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Plant functional types and ecosystem function in Mediterranean shrubland

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Abstract. This study attempts to identify Plant Functional Types (PFTs) within the scrub vegetation of the stabilized sand dunes of the Doñana National Park (southwestern Spain) and to explore possible links with ecosystem function. Two 10-km long transects were sampled along a gradient of water table depth from elevated and dry dunes to a border area close to the salt marsh.

A matrix of cover values for 20 woody species × 58 plots and a matrix of 24 morphological and physiological traits × 20 species were analysed by means of DCA and TWINSPAN to identify the main vegetation types and PFTs. In order to know the predominant plant traits, the matrix of 20 species × 58 plots was multiplied by the 24 traits × 20 species matrix. The resulting 24 traits × 58 plots matrix was analysed by means of DCA.

The main vegetation types coincide with the previous descriptions of the Park with *Juniperus phoenicea* woodland and xerophytic species dominating the top of the dunes and hygrophytic species with isolated *Quercus suber* trees in the depressions. Previous classifications of Mediterranean woody plants resulted in two main PFTs. The present analysis confirmed these two groups: *maquis* versus *garrigue*, but added four new groups. The analysis of the traits × plots matrix revealed that the main trend of variation is related to the water table gradient, while the traits related to the species of mature plant communities had little weight in the analysis because these communities are restricted to isolated patches.

Keywords: Doñana; Plant trait; Regeneration; Water potential; Water table depth.

Nomenclature: Valdés et al. (1987).

Introduction

The significance of morphological and physiological traits enabling plants to persist, compete and regenerate under different environmental constraints, has been known since the days of Aristotle and Theophrastos. One major application of the trait concept is the classification of plants (Skarpe et al. 1996). Noble & Gitay (1996) recognized five categories of plant classification according to the main aim of the study:

1. Phylogeny (traditional taxonomy);
2. Structure (life forms);
3. Resource use (guilds);
4. Response to a defined perturbation response group;
5. Role in ecosystem function (functional groups).

The use of Plant Functional Types (PFTs) for plant classification has increased in recent years (Woodward & Cramer 1996). PFTs can be defined as sets of plants exhibiting similar responses to environmental conditions and having similar effects on the dominant ecosystem process (Walker 1992; Noble & Gitay 1996; Díaz & Cabido 1997).

With the help of PFTs we are able to summarize the enormous complexity of individual species and populations into a relatively small number of general recurrent patterns (Walker 1992; Grime et al. 1997). Different PFTs are expected to play different roles in terms of matter and energy processes in ecosystems. Therefore, their identification and the estimation of their abundance is highly relevant to the assessment of ecosystem function (Gitay & Noble 1997).

In Mediterranean shrubland ecosystems of the Southern Iberian Peninsula, PFTs have been identified on the basis of leaf, flower and fruit characteristics (Herrera 1984, 1992; Alés 1993; Gallego Fernández et al. 1997). In annual plants they have been identified on the basis of plant size and other morphological traits (Fernández Ales et al. 1993).

In the present contribution, we aim at identifying PFTs in Mediterranean woody vegetation looking at both morphological and physiological features and to explore the role of the main plant traits in ecosystem function, particularly in relation to water availability and succession. In addition we wish to identify the relation of those plant traits along a wide gradient of water table depth which characterizes the stabilized dune sands of Doñana National Park. We followed the protocol developed by Díaz & Cabido (1997) on the basis of easily-measurable plant traits, both from published data and from our own field work, completed with physiological measurements like leaf water potential and costs of leaf growth and maintenance. Patterns were detected from individual to ecosystem level.

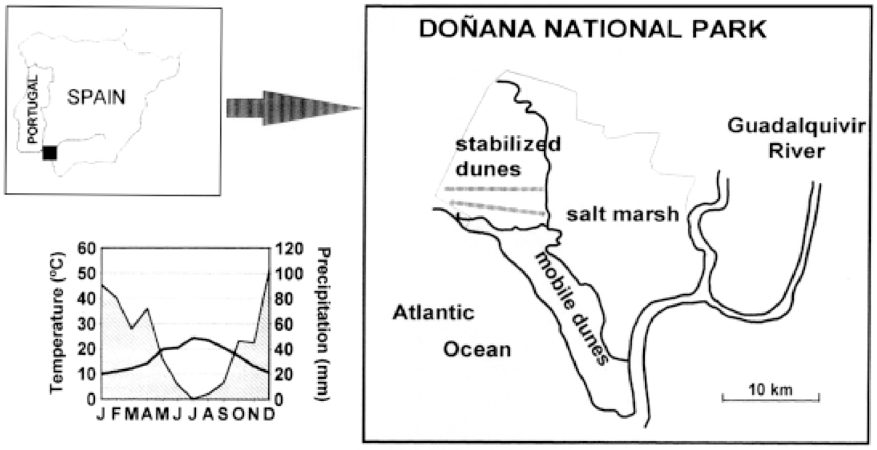

Fig. 1. Map showing the location of Doñana National Park. Transects are marked and names of the three ecological units of the Park given. The dotted lines mark the boundaries of the Park.

Steep gradients, in which sharp changes can be observed along relatively short distances, are particularly appropriate for the study of the relationships between natural vegetation and climatic conditions (Díaz & Cabido 1998). Doñana National Park was chosen to start with this methodology because the distribution of shrubland is well-known, environmental gradients are well-defined and there are many published studies on shrub species. A steep gradient of water availability can be found within the Park under uniform sandy soil conditions.

Material and Methods

Study area

Doñana National Park is located in southwestern Spain, facing the Atlantic Ocean. It has a Mediterranean-type climate with some oceanic influences: milder temperatures, higher air moisture and rainfall than further inland. Annual rainfall is 565 mm on average, but can exceed 1000 mm or remain below 300 mm. 80 % of the rainfall occurs in the period October-March, with a maximum in December and January with close to 90 mm/month and no rain in July and August (García Novo et al. 1996).

The Park has been described as a wide ecotone between the sands of the continental platform and the marsh. A topographical W-E gradient exists in the stabilized dunes of the Park, from the elevated and drier western border at 40 m a.s.l., to the low-lying eastern border close to the marsh at 2 - 3 m a.s.l., which corresponds to a gradient of water table depth. Within this large-scale gradient, small-scale gradients occur in association with dune topography, which have been described by Muñoz Reinoso (1997). Their dynamics in relation to rainfall fluctuations have been analysed by Zunzunegui et al. (1998). Different types of scrub communities have been identified on the stabilized dunes in response to the general water table level gradient (García Novo 1997; García Novo & Merino 1995, 1997 among many others). As water table depth increases, vegetation types replace one another, from grassland to 'monte negro' scrub on moist soils, to 'monte intermedio' scrub on dry soils with some occasional phreatic water supply, to 'monte blanco' scrub on the higher and drier sands, where rainfall is the only water supply (García Novo et al. 1996).

Methods

Two transects of 10 km each were sampled along this wide gradient of the stabilized dunes (Fig. 1). In each, 5 m × 5 m plots were established for quantitative cover measurements of the scrub (along four parallel 5-m lines). Topography and water table level were measured in the centre of each plot. In total 58 plots were sampled.

We selected 24 vegetative- and functional plant traits measured at the individual plant level, using both the literature as well as field measurements, according to the following criteria:

1. They should express plant morphology.
2. They should be related to plant responses to resource availability and to environmental stress factors.
3. They should express the capacity to colonize new areas and to re-establish after disturbance.
4. They should provide information on plant relationships with pollinators and seed dispersers.
5. They should be easy to measure in the field or in the laboratory.

The list of traits and the source of information are presented in Table 1.

Table 1. Traits recorded on the 20 shrub species of the stabilized dunes of Doñana National Park.

Trait	Description	Classes in the matrix
Age[5]	Average plant age	1 = 5 - 25; 2 = 25 - 50; 3 = 50 - 100; 4 = > 100
Height[7]	Average plant height	1 = < 60 cm; 2 = 60 -100 cm; 3 = 100 cm - 3 m; 4 = 3 - 5 m; 5 = > m.
Diameter[1;5]	Average canopy diameter	1 = < 50 cm; 2 = 50 -100 cm; 3 = 1 - 2 m; 4 = 2 - 3 m; 5 = > 3.5 m
Leaf size[7]	Average leaf area	1 = < 0.10 cm^2; 2 = 0.10 - 0.25 cm^2; 3 = 0.25 - 2.25 cm^2; 4 = 2.25 - 12.25 cm^2
Leaf colour[1;5]		1 = all green; 2 = green and white; 3 = all white
Leaf margin[5;7]		1 = entire; 2 = revolute; 3 = lobed
Leaf texture[5;7]		1 = malacophyll; 2 = semi-sclerophyll; 3 = sclerophyll
Leaf hairiness[5;7]		1 = not hairy; 2 = hairy lower side; 3 = hairy upper side
Leaf duration[5;7]		1 = < 6 month; 2 = 6 - 14 month; 3 = 14 - 26 months; 4 = 26 - 28 months
L/S[1;5]	No. of leaves per 10 cm of stem	1 = < 10; 2 = 10 - 20; 3 = 20 - 50; 4 = 0 - 100; 5 = 100
Stem diameter[1;5]	Measured at ground level	1 = < 2 cm; 2 = 2 - 5 cm; 3 = 5 - 10 cm; 4 = < 20 cm
Bark consistency[1;5]		1 = smooth; 2 = fibrous; 3 = corky
Spininess[8]		1 = absent; 2 = with spine
Underground stem[1;5]		1 = lignotubers; 2 = others
Root morphology[3;5]		1 = tap root; 2 = horizontal roots; 3 = vertical - horizontal roots
Root depth[3;5]		1 = < 25 cm; 2 = 25 - 50 cm; 50 - 100 cm; 4 = > 100 cm
Regeneration[2;5]	Vegetative regeneration after fire	1 = plant killed 2 = from epicormic buds; 3 = from non epicornic buds; 4 = from epicornic and non epicornic buds
Fruit dehiscence[8]		1 = dry indehiscent; 2 = dry dehiscent; 3 = fleshy indehiscent; 4 = fleshy
Fruit type[8]		1 = capsule; 2 = cone; 3 = nutlet ; 4 = legume; 5 = achene; 6 = drupe; 7 = berry Pol-
lination[8]	Type of pollination	1 = zoophyllous; 2 = anemophyllous
Slwp[1;4;6]	Summer leaf water potential	1 = < – 2 MPa; 2 = – 2 - – 3 MPa; 3 = – 3 - – 4.5 MPa; 4 = > – 4.5 MPa
Wlwp[1;4;6]	Winter leaf water potential	1 = < – 0.5 MPa; 2 = – 0.5 - – 0.6 MPa; 3 = - 0.6 - – 0.7MPa; 4 = > – 0.7 MPa
Cost of growth[9]	Cost of leaf growth	1 = < 1.5 ; 2 = 1.5 - 1.6; 3 = > 1.8 g glucose $g(dw)^{-1}$
Cost maintenance[9]	Cost of leaf maintenance	1 = < 0.0130; 2 = 0.0130 - 0.0140; 3 = > 0.0140 g glucose $g(dw)^{-1}$ day^{-1}

[1]Field observation; [2]García Novo (1977); [3]Martínez et al, (1998); [4]J. Merino et al. (1976); [5]J. Merino in Specht (1988).
[6]O. Merino. et al. (1995); [7]Orshan (1989); [8]Valdés et al. (1987); [9]J. Merino (1987).

Data analysis

The matrix of 20 species × 58 plots resulting from the transect sampling was subjected to standard multivariate ordination and classification techniques (DCA and TWINSPAN) so as to identify the main floristic scrub types. Here we used the methodology of Díaz & Cabido (1997).

The scales of measurements of plant attributes were originally continuous, categorical or binary, but they were all transformed into categorical or binary scales prior to the analysis. We subjected the 24 traits × 20 species matrix to DCA and TWINSPAN in order to identify groups of species with similar traits. The species clusters were assumed to represent PFTs at the species level (Keddy 1992; García Mora et al. 1999).

In order to identify the predominant plant traits along this large gradient the matrix of 20 species × 58 plots (floristic) was multiplied by the matrix of 24 traits × 20 species. The result was a matrix of 24 traits × 58 plots that was analysed by means of DCA.

Results

Floristic analysis

Through the analysis of the sites × species matrix the main types of scrub of the stabilized dunes in the Park could be distinguished. The main trend of variation of the DCA is related to the depth of the water table.

Fig. 2 shows the results of the DCA, together with a schematic drawing of the topographic gradient and the dominant shrub species. The groups of plots defined by TWINSPAN analysis are the following:

1. On dune tops, where the water table is always deeper than 6 m, plant cover is dominated by *Juniperus phoenicea.*
2. Xerophytic scrub of the top of the dunes, with a water table deeper than 4 m. Dominant species are *Cistus libanotis, Halimium commutatum, Helichrysum picardii, Lavandula stoechas, Rosmarinus officinalis, Stauracanthus genistoides* and *Thymus mastichina.*
3. Xerophytic scrub of the dune slopes, with water table depth between 2 and 4 m. Dominant species are *Halimium halimifolium,* and *Ulex australis.*
4. Hygrophytic scrub of the dune valleys, with a water table depth between 1 and 2 m. Dominant species are: *Calluna vulgaris, Cistus salvifolius, Daphne gnidium, Erica scoparia, Myrtus communis* and *Phillyrea angustifolia.*
5. These hygrophytic areas present occasional patches with *Pistacia lentiscus* and *Quercus suber.*
6. Hygrophytic scrub of the depressions, with the water table being shallower than 1 m and common flooding in wet winters. The dominant species are *Erica ciliaris* and *Ulex minor.*

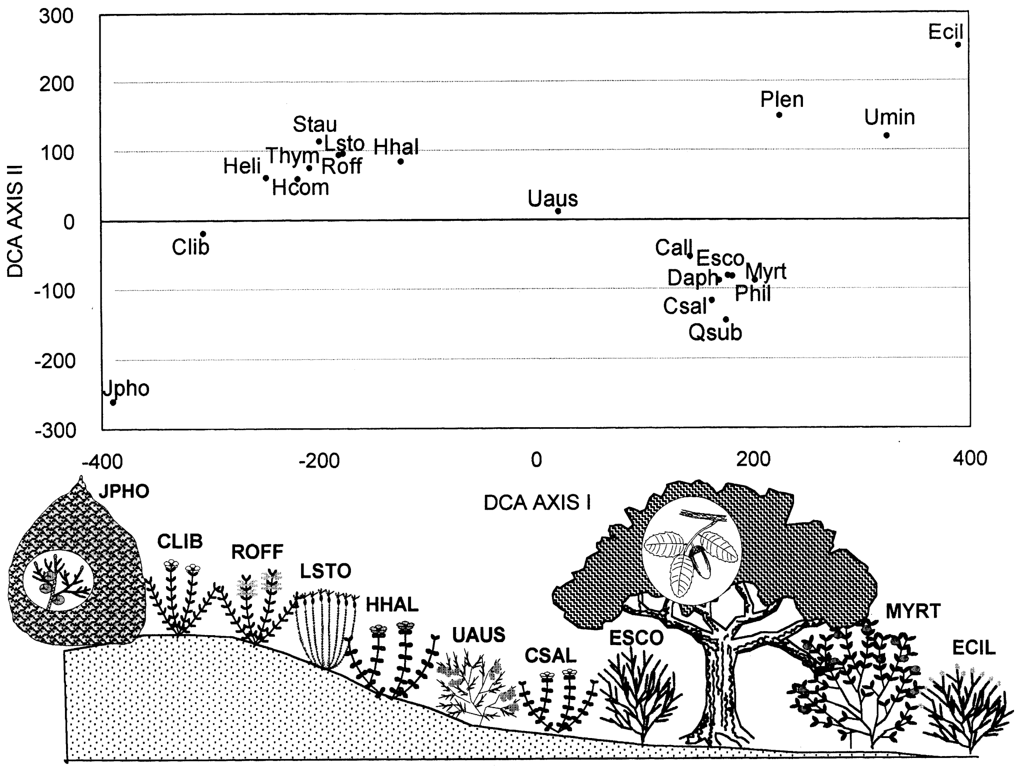

Fig. 2. Results of the DCA-analysis of species × sites matrix and approximate location of main species along the topographic gradient. Abbreviations: Call: *Calluna vulgaris*; Clib: *Cistus libanotis*; Csal: *Cistus salvifolius;* Daph: *Daphne gnidium*; Ecil: *Erica ciliaris*; Esco: *Erica scoparia*; Hcom: *Halimium commutatum*; Heli: *Helichrysum picardii*; Hhal: *Halimium halimifolium*; Jpho: *Juniperus phoenicea*; Lsto: *Lavandula stoechas*; Myrt: *Myrtus communis*; Phil: *Phillyrea angustifolia*; Plen: *Pistacia lentiscus*; Qsub: *Quercus suber*; Roff: *Rosmarinus officinalis*; Stau: *Stauracanthus genistoides*; Thym: *Thymus mastichina*; Uaus: *Ulex australis*; Umin: *Ulex minor.*

PFT-analysis

We distinguished seven PFTs on the basis of the TWINSPAN-classification of the traits × species matrix (Fig. 3). The main trend of variation as reflected by the DCA-analysis (axis 1) separates plants with hairy leaves and more negative leaf water potentials, which are obligate seeders after fire (positive end), vs. sprouters with many small leaves per stem length (negative end). The second trend of variation (axis 2) separates plants with fleshy fruits (drupe or berry) towards the negative end (Fig. 4).

As PFTs 5 and 6 are not clearly distinguished in the DCA-analysis they can be merged into a single group. After this fusion our system includes six PFTs.

PFT A: Large shrubs, with a high number of small leaves per stem unit of length, fibrous bark, moderately negative leaf water potentials, high costs of leaf growth and low cost of leaf maintenance, generally with the capacity to sprout after a fire (Vilà 1997); formed by *Ericaceae – Calluna vulgaris, Erica ciliaris, E. scoparia.* This type occurs optimally in intermediate, mesic sites along the water table depth gradient, and keeps an adequate water status throughout the year. They have been considered as water stress avoiders by Merino et al. (1995). They are very sensitive to unusual changes in soil water accessibility, like severe periods of drought typical of Mediterranean climate (field observations).

PFT B: This type is based on the small tree *Juniperus phoenicea* ssp. *turbinata.* Individuals have a conic shape from the juvenile stage onwards. They sprout after fire. Plants have many scale-like leaves per stem length all the way along the branches, forming a quite homogeneous layer around the crown (Villar 1997). Type B has the lowest costs of leaf maintenance, moderate leaf growth costs, and a considerable leaf water potential. High water stress may occur during the summer months. Martínez García & Rodríguez (1988) and Martínez García et al. (1998) suggested that the root biomass distribution is superficial, which agrees with the observations of Tsiourlis (1992) on *J. phoenicea* woodland in the Greek phrygana.

PFT C: Formed by the relatively large evergreen tree *Quercus suber*, with a long life span, the trunk protected

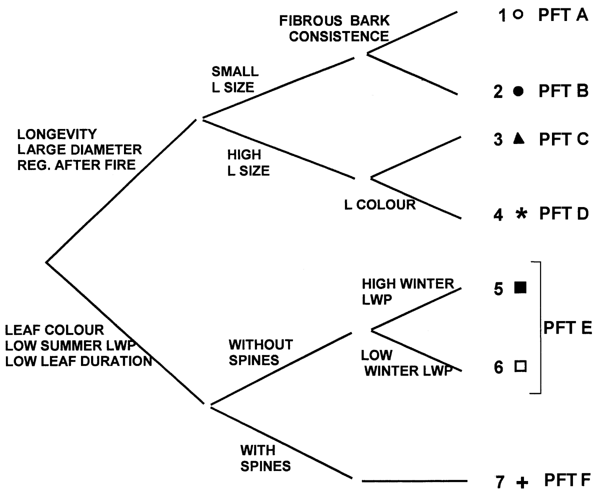

Fig. 3. Plant functional types defined by the TWINSPAN-analysis of the traits × species matrix and the main trait indicators for each division. See text for abbreviations.

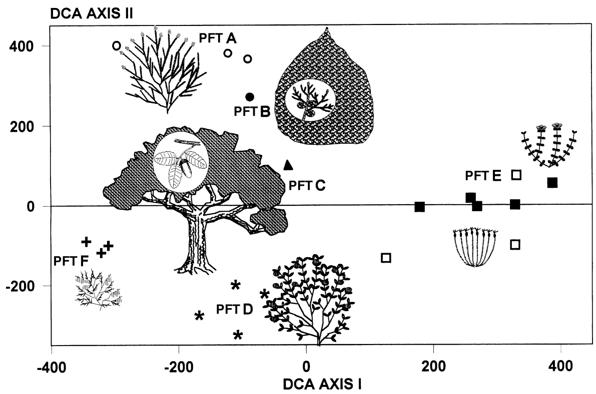

Fig. 4. DCA-ordination of the traits × species matrix; the PFTs distinguished by TWINSPAN are shown and a schematic drawing of example species is presented.

by cork and large leaves, which are sclerophyllous and pubescent on the under side. The trees sprout after fire (Pausas 1997). This tree is drought-resistant and it can grow on very poor soils, due to its structural and physiological xerophytic adaptations (Oliveira et al. 1992). It forms woodlands rarely exceeding 5 m in height. This type is associated with the drier outcrops (sand bars) of the stabilized dunes.

PFT D: Shrubs of mature scrub. Plants have large and tall canopies, a long life span, high leave maintaining costs – leaves can be kept for more than one year. Fruits are fleshy (drupe or berry). Plants sprout after fire. Leaf water potential is high (less negative) in winter and summer. Species in this group include *Daphne gnidium, Myrtus communis, Phillyrea angustifolia* and *Pistacia lentiscus.*

PFT E: Pioneer shrubs with small canopies, hairy leaves, zoophyllous pollination, dry fruit type, and no underground stems They generally do not sprout after fire but germination is stimulated by fire (Lloret 1998; Clemente et al. 1996) and they show low leaf water potential figures in summer, which can reach values lower than – 8 MPa. Species of this type are *Cistus libanotis*, *C. salvifolius, Halimium commutatum, H. halimifolium, Helichrysum picardii, Lavandula stoechas, Rosmarinus officinalis* and *Thymus mastichina.*

PFT F: Legume shrubs with spines or thorns – *Stauracanthus genistoides, Ulex minor* and *U. australis*. Leaves are absent or very much reduced in size and short-lived, a feature which allows the species of this type to maintain less negative water potentials. They can both sprout after fire and establish from seeds. Spinyness can be an adaptation to withstand summer drought. We have measured high leaf water potentials in some of these species in summer in the drier areas. Terradas (1991) suggested that spines are probably an adaptation in order to reduce herbivory and to maintain positive total carbon budgets. Browsing of new twigs can result in a cushion-like canopy.

From PFTs to ecosystem function

The ordination of the traits × sites matrix closely resembles that of the floristic gradient in relation to water table level. DCA-axis 1 is associated with the depth of the water table. Only the group of plots with *Juniperus phoenicea*, linked to the driest areas, is located in an unexpected position, in the middle of the gradient (Fig. 5).

Two groups of traits seem to be related to both extremes of the main gradient: at the left extreme of the fist ordination axis we find small shrub species, obligate seeders after fire, with hairy leaves, negative leaf water potentials, lower costs of leaf production, at the right extreme we find the larger shrub species with many small leaves per stem length, less negative leaf water potentials, higher costs of leaf growth, and with underground stems and vegetative regeneration after fire.

Traits corresponding to mature scrub and *Quercus* woodland, have a lower weight in this analysis, because of the degree of disturbance of the vegetation, which reduces the occurrence of these plant types to small patches in Doñana National Park.

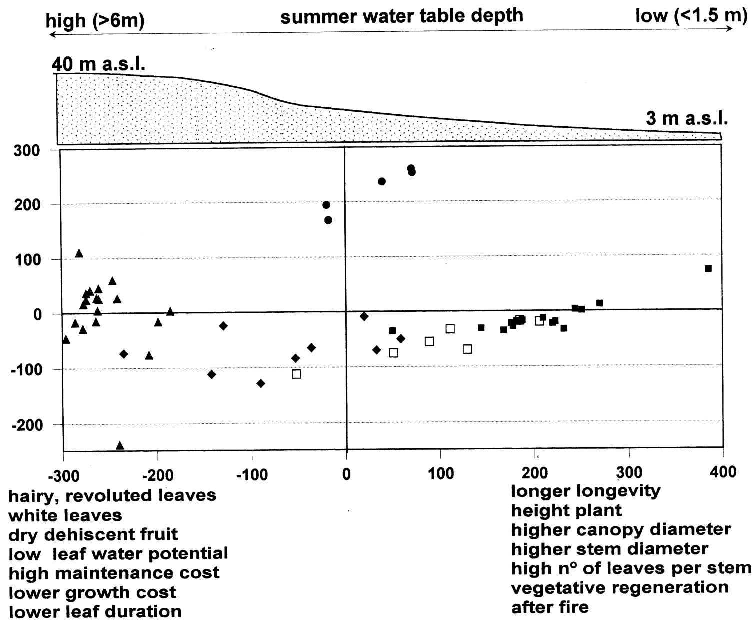

Fig. 5. DCA-ordination of the traits × sites matrix. The main gradient of topography and water table depth is also displayed in the figure. The symbols represent the groups of plots following the TWINSPAN-analysis of the floristic matrix. Filled circles: *Juniperus* woodland; triangles: xerophytic shrubland of the top of the dune, rhomboids: xerophytic shrubland of the dune slope, open squares: hygrophytic scrub of the dune valleys, filled squares: hygrophytic scrub of the depressions.

Discussion

In previous classifications of Mediterranean woody plants two main groups were distinguished, which correspond to our PFT D (tall shrubs) and PFT E (pioneer shrubs). Margaris (1981) suggested two main adaptation syndromes, *maquis* species, corresponding to typical sclerophyllous woody plants and *phrygana* species (equivalent to the 'botha', 'tomillares', 'barrocales', 'garrigue' and similar vegetation types). Similar views have been discussed by Orshan (1989) and Terradas (1991). The maquis plants, which maintain the same kind of leaves throughout the year, may be equivalent to PFT D, while phrygana plants, characterized by a marked seasonal leaf heteromorphism may be equivalent to PFT E.

The classification of Herrera (1984, 1992) only considered two large functional types: type I which corresponds to pioneer species with large flowers and non-edible fruits (PFT E) and type II which is related to mature scrub with small flowers and fleshy fruits (PFT D).

These previous classifications with two large PFTs, offer no place for many Mediterranean shrub species, as these do not fit either category. Our results suggest that the two-group classification may be enlarged so as to distinguish four new PFTs: A, B, C and F.

The analysis of the traits × sites matrix emphasizes the role of plant features in the ecosystem. The main trend of variation as reflected by the DCA-analysis (axis 1) is related to a gradient of water table depth, where plots dominated by xerophytic scrub appear in one end of the gradient, and plots of hygrophytic scrub occupy the other end. However some patterns emerge as described below.

The second trend of variation (axis 2) seems to be related to successional stages. Plots dominated by *Juniperus phoenicea,* which occur in the driest areas, appear in the middle of the water availability gradient and at the upper end of axis 2. Formations of *J. phoenicea* represent the climax stage of succession in the dry habitats of the stabilized dunes in the Park (Villar et al. 1997).

The results of this analysis do not discriminate mature scrub from *Quercus suber* woodlands because the latter are of little importance in the ecosystems of the Park. It is known that *Q. suber* populations have decreased in the Mediterranean, mainly due to improper land and crop management (Oliveira et al. 1992). In the low-lying areas of Doñana, the former woodland type was composed of *Q. suber*. Lumbering, prescribed fires and overgrazing destroyed most of these woodlands which formerly dominated the Park vegetation (Granados et al. 1988), and reduced them to small remnant thickets. Forest degradation has also resulted in destruction of the rich organic original soil and in impoverishment of the sandy soils (García Novo 1997).

A hypothetical model of the ordination of the traits × sites matrix would be formed by two parallel lines along the DCA-axis I, both representing the water availability gradient of vegetation. One of the lines would represent low shrub species – r-strategists – and the other one taller woody species of woodland and mature scrub – K-strategists. Thus, human disturbance leads to this substitution of K-strategists by r-strategists, a process which is very old in Mediterranean habitats. Maquis-type isomorphic plants in mature communities are K-strategists, with slow energy use, while garrigue-type pioneer stages in disturbed sites can follow r-strategies (Terradas 1991).

In Doñana, as in other areas of the Mediterranean basin, the vegetation is a mosaic of pioneer communities with patches of mature scrub and *Quercus suber* formations. The recovery of the original forest through the protection of areas with scrub is not possible because the formerly rich soils have been destroyed. Scrub communities remain stable nowadays and they have diversified towards different types of PFTs, which in our model correspond to PFTs A, E and F.

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References

Ales E.E. 1993. *Sindromes ecológicos en la vegetación de matorral*. Ph.D. Thesis, Universidad de Sevilla.

Clemente, A.S., Rego, F.C. & Correira, O.A. 1996. Demographic patterns and productivity of post-fire regeneration in Portuguese Mediterranean maquis. *Int. J. Wildland Fire* 6: 5-12.

Díaz, S. & Cabido, M. 1997. Plant functional types and ecosystem function in relation to global change: an multiscale approach. *J. Veg. Sci.* 8: 463-474.

Díaz, S., Cabido, M. & Casanoves, F. 1998. Plant functional traits and environmental filters at regional scale. *J. Veg. Sci.* 9: 113-122.

Fernández Alés, R., Laffarga, J.M. & Ortega, F. 1993. Strategies in Mediterranean grassland annuals in relation to stress and disturbance. *J. Veg. Sci.* 4: 313-322.

Gallego Fernández, J.B., Ales, E.E. & García Novo, F. 1997. *Application and ecological roles of morpho-functional syndromes to the Mediterranean shrubland in abandoned cultural landscape of the Sierra de Grazalema (South Spain)*. Conference Abstracts IAVS Symposium Ceske Budejovice, August 1997.

García Mora, M.R., Gallego-Fernández, J.B. & García-Novo, F. 1999. Plant functional types in coastal foredunes in relation to environmental stress and disturbance. *J. Veg. Sci.* 10: 27-34.

García Novo, F. 1977. The effects of fire on the vegetation of Doñana National Park. In: Mooney H.A. & Conrad, C.E. (eds.) *Proc. Symp. Environmental Consequences of Fire and Fuel Management in Mediterranean Ecosystems*, USDA For. Serv. Gen. Techn. WO-3. U.S. Department of Agriculture, California, pp. 318-325.

García Novo, F. 1997. The ecosystems of Doñana National Park. In: García Novo, F., Crawford, R.M.M. & Díaz Barradas, M.C. *The ecology and conservation of European dunes*, pp. 97-116. Universidad de Sevilla, Sevilla.

García Novo, F. & Merino, J. 1997. Pattern and processes in the dune system of Doñana National Park, South-western Spain. In: van der Maarel, E. (ed.) *Dry coastal ecosystems. Part C. General aspects*, pp. 453-468. Elsevier, Amsterdam.

García Novo, F., Zunzunegui, M., Muñoz Reinoso, J.C., Gallego Fernández, J.B. & Díaz Barradas, M.C. 1996. Surface and groundwater control on ecosystem development: the case of Doñana National Park (SW Spain). In: Cruz San Julian, J. & Benavente J. (eds.) *Wetlands: A multiapproach perspective*, pp. 81-101. Universidad de Granada, Granada.

Gitay, H. & Noble, I.R. 1997. What are plant functional types and how should we seek them? In: Smith, T.M., Shugart, H.H & Woodward, F.I. (eds.) *Plant functional types*, pp. 3-19. Cambridge University Press, Cambridge.

Granados Corona, M., Martín Vicente, A. & García Novo, F. 1988. Long-term vegetation changes on the stabilized dunes of Doñana National Park (SW Spain). *Vegetatio* 75: 73-80.

Grime, J.P. et al. 1996. Functional types: testing the concept in Northern England. In: Smith, T.M., Shugart, H.H. & Woodward, F.I. (eds.) *Plant functional types*, pp. 122-150. Cambridge University Press, Cambridge.

Herrera, C. 1984. Tipos morfológicos y funcionales en plantas del matorral mediterráneo en el sur de España. *Stud. Oecol.* 5: 7-34.

Herrera, C. 1992. Historical effects and sorting processes as explanations for contemporary ecological patterns: character syndromes in mediterranean woody plants. *Am. Nat.* 140: 421-446.

Keddy, P.A. 1992. Assembly and response rules: two goals for predictive community. *J. Veg. Sci.* 3: 157-164.

Lloret, F. 1998. Fire, canopy cover and seedling dynamics in Mediterranean shrubland of northeastern Spain. *J. Veg. Sci.* 9: 417-430.

Margaris, N.S. 1981. Adaptative strategies in plants dominating Mediterranean-type ecosystems. In: di Castri, F., Goodall, D.W. & Specht, R.L. (eds.) *Mediterranean shrublands*, pp. 309-315. Elsevier, New York, NY.

Martínez García, F. & Rodríguez J.M. 1988. Distribución vertical de las raíces del matorral de Doñana. *Lagascalia* 15: 549-557.

Martínez, F., Merino, O., Martín, A., García Martín, D. & Merino, J. 1998. Belowground structure and production in a Mediterranean sand dune shrub community. *Plant Soil* 201: 209-216.

Merino, J. 1987. The cost of growing and maintaining leaves of Mediterranean plants. In: Tenhunen, J.D., Catarino, F.M., Lange, O.L. & Oechel, W.C. (eds.) *Plant response to stress: functional analysis in Mediterranean ecosystems*, pp. 553-564. Springer-Verlag, Berlin, Heidelberg.

Merino, J., García Novo, F. & Sánchez Díaz, M. 1976. Annual fluctuation of water potential in the xerophitic shrub of Doñana Biological Reserve (Spain). *Oecol. Plant.* 11: 1-11.

Merino, O., Villar, R., Martín, A., García, D. & Merino, J. 1995. Vegetation response to climatic change in a dune ecosystem in Southern Spain. In: Moreno, J.M. & Oechel, W.C. (eds.) *Global change and mediterranean type eco-*

systems. Ecological Studies 117, pp. 225-238. Springer-Verlag, New York, NY.

Muñoz Reinoso, J.C. 1997. *Patrón espacio temporal del matorral de la reserva biológica de Doñana y sus relaciones con el acuífero Almonte-Marisma.* Ph.D. Thesis, Universidad de Sevilla, Sevilla.

Noble, I.R. & Gitay, H.A. 1996. A functional classification for predicting the dynamics of landscapes. *J. Veg. Sci.* 7: 329-336.

Oliveira, G., Correia, O.A., Martins-Louçâo, M.A. & Catarino, F.M. 1992. Water relations of cork-oak (*Quercus suber* L.) under natural conditions. *Vegetatio* 99-100: 199-208.

Orshan, G. (ed.) 1989. *Plant pheno-morphological studies in Mediterranean type ecosystems.* Kluwer Academic Publishers, Dordrecht.

Pausas, J.G. 1997. Resprouting of cork-oak (*Quercus suber* L.) after fire in NE Spain. *J. Veg. Sci*. 8: 703-706.

Skarpe, C. 1996. Plant functional types an climate in a southern African savanna. *J. Veg. Sci.* 7: 397-404.

Specht, R.L. (ed.) 1988. *Mediterranean-type ecosystems a data source book.* Kluwer Academic Publishers, Dordrecht.

Terradas, J. 1991. Mediterranean woody plant growth-forms, biomass and production in the eastern part of the Iberian Peninsula. In: Ros, J.D. & Prat, N. (eds.) Homage to Ramón Margalef; or Why is such pleasure in studying nature. *Oecol. Aquat.* 10: 337-349.

Tsiourlis, G.M. 1992. Etude d'un écosystème de maquis à *Juniperus phoenicea* L. (Naxos, Cyclades, Grèce): Structure spatiale et phytomasse des appareils racinaires. *Bull. Ecol.* 23: 71-81.

Valdés, B., Talavera, S. & Fernández Galiano, E. (eds.) 1987. *Flora vascular de Andalucía Occidental.* Ketres Editora, Barcelona.

Vilà, M. 1997. Effect of root competition and shading on resprouting dynamics of *Erica multiflora*. *J. Veg. Sci*. 8: 71-80.

Villar, R., Martínez, F., Martín, A. & Merino, J. 1997. Biomass of the *Juniperus phoenicea* forest in the sand dune ecosystems of the Doñana National Park. In: García Novo, F.; Crawford, R.M.M. & Díaz Barradas, M.C. (eds.). *The ecology and conservation of European dunes*, pp. 135-141. Universidad de Sevilla, Sevilla.

Walker, B.H. 1992. Biodiversity and ecological redundancy. *Conserv. Biol.* 6: 18-23.

Woodward, F.I. & Cramer, W. (eds.). 1996. Plant functional types and climatic change. *J. Veg. Sci.* 7: 305-430.

Zunzunegui, M., Díaz Barradas, M.C. & García Novo, F. 1998. Vegetation fluctuation in Mediterranean dune ponds in relation to rain fall variation and water extraction. *Appl. Veg. Sci.* 1: 151-160.

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