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.


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.
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.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Description</th>
<th>Classes in the matrix</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age</td>
<td>Average plant age</td>
<td>1 = 5 - 25; 2 = 25 - 50; 3 = 50 - 100; 4 = &gt; 100</td>
</tr>
<tr>
<td>Height</td>
<td>Average plant height</td>
<td>1 = &lt; 60 cm; 2 = 60 -100 cm; 3 = 100 cm - 3 m; 4 = 3 - 5 m; 5 = &gt; m.</td>
</tr>
<tr>
<td>Diameter</td>
<td>Average canopy diameter</td>
<td>1 = &lt; 50 cm; 2 = 50 -100 cm; 3 = 1 - 2 m; 4 = 2 - 3 m; 5 = &gt; 3.5 m</td>
</tr>
<tr>
<td>Leaf size</td>
<td>Average leaf area</td>
<td>1 = &lt;0.10 cm²; 2 = 0.10 - 0.25 cm²; 3 = 0.25 - 0.25 cm²; 4 = 0.25 - 12.25 cm²</td>
</tr>
<tr>
<td>Leaf colour</td>
<td>1 = all green; 2 = green and white; 3 = all white</td>
<td></td>
</tr>
<tr>
<td>Leaf margin</td>
<td>1 = entire; 2 = revolute; 3 = lobed</td>
<td></td>
</tr>
<tr>
<td>Leaf hairs</td>
<td>1 = malacophyll; 2 = semi-sclerophyll; 3 = sclerophyll</td>
<td></td>
</tr>
<tr>
<td>Leaf texture</td>
<td>1 = not hairy; 2 = hairy lower side; 3 = hairy upper side</td>
<td></td>
</tr>
<tr>
<td>L/S</td>
<td>No. of leaves per 10 cm of stem</td>
<td>1 = &lt; 10; 2 = 10 - 20; 3 = 20 - 50; 4 = 0 - 100; 5 = 100</td>
</tr>
<tr>
<td>Stem diameter</td>
<td>Measured at ground level</td>
<td>1 = &lt; 2 cm; 2 = 2 - 5 cm; 3 = 5 - 10 cm; 4 = &lt; 20 cm</td>
</tr>
<tr>
<td>Bark consistency</td>
<td>1 = smooth; 2 = fibrous; 3 = corky</td>
<td></td>
</tr>
<tr>
<td>Spines</td>
<td>1 = absent; 2 = with spine</td>
<td></td>
</tr>
<tr>
<td>Underground stem</td>
<td>1 = lignotubers; 2 = others</td>
<td></td>
</tr>
<tr>
<td>Root morphology</td>
<td>1 = tap root; 2 = horizontal roots; 3 = vertical - horizontal roots</td>
<td></td>
</tr>
<tr>
<td>Root depth</td>
<td>1 = &lt; 25 cm; 2 = 25 - 50 cm; 50 - 100 cm; 4 = &gt; 100 cm</td>
<td></td>
</tr>
<tr>
<td>Regeneration</td>
<td>Vegetative regeneration after fire</td>
<td>1 = plant killed; 2 = from epicormic buds; 3 = from non epicormic buds; 4 = from epicormic and non epicormic buds</td>
</tr>
<tr>
<td>Fruit dehiscence</td>
<td>1 = dry indehiscent; 2 = dry dehiscent; 3 = fleshy indehiscent; 4 = fleshy</td>
<td></td>
</tr>
<tr>
<td>Fruit type</td>
<td>1 = capsule; 2 = cone; 3 = nutlet; 4 = legume; 5 = achene; 6 = drupe; 7 = berry Pol.</td>
<td></td>
</tr>
<tr>
<td>Slwp</td>
<td>Type of pollination</td>
<td>1 = zoophyllous; 2 = anemophyllous</td>
</tr>
<tr>
<td>Wlwp</td>
<td>Summer leaf water potential</td>
<td>1 = &lt; -2 MPa; 2 = -2 - -3 MPa; 3 = -3 - -4.5 MPa; 4 = -4.5 - -4.5 MPa</td>
</tr>
<tr>
<td>Winter leaf water potential</td>
<td>1 = &lt; -0.5 MPa; 2 = -0.5 - -0.6 MPa; 3 = -0.6 - -0.7MPa; 4 = -0.7 MPa</td>
<td></td>
</tr>
<tr>
<td>Cost of growth</td>
<td>Cost of leaf growth</td>
<td>1 = &lt; 1.5; 2 = 1.5 - 1.6; 3 = &gt; 1.8 g glucose (gdw)^{-1}</td>
</tr>
<tr>
<td>Cost maintenance</td>
<td>Cost of leaf maintenance</td>
<td>1 = &lt; 0.0130; 2 = 0.0130 - 0.0140; 3 = &gt; 0.0140 g glucose (gdw)^{-1} day^{-1}</td>
</tr>
</tbody>
</table>


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 TWINSPLAN) 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 TWINSPLAN 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 TWINSPLAN 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 ladanifera, 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. Hydrophytic scrub of the dune valleys, with a water table depth between 1 and 2 m. Dominant species are Calluna vulgaris, Cistus salviifolius, Daphne girdium, Erica scoparia, Myrtus communis and Phillyrea angustifolia.
5. These hydrophytic areas present occasional patches with Pistacia lentiscus and Quercus suber.
6. Hydrophytic 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.
We distinguished seven PFTs on the basis of the TWINSPAN-classification of the traits \times 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, which are obligate seeders after fire (positive end), vs. sprouters with many small leaves per stem length (negative end). 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
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 leaf 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 g nidium*, *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. salvi folius*, *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 first 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.
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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