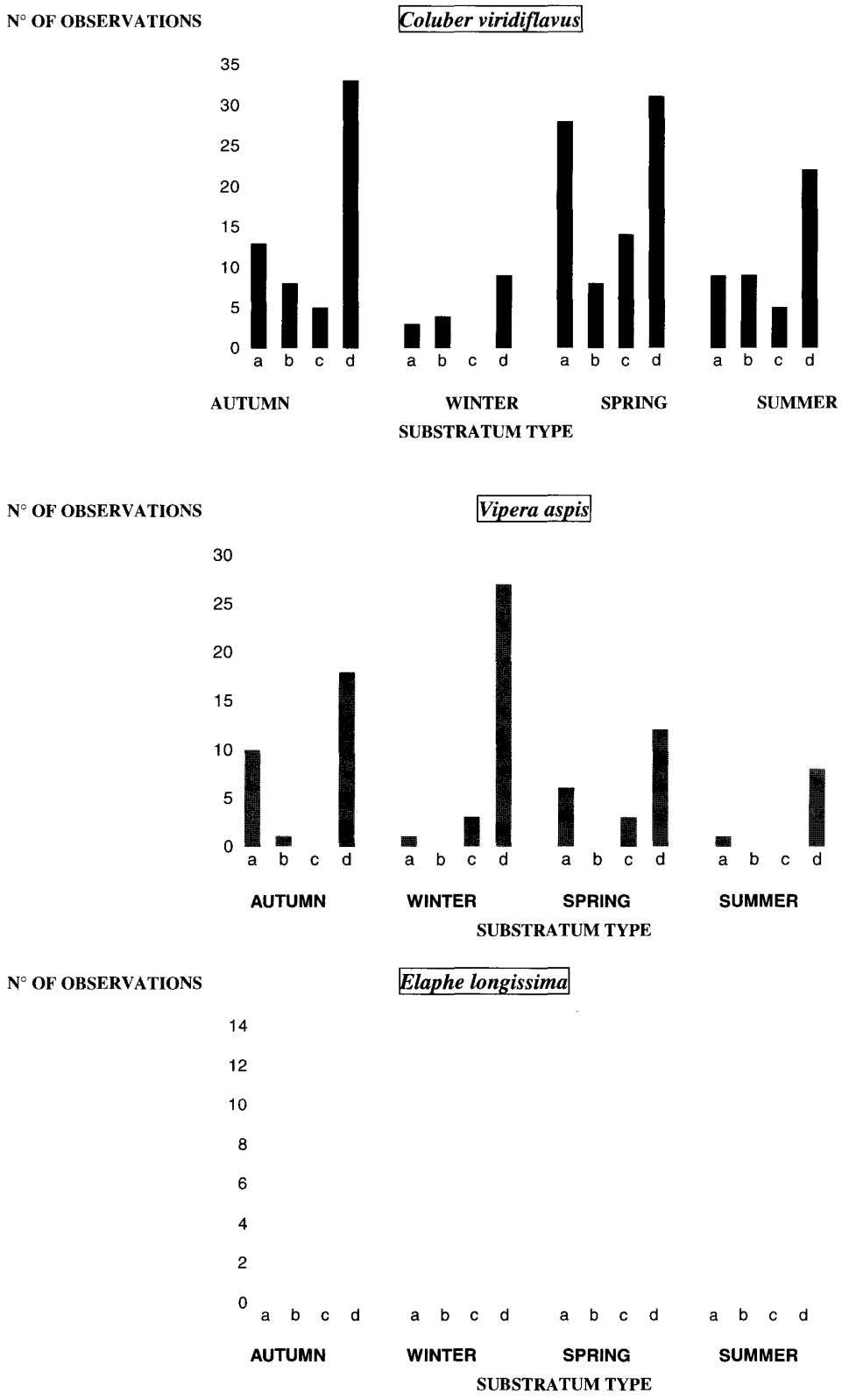

Figure 4. Seasonal variations of the numbers of snakes observed in the various substratum types available in the study area. For symbols relative to the various substratum types, see the text

DISCUSSION

Pooling the three species of snakes studied in this paper, it resulted an average total density slightly exceeding 5 individuals × ha^{-1}. This density is very similar to the values calculated in other areas of Mediterranean central Italy with low anthropic disturbance (Filippi, 1995). Thus, it seems that the study area could be well representative of other snake assemblages in Mediterranean central Italy. However, our estimates of population sizes and density have some shortcomings that are quite often found in snake studies published to date. Indeed, snake populations are quite difficult to census carefully, and in our study case the surface of the study area (about 120 ha), compared with the high mobility of the two colubrids (Naulleau, 1989; Ciofi & Chelazzi, 1991, 1994), suggests the possibility of high emigration and/or immigration rates through the borders. Thus, it is likely that our study populations have an open structure that may overestimate the true population sizes and densities of snakes, especially in the case of *Coluber viridiflavus* and *Elaphe longissima,* that experienced low recapture rates during our research period. In this regard, it is in fact surprising that these two latter species, although being considerably larger, exhibited higher population sizes and densities than *Vipera aspis*, whereas it is well known that higher densities of small snakes compared with large snakes should be expected (Peters & Wassenberg, 1983; Luiselli *et al.,* 2000).

As for micro-habitat utilization is concerned, our data demonstrated that the three species were relatively different from each another. Conversely, they are relatively similar in terms of macro-habitats, being generalist species with a preference for wooded and bushy sites (Bruno & Maugeri, 1990; Luiselli & Rugiero, 1990). These interspecific differences were even more marked if we consider the seasonal patterns in micro-habitat utilization, especially in *Vipera aspis* and in *Coluber viridiflavus.* It is likely that such interspecific micro-habitat differences could be linked to multiple reasons, either synecological (to limit resource overlap among species with very similar feeding habits, cfr. Capizzi & Luiselli, 1996) or autoecological (species-specific thermal and physiological exigences). In this regard it is not surprising that *Coluber viridiflavus*, an heliophilous colubrid with high body temperatures for activity (Scali & Zuffi, 1994; Capula *et al.,* 1997), was frequently observed in the hot and dry micro-habitats, whereas the same was not true for the other two species. Indeed, *Elaphe longissima* is particularly linked to forested areas (Naulleau, 1984; Luiselli & Capizzi, 1997), and *Vipera aspis,* although also present in areas with thick and arboreal vegetation, is more linked to mesophilous bushes and Mediterranean maquis (Naulleau, 1984; Bruno & Maugeri, 1990; Luiselli & Capizzi, 1997).

Contrary to what happened with micro-habitat utilization, the three species of snakes were similar in terms of substratum type utilization, and they did not use the various available substratums on the basis of their relative availability in the field. In general terms, tree clustering analyses indicated that *Coluber viridiflavus* and *Vipera aspis* are clustered together as for micro-habitat utilization (Figure 5), whereas *Coluber viridiflavus* and *Elaphe longissima* are clustered together as for substratum type utilization (Figure 6). However, there was a clear evidence that, as regards to both micro-habitat and substratum use, *Coluber viridiflavus* was the most generalist species, whereas *Elaphe longissima* was the most specialized species, and *Vipera aspis* was intermediate between the two colubrids.

In conclusion, our study suggests that *Elaphe longissima* and *Vipera aspis* are relatively similar in terms of ecological requirements in Mediterranean central Italy, not only as for trophic preferences (cf. Capizzi & Luiselli, 1996), but also as for substratum type utilization, although the former is clearly more linked to forested spots than the latter. On the grounds of all these matters, it is now quite clear why these two phylogenetically and morphologically diverging species are influenced in a relatively similar way by external factors such as, e.g., habitat loss, habitat residual, numbers of fencerows connecting two isolated good forested areas, etc. (Luiselli & Capizzi, 1997), although one species (*Vipera aspis*) is strictly terrestrial (e.g. see Saint Girons, 1952, 1957, 1975, 1996), and the other species (*Elaphe longissima*) is also an excellent climber (Naulleau, 1984, 1989; Naulleau & Bonnet, 1995). This relative similarity between *Elaphe longissima* and *Vipera aspis* may be not the case in other European regions, e.g. in central

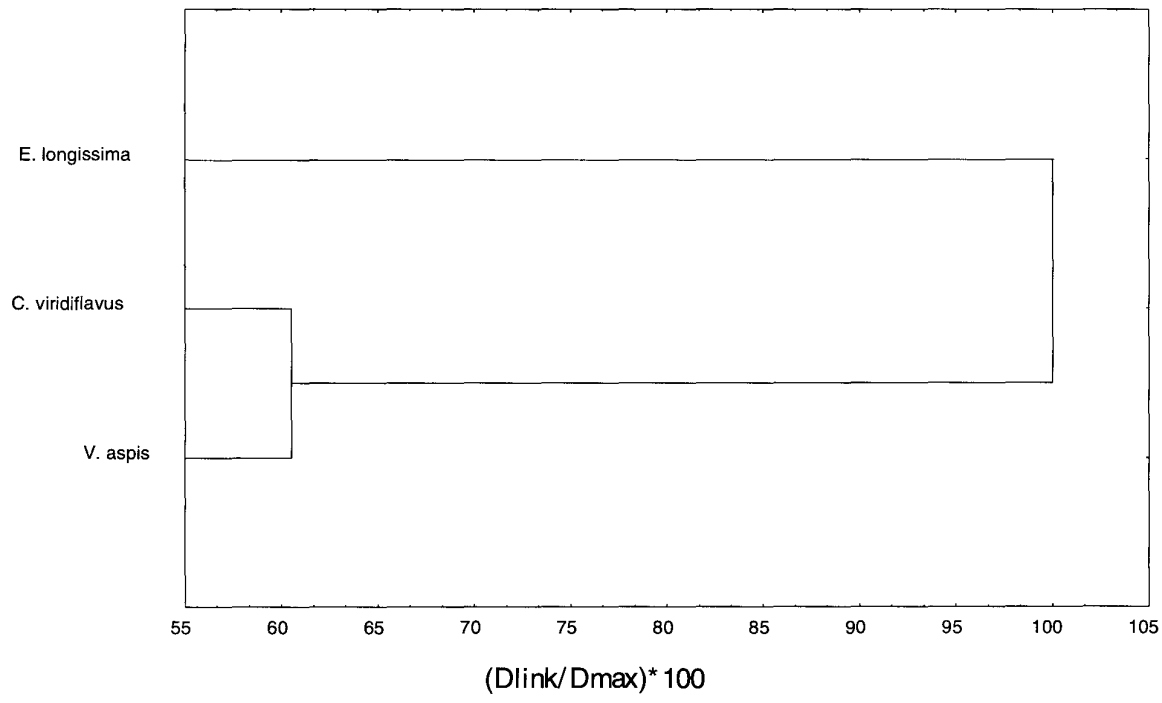

Figure 5. Tree diagram (UPGMA method, standardized to 100%) on the similarities between snake species in terms of microhabitat utilization

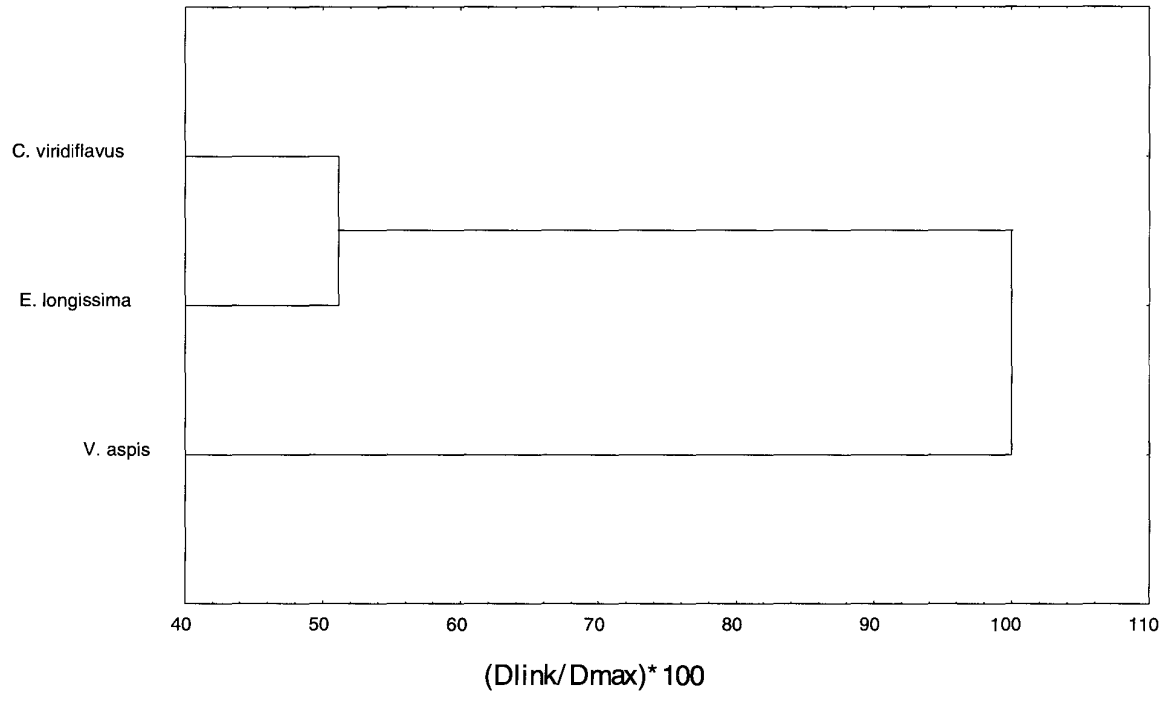

Figure 6. Tree diagram (UPGMA method, standardized to 100%) on the similarities between snake species in terms of substratum type utilization

France, where their ecological requirements are known to diverge considerably (Naulleau, 1984).

Acknowledgements

We are gratefully indebted to Dr U. Agrimi, Dr F.M. Angelici, Dr D. Capizzi, Dr M. Capula, Dr A. Mozzorecchia, Dr G. Dell'Omo, and Dr L. Rugiero for having given some original data on the snake-fauna of the study area. The manuscript also benefitted from helpful criticisms by three anonymous referees, Dr M. Capula, and Dr F.M. Angelici, whereas the inspiration of this research project came from vigorous discussion with Dr D. Capizzi and Dr M. Capula. Dr M.A.L. Zuffi is also thanked for helpful discussion and exchange of information. Thanks a lot to all of them! Funds to support this research were indirectly provided by H.F.I.Z.V (to L.L.).

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Réflexions sur l'évolution de la flore et de la végétation au Maghreb méditerranéen

P. QUÉZEL

IBIS Press, Paris : 117 p. (2000).

Nul autre que P. Quézel n'aurait pu réunir dans un petit opuscule d'à peine plus de 100 pages une masse aussi considérable d'informations et de références sur l'origine, l'état actuel et l'évolution alarmante de la flore et de la végétation de l'Afrique du Nord méditerranéenne.

Après avoir défini le cadre géographique et écologique de son étude, limitée à la zone non saharienne (soit approximativement la région située au nord de l'isohyète 100 mm) l'auteur résume dans une première partie les données les plus récentes sur l'origine multiple des éléments constitutifs de la flore actuelle et le contexte paléo-écologique de leurs migrations et de leur installation au sud de la Méditerranée, en mettant en évidence l'intérêt exceptionnel du "conservatoire botanique canarien" pour l'interprétation biogéographique de la flore du Maghreb.

Dans une deuxième partie, P. Quézel présente une analyse très synthétique des informations disponibles sur la flore et de la végétation actuelles du Maghreb.

La richesse de la flore en endémiques et sa répartition par éléments floristiques reflètent à la fois la grande diversité des conditions écologiques et l'histoire mouvementée de sa mise en place.
Encore qu'inégalement documentées sur l'étendue du territoire concerné, les menaces d'appauvrissement et de banalisation de la flore de cette région doivent être prises au sérieux et témoignent de l'urgence à mettre en œuvre les programmes de conservation actuellement en cours de gestation.

La description de la végétation tire un remarquable parti de l'expérience personnelle de l'auteur et des observations qu'il a accumulées sur le terrain depuis une cinquantaine d'années dans l'ensemble de la région méditerranéenne. Dans son opinion, et à l'exception des milieux édaphiques particuliers ou des climats extrêmes de haute montagne, la végétation potentielle de toute la zone envisagée est essentiellement arborée : groupements forestiers, "pré-forestiers" et "pré-steppiques". Les steppes du Maghreb méditerranéen sont elles-mêmes inter-prétées comme le résultat de la dégradation anthropique de formations arborées "pré-steppiques". Notons que cette interprétation semble s'opposer résolument à celle de Ch. Sauvage (Sauvage, 1963, Ionesco & Sauvage, 1963) qui, à la suite de L. Emberger, tenait pour climaciques (quoique par ailleurs dégradées) les steppes, arborées ou non, de l'étage bioclimatique aride ou des abords de l'étage bioclimatique de haute montagne. Mais peut-être s'agit-il essentiellement de divergences de vocabulaire dans la désignation des formations végétales climaciques de transition entre bioclimats potentiellement forestiers et bioclimats asylvatiques : les termes de *"séries forestières pré-steppiques"* (Abi-Saleh, Barbero, Nahal & Quézel, 1976) ou de *"forêt-steppe"* de la figure 3 ne désignent-ils pas les mêmes formations que les *"steppes arborées"* de Sauvage ?

En une vingtaine de pages, les différentes composantes de la végétation arborée du Maghreb sont présentées par étages thermiques (déterminés essentiellement par l'altitude), suivies de leurs formes de dégradation (matorrals, steppes et "pelouses" à thérophytes – ces dernières correspondant aux "ermes" de la terminologie de Ionesco et Sauvage, loc. cit.) et enfin des principaux types de végétation à déterminisme édaphique ou de haute montagne.

La troisième et dernière partie s'appuie sur nombre d'éléments descriptifs de la précédente pour dénoncer l'accélération récente des processus de dégradation anthropique du tapis végétal : quels qu'en soient les mécanismes (coupes délictueuses, défrichements anarchiques pour les cultures vivrières ou localement celle du chanvre, substitution de reboisements d'essences exotiques aux reliques forestières, surpâturage et incendies, urbanisation...), les effets se traduisent globalement par un recul de la forêt naturelle et une "steppisation" lourds de conséquences sur les sols et le climat. Dans un contexte aggravé par les perspectives planétaires de changement climatique global, on ne peut que partager les préoccupations et le pessimisme de P. Quézel devant la

désertisation causée par une explosion démographique incompatible avec les ressources limitées de la nature maghrébine. Où chercher les bases scientifiques du développement durable et respectueux d'un patrimoine naturel encore riche, mais pour combien de temps ?

Indispensable à tous ceux qui souhaitent bénéficier de l'expérience exceptionnelle de P. Quézel sur la flore et la végétation du Maghreb, ce petit livre offre par surcroît une bibliographie abondante. Il est malheureusement desservi par l'imperfection de sa forme : nombreuses coquilles, affectant notamment l'orthographe des noms scientifiques et la ponctuation, omission de plusieurs références bibliographiques citées dans le texte... Espérons que le succès qu'il mérite lui vaudra rapidement une réédition corrigée !

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Joël MATHEZ
Institut de Botanique, Université de Montpellier II, 163 rue A. Broussonnet, 34000 Montpellier

The Birds of Corsica (BOU Checklist Series : 17)

J.C. THIBAULT & G. BONACCORS

British Ornithologists' Union, Hertfordshire, 171 p. (1999).
BOU, c/o The Natural History Museum, Akeman Street, Tring Hertfordshire HP23 6AP, UK. Prix : £22, port compris.

Publié dans le cadre de la déjà longue série des listes ornithologiques commentées de la British Ornirthologists' Union (BOU), l'ouvrage que nous proposent Jean-Claude Thibault et Gilles Bonaccorsi offre une mise à jour remarquable et bien venue de la riche avifaune corse, à laquelle aucun document de synthèse n'avait été consacré depuis 1983.

Après une présentation rapide de l'histoire géologique, de la géographie, des milieux naturels et de la mise en place de l'avifaune de la quatrième plus grande île de Méditerranée, les auteurs précisent et commentent le statut, la dynamique récente et l'écologie de plus de 320 espèces d'oiseaux observées en Corse, qu'il s'agisse d'espèces nicheuses, migratrices ou simplement accidentelles. Bien évidemment, le texte consacré à chacune des espèces varie fortement en longueur et en détail, de quelques lignes pour quelques espèces d'observation anecdotique à une page entière pour certains « joyaux » de l'avifaune Corse, telle la Sittelle corse endémique *Sitta whiteheadi*. Les auteurs ont à très bon escient ajouté à cette liste commentée, un jeu de données chiffrées en 16 tableaux concernant différents recensements récents et anciens réalisés sur les zones humides ou les îlots littoraux de Corse. Un jeu d'un trentaine de photographies en couleur agrémente l'ouvrage, qui se termine par une bibliographie conséquente, riche d'environ 400 références. En conclusion, il s'agit-là d'un petit livre bien conçu, dense, concis et riche en informations, qui met parfaitement en exergue la valeur et la diversité de l'avifaune Corse. Nul doute que sa publication en langue anglaise, si elle a pu étonner de prime abord, lui assurera la large diffusion et le succès qu'il mérite auprès de la communauté scientifique tout autant qu'auprès des ornithologues amateurs.

Eric VIDAL
Institut Méditerranéen d'Ecologie et de Paléoécologie (IMEP, UMR 6116), Université d'Aix-Marseille III, Faculté des Sciences et Techniques de Saint-Jérôme. Case 461. F - 13397 Marseille Cedex 20.

Ecology, biogeography and management of *Pinus halepensis* and *P. brutia* forest ecosystems in the Mediterranean Basin

G. NE'EMAN & L. TRABAUD (coords.)

Backhuys Publishers, Leiden : 407 p. (2000).

Le pin d'Alep et le pin brutia comptent parmi les essences les plus fréquentes du pourtour méditerranéen, le premier s'étendant essentiellement depuis le Maroc jusqu'à la Grèce continentale, tandis que le second se rencontre en Méditerranée orientale, surtout en Turquie mais aussi en Syrie, au Liban et sur les îles de la mer Egée. L'ensemble des peuplements couvre environ 7 millions d'hectares et ces deux arbres à stratégie de vie de type expansionniste sont favorisés par la déprise agricole dans bon nombre de situations, mais aussi par les incendies de forêts. De nombreuses études biologiques, écologiques et écophysiologiques ont été consacrées à ces deux ligneux, mais une synthèse accessible à un public plus large s'imposait. Ainsi, après le récent ouvrage « *Ecology and biogeography of Pinus* » (Richardson, 1998), consacré à l'ensemble des pins du globe, un travail plus précis sur les pins circum-méditerranéens du groupe *halepensis-brutia* s'imposait. Le grand mérite des deux coordinateurs est d'avoir réussi le tour de force de réunir des spécialistes de divers horizons pour réaliser une synthèse cohérente et fouillée, se divisant en 29 chapitres groupés en quatre parties.

La première partie (10 chapitres), consacrée à la taxonomie et à l'autécologie, débute par une présentation biogéographique et taxonomique (P. Quézel), auxquels font suite plusieurs chapitres comparant notamment la diversité génétique et l'écophysiologie (G. Schiller), la germination (C.A. Thanos) et les modalités de reproduction (C.A. Thanos & E.N. Daskalakou et A. Shmida *et al.*) de ces deux pins. On regrettera toutefois que le chapitre traitant de dispersion, prédation et sérotinie (R. Nathan & G. Ne'eman) ne se limite qu'au seul pin d'alep, et que les aspects paléoécologiques ne soient abordés que sous l'angle restreint de la signification palynologique de ce pin, conclusions de plus bâties sur les bases fragiles de sondages polliniques marins ou archéologiques (M. Weinstein-Evron & S. Lev-Yadun). Cette partie s'achève par une synthèse traitant de l'ensemble des 7 pins méditerranéens non indigènes et à caractère envahissant de l'hémisphère austral (D.M. Richardson) ; parmi eux, *P. halepensis* était déjà considéré comme très dynamique en 1855 dans la région du Cap, alors que *P. brutia* semble nullement envahissant.

La deuxième partie (9 chapitres) traite de multiples aspects écologiques et dynamiques liés à ces forêts de pins. Un premier paragraphe concerne la diversité et la composition spécifique des forêts de pin d'Alep de Méditerranée orientale (P. Kutiel). Plusieurs chapitres abordent la dynamique de ces forêts, que ce soit sous l'angle des perturbations et de la balance hydrique (M.A. Zavala), de la banque de graines du sol (I. Izhaki & G. Ne'eman), de la production et de la décomposition de la litière (M. Arianoutsou & C. Radea), ou du rôle des mycorrhizes (M. Honrubia). Puis sont considérées l'incidence des invertébrés phytophages (Z. Mendel) et une description de communautés d'oiseaux (I. Izhaki) ou de mammifères (A. Haim), sans relier toutefois ces données à des processus sylvigénétiques essentiels comme les taux de prédation ou de dispersion des graines. De plus, l'ensemble de cette partie souffre de trop forts déséquilibres taxonomique : *Pinus halepensis* est le plus souvent uniquement considéré, et géographique : les études de cas sont surtout centrées en Méditerranée orientale, notamment en Israël.

La troisième partie aborde l'écologie du feu, perturbation majeure affectant ces forêts, mais aussi véritable « moteur » de leur dynamique. La régénération post-incendie des forêts de pin d'Alep est tout d'abord étudiée, en Méditerranée occidentale (L. Trabaud) et orientale (M. Arianoutsou & G. Ne'eman), puis celle du pin brutia (C.A. Thanos & M.A. Doussi). Un chapitre synthétique regroupant et discutant l'ensemble de ces données aurait sans doute été plus profitable au lecteur. La gestion des pinèdes brûlées en Israël (G. Ne'eman & A. Perevolotsky) et les méthodes de prévention du feu dans les pinèdes de Méditerranée occidentale (V. Leone *et al.*) terminent ce volet.

La dernière partie est consacrée aux techniques d'agroforesterie (M. Etienne) et de gestion sylvo-pastorale, en Grèce (C.N. Tsiouvaras) ou dans les plantations

d'Israël (O. Bonneh), pour s'achever sur l'étude de l'impact des pollutions atmos-phériques sur les pinèdes (J. Barnes *et al.*).

L'ensemble de l'ouvrage représente une synthèse précieuse, bien documentée et réalisée, sur la dynamique et la gestion de ces forêts majeures du paysage méditerranéen. La portée générale de cette monographie est toutefois quelque peu amoindrie par l'existence de plusieurs études de cas, localisées le plus souvent en Méditerranée orientale. Le recours à des mises en parallèle plus fréquentes entre pin d'Alep et pin brutia, comme cela est réalisé dans la première partie de l'ouvrage, aurait sans doute contribué à mieux dégager les originalités ou, au contraire, les similitudes fonction-nelles et dynamiques de ces deux types quasi vicariants d'espèces et de forêts.

Frédéric MÉDAIL
Institut Méditerranéen d'Ecologie et de Paléoécologie (IMEP, UMR 6116), Université d'Aix-Marseille III, Faculté des Sciences et Techniques de Saint-Jérôme. Case 461. F - 13397 Marseille Cedex 20.

Camargue, canards et foulques ; fonctionnement et devenir d'un prestigieux quartier d'hiver

A. TAMISIER & O. DEHORTER

C.O.GARD, Nimes, 369 p. (1999).

This book provides an overview of the ecological functioning of a wintering area for waterfowl in the Camargue delta. The book is written in French and divided into four distinct sections. The first section provides a description of the Camargue, including the habitat types and its ducks and coots. The description emphasises habitat changes that have occurred over the last 50 years in relation to human activity. In the second section, an impressive amount of long term data are presented on several topics: bird numbers and trends over years and season, diets, feeding behaviour, and resource partitioning resulting in diurnal and nocturnal spatial distributions. Time budgets and energetics are used in explaining the daily and seasonal activity of ducks and their habitat use. The third section presents the social organisation of ducks and coots leading to an analysis of the adaptive significance of the spatio-temporal organisation within a functional unit framework. Finally, adding a comparison with three other major wintering areas in Senegal, Tunisia and Louisiana, the authors discuss life history traits presented in previous chapters in the context of wintering strategies for ducks. They emphasise that breeding strategies are strongly influenced by wintering strategies. The last section addresses conservation topics taking into account the role and the impact of human activity, principally hunting, on habitat management, waterfowl behaviour and wintering numbers. Finally, they discuss the carrying capacity of the Camargue for wintering ducks and the place of Nature within a human altered landscape. The book is well organised and well presented with many illustrations, figures and pictures that accurately support the text. Moreover, each chapter is very well synthesised in a one-page summary.

The book is based on 30 years of original scientific research and presents a convincing global picture of the ecological functioning of one of the most important wintering area in Europe. This would not be possible without an impressive knowledge of, and passion for, this region. The authors effectively use a scientific approach for collecting and analysing data for waterfowl to address broader questions of conservation and the future of the Camargue. For this purpose, the writing is definitively oriented to be accessible to a large but concerned public. The book should be a useful tool for managers and decision-makers ranging from local landowners to regional representatives. Finally, an English translation would make the book available for a larger audience.

Nicolas SADOUL
Station Biologique de la Tour du Valat, Le Sambuc, 13200 Arles.

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 êtres analysés seront envoyés aux Editeurs.

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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.
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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, 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.

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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 :

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- 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.

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Les mots « figures » et « tableaux » annoncés dans le texte sont écrits en toutes lettres et en minuscules. Indiquer le nom d'auteur et l'année de publication (mais indiquer tous les auteurs dans la bibliographie). Exemples: « Since Dupont (1962) has shown that... », or « This is in agreement with previous results (Durand *et al.*, 1990 ; Dupond & 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.*

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Ecologia Mediterranea publishes original research report and reviews in the fields of fundamental and applied ecology of Mediterranean areas, except descriptive articles or articles about systematics. The editors of Ecologia Mediterranea invite original contributions in the fields of: bioclimatology, biogeography, conservation biology, population biology, genetic ecology, landscape ecology, microbial ecology, vegetal and animal ecology, ecophysiology, palaeoecology, palaeoclimatology, but not marine ecology. Symposium proceedings, review articles, methodological notes, book reviews and comments on recent papers in the journal are also published. 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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- 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.

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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* Linnée).

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