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REGULAR PAPER

A comparative study of leaf trait relationships in coastal dunes in southern Spain

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Background and aims – Coastal dunes of southern Spain are an original Mediterranean ecosystem, hotspot of biodiversity, insufficiently studied under the functional ecology. We explore co-variation patterns among leaf traits (size, specific leaf area (SLA), nutrient concentrations (N, P, K…), deciduousness and leaf consistence), and growth form in 78 native coastal dune species.
Methods – Three coastal dunes of contrasting climatic conditions were sampled and differentiated between fixed and mobile dunes. Species were classified based on growth form, deciduousness and leaf consistence. Leaf samples were collected following Cornelissen et al. (2003) and soil samples were also analysed by ICP-OES and elemental analysis.
Key results – Positive co-variation patterns of SLA and leaf [N], and of leaf [N] and leaf [P], were found in two of three sites. Fixed dunes, with a higher proportion of large shrubs, evergreens, and sclerophyllous species, had lower values of SLA and foliar nutrients, and higher values of [C] than mobile dunes. The topsoil of fixed dunes had less [Ca] than in mobile dunes and this was reflected in foliar concentrations. The Mediterranean-subdesert dunes, had a distinct pattern of trait variation.
Conclusion – Mediterranean-subdesert coastal dunes are characterized by lower values of leaf [N] and higher values of leaf [Ca] and [Fe] than in other Mediterranean ecosystems and by a broad correlation among SLA, leaf [N], [P] and [K]. Mediterranean-subdesert dunes showed a predominance of xerophytic malacophyllous strategy, whereas Mediterranean -oceanic dunes are dominated by stress tolerant species. Mobile dunes showed a leaf strategy closer to the observed on Mediterranean -subdesert dunes but with a relevantly higher leaf [Ca].

Key words – Mediterranean coastal dunes, specific leaf area, leaf nutrient concentrations, leaf consistence, deciduousness.

INTRODUCTION

Leaf functional traits such as leaf structure and nutrient content are key determinants of biogeochemical cycles that link soil, climate and atmosphere (Reich et al. 2007). Thus, characterization of leaf functional traits is an important tool in the prediction of ecosystem functioning (Norby & Luo 2004, He et al. 2006).

Previous researches have revealed strong relationships among a suite of leaf functional traits, which have been referred to as "leaf economics spectrum" (Wright et al. 2004). These relationships have been interpreted as evidence of coordinated leaf physiological strategies, reflecting adaptive strategies and/or biomechanical constraints (Ackerly & Reich 1999). In general, leaf economic spectrum runs from species with cheaply constructed leaf area but short duration return on investment, to species with low specific leaf area (SLA) and long leaf lifespan. Higher nitrogen and phosphorous concentration are associated with high SLA (Wright et al. 2004). High values of SLA have also been associated to productive habitats, whereas low values are characteristic of unproductive habitats in which the mean residence time of nutrients tends to be maximized through longer leaf longevity (Lavorel & Garnier 2002). Contrasting leaf traits have also been found among major functional groups. Herbs and deciduous trees tend towards the higher SLA and evergreen shrubs and trees towards the lower SLA, but there is wide overlap between growth forms (Westoby & Wright 2006).

Leaf nitrogen [N] is the mineral element that plants require in the largest amounts. It is integral to the proteins of photosynthetic machinery and it is, in addition with phosphorous [P], a constituent of many plant cell components,

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including amino and nucleic acids (Wright et al. 2005, Hu & Schmidhalter 2005). Other nutrients such as K, Ca, Fe, Mg and Mn are less often studied in relation to leaf functional traits (Niinemets & Kull 2003). Mineral nutrient concentrations in leaves vary depending on genetic factors and phylogenetic constraints (Broadley et al. 2003), but they are also influenced by local soil conditions (Hobbie & Gough 2002).

Considerable attention has been focused on the ecological significance of leaf size (LS) variation (Givnish & Vermeij 1976, Chiariello 1984). Leaf size directly affects light interception and leaf balance, and leaves are often smaller in species occupying habitats with high light, low nutrients and low moisture availability (e.g. Körner et al. 1991, Niinemets & Kull 1994), conditions that are also associated with thick leaves, low nitrogen content and low photosynthetic rates (Reich et al. 1992).

Although Mediterranean-type ecosystems provide a good scenario for examining the relationships between leaf traits (Ackerly et al. 2002), scarce reports have been published on leaf trait relationships in the Mediterranean coastal dunes. Coastal dune systems are defined by particular environmental conditions such as the wind, drought, salt spray, soil salinity, high intensity of light and temperature and low nutrient content (Ley Vega de Seoane et al. 2007, Fenu et al. 2012), which involve specific functional strategies that characterize its particular vegetation (García-Mora et al. 1999, Ley Vega de Seoane 2007). Additionally, their conservation statement involves a second reason of interest for its functional study. Coastal dunes are extremely fragile and very vulnerable to the human activity, which is particularly striking in the Mediterranean (Curr et al. 2000). The current situation of coastal dune ecosystems constitutes a serious danger for all the ecosystem services that they provide, such as protection against sea waves, wind, floods or erosion (Kiehl & Isermann 2007) and for the survival of the important habitats and endangered species they include. This is the case of coastal dunes with *Juniperus* sp. or Atlantic decalcified fixed dunes (*Calluno-Ulicetea*), which are catalogued as habitats of priority interest according to Red Natura 2000 (VV.AA. 2009).

The objective of this study was to explore, for the very first time, patterns of (co)variation of leaf functional traits in 78 perennial species on coastal dunes in southern Spain with differences within the Mediterranean macroclimate (Mediterranean-oceanic, Mediterranean-subtropical, Mediterranean-subdesert) and between dune sectors (mobile semi-fixed and fixed dunes). We test the hypothesis that coastal dunes could be differentiated from other habitats in terms of the leaf economic spectrum, based on its particular environmental conditions (such as soil nutrient content). We also test the hypothesis that leaf functional patterns in coastal dunes are affected by climate and sea proximity and that there are different leaf functional patterns related to the functional groups which are represented in these ecosystems.

MATERIAL AND METHODS

Study area

The study was carried out in three coastal dunes in Souther Spain with different Mediterranean climate (DERA 2013): Parque Natural (P.N.) del Estrecho in Cádiz (Mediterranean-oceanic climate) (52 species), Monumento Natural (M.N.) de Artola-Cabopino in Málaga (Mediterranean-subtropical) (34 species) and P.N Cabo de Gata-Níjar in Almería (Mediterranean-subdesert) (24 species) (fig. 1).

Climatic data were obtained from Rivas-Martínez (1996–2009). In P.N. del Estrecho, the average annual rainfall is 794 mm, with maximum values in November (133 mm) and minimum in August (0 mm). Annual temperatures are milder than in the other two dunes (mean-minima of 13.4°C in January and mean-maxima of 23.5°C in August). M.N. Artola-Cabopino shows an average annual rainfall of 659 mm, with similar rainy season to P.N. del Estrecho. January was also the coldest month (mean-minima of 12.5°C) and August the hottest (mean-maxima 24.5°C). P.N Cabo de Gata-Níjar shows the driest dunes (average annual rainfall of 308 mm) and a different rainy season (maximum rainfall values are observed in March and December, 40 mm). The seasonal amplitude of temperature is different from the other studied dunes, with mean-minima of 10.8°C in January and mean-maxima of 25.9°C in August.

Three dunes sectors were recognized, depending on the distance from the sea and which have contrasting vegetation structure (e.g. Brown & McLachlan 1994, Van der Maarel 1997). In this study, the nomenclature of dune sectors was the one based up on sands mobility (Van der Maarel 1993): fixed dunes, semi-fixed and mobile dunes. However, the two last dunes were unified in this work in one common sector. Fixed dunes are formed by shrubs and trees and represent the mature stage of the ecosystem. Mobile semi-fixed dune vegetation is constituted by communities of herbs and small shrubs, which are adapted to the intense disturbance that is associated to the proximity of the sea (Costa-Pérez & Valle-Tendero 2004, Ley Vega de Seoane 2007).

Samples and measurements

Data were gathered for 78 major representative perennial species with the highest cover values (Van der Maarel 1993, Costa-Pérez & Valle-Tendero 2004, Navarro et al. 2006) in the period of 2009–2012. Voucher specimens of the studied species were stored in the MGC Herbarium. Botanical nomenclature follows Castroviejo (1986–2007).

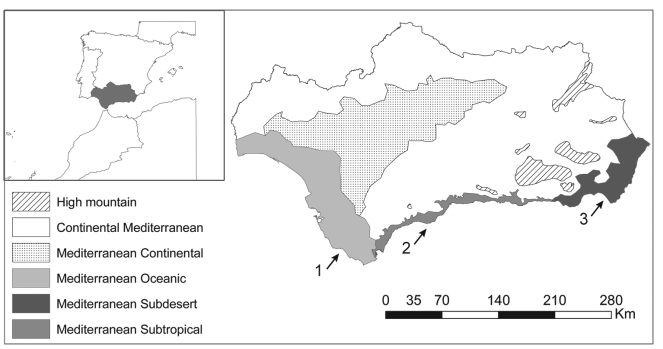


Figure 1 – Different climates in southern Spain and study areas. Black arrows show the study areas: 1, P.N. del Estrecho; 2, M.N. Artola-Cabopino; 3, P.N. Cabo de Gata-Níjar. Data source: DERA (2013).

We classified each species based on growth form, deciduousness and leaf consistence, which yielded different major functional groups of species. These functional groups provided the possibility of describing natural correlations between leaf functional traits. Within growth forms, we distinguished trees (woody plants with main canopy elevated on a substantial trunk), larger shrubs (woody plants taller than 0.8 m with main canopy deployed relatively close to the soil surface on one or more relatively short trunks), small shrubs (woody plants up to 0.8 m tall) and perennial herbs (not woody plants). Within deciduousness, we differentiated among deciduous species (plants which lost their leaves during a determinate period of time), semi-deciduous (plants which reduced their green structures during summer to brachyblasts) and evergreen species (plants that maintain their leaves along the year). Finally, species were differentiated according to their leaf consistence by distinguishing between malacophyllous (soft leaves) and sclerophyllous (hard leathery leaves).

Leaf samples were collected by following the methodology of Cornelissen et al. (2003). Fully expanded and hardened leaves were collected throughout the year (mainly in spring) from random adult plants in full-light situations and without obvious symptoms of pathogen, herbivore attack or substantial cover of epiphylls. Between ten and twenty leaves were collected from at least five individuals of each species. Leaves were transported to the laboratory in plastic bags and stored in low temperatures (2–6°C) during less than 24 hours prior to measurements.

Soil samples were collected in the three different dune sectors (fixed, semi-fixed and mobile) at each location (P.N. del Estrecho, M.N. Artola-Cabopino and P.N. Cabo de Gata-Níjar) in spring 2010. They were randomly taken in three replicates in the 0–20 cm soil layer under the canopy covered zone in fixed dunes, and in the proximity of shrub stumps in mobile and semi-fixed dunes. The three replicates of each sample were air dried and individually processed for chemical analysis. Soil samples were extracted in $AcNH_4$ pH 7 (for major nutrients: Ca, Mg, K), or with $AcNH_4$-EDTA pH 8.5 for [Fe], [Mn] and [P]. Nutrients were determined by ICP-OES, except [N] whose concentration was obtained by elemental analyser.

Leaf size (LS) was measured by scanning and digitalizing fresh leaves. Images were subsequently processed using Visilog 6.3 image analysis software. For the measurements of leaf size, leaf laminas (or leaflets in compound leaves) without petiole or rachis were analysed, whereas for calculating specific leaf area (SLA), entire leaves were used (Cornelissen et al. 2003). Leaf size of species was differentiated in Raunkiær-Orshan classes (Orshan 1989). Leaf dry mass was determined after oven drying at 60°C for at least 72 h. Specific leaf area is the one-sided area of a fresh leaf divided by its oven-dry mass (Cornelissen et al. 2003).

To determine the leaf nutrient contents, dried leaves from SLA analysis were used after removing any petiole or rachis (Cornelissen et al. 2003). These leaves were ground with a mortar and pestle. [N] and [C] were obtained by elemental analyser (Perkin-Elmer 2400), whereas the rest leaf nutrients (Ca, K, Fe, Mg, Mn and P) were determined by dissolving in concentrated HCl and subsequently analysed with ICP OES (Varian Vista MPX).

Data analyses

All statistical analyses were performed with SPSS 15.0 (SPSS Inc). Continuous characters (leaf nutrient content, LS and SLA) were $\log_{10}$-transformed prior to statistical analysis in order to normalise their distributions. Kolmogorov-Smirnov test confirmed the normality assumptions ($P > 0.05$).

We used MANOVA to examine responses of leaf traits to functional groups. The MANOVA model included growth forms (four levels), deciduousness and leaf consistence (two levels each) as fixed effects, leaf traits (leaf size, specific leaf traits and leaf nutrient content) as dependent factor, and all interactions. If a MANOVA was significant, we then conducted protected univariate tests to examine how each response variable was affected by treatments (Scheiner 1993).

Linear correlation and regression techniques were used to analyse the relationship among leaf traits.

Two-way ANOVA and nonlinear principal components analysis (NLPCA, de Leeuw 1982) were performed for the differentiation among functional traits in coastal dunes. It was performed by the program CATPCA, included in the software SPSS 15.0 (SPSS Inc). NLPCA can handle variables of different type simultaneously and deal with nonlinear relationships between variables. Alpha of Cronbach was calculated (Cronbach 1951) for each extracted component. If this value was high to a specific component, it would be interpreted as an indicator of the weight of the component. In addition, it serves to explain the total variance. In general, an alpha value of 0.7 or greater is considered reliable (Bland & Altman 1997).

RESULTS

In coastal dunes in southern Spain shrubs with malacophyllous and deciduous or semi-deciduous leaves were predominant (table 1).

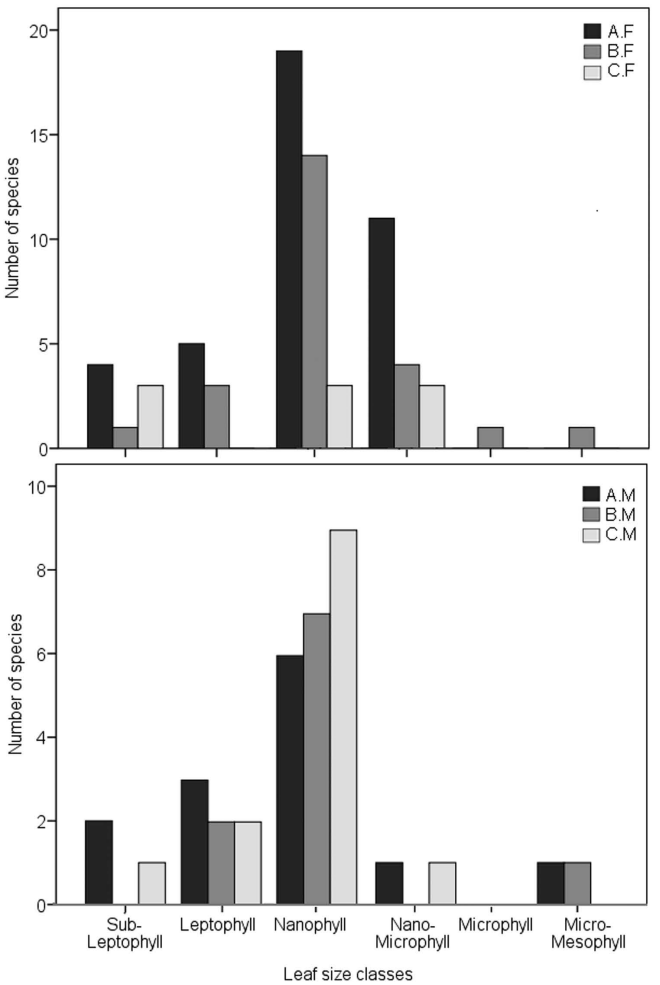
Soil characteristics of the study areas are included in table 2. Site differences in soil nutrient content resulted from significantly higher [Ca] in mobile semi-fixed dunes in P.N. Cabo de Gata-Níjar (table 2) and higher [Mn] in M.N. Artola-Cabopino (table 2) than in the other dunes.

Leaf functional traits in coastal dunes

Leaf size (LS) spanned 10^4 ranges, from 10^{-2} to 10^2 cm^2 (electronic appendix 1). Maximum values were found in *Eryngium maritimum*, on M.N. Artola-Cabopino (36.4 cm^2), whereas species on P.N. Cabo de Gata-Níjar showed the minimum LS (0.03 cm^2) (e.g. *Thymelea hirsuta* and *Thymus hyemalis* on fixed dunes, *Salsola vermiculata* on mobile semi-fixed dunes). Nanophyll was the dominant leaf size class (from 70% of species on mobile semifixed dunes in M.N. Artola-Cabopino to 33.3% on fixed dunes in P.N. Cabo de Gata-Níjar) (fig. 2). Microphyll and micro-mesophyll species were shown in less than 10% of species in all the studied dunes (fig. 2).

Table 1 – Major functional groups for the studied species in coastal dunes in southern Spain.
F, fixed dunes; M, mobile and semi-fixed dunes.

	P.N. del Estrecho		M.N. Artola-Cabopino		P.N. Cabo de Gata-Níjar	
	F	M	F	M	F	M
Number of species	39	13	24	13	11	10
Growth forms						
Perennial herbs	1	5	1	3	0	5
Small shrubs	13	8	8	10	7	5
Large shrubs	19	0	10	0	4	0
Trees	6	0	5	0	0	0
Deciduousness						
Evergreen	17	1	10	3	5	1
Semi-deciduous	15	6	9	7	2	4
Deciduous	7	6	5	3	4	5
Leaf consistence						
Sclerophyllous	17	1	12	1	5	1
Malacophyllous	22	12	12	12	6	9



► **Figure 2** – Leaf size classes by Raunkiaer-Orshan (Orshan 1989). A, P.N. del Estrecho; B, M.N. Artola-Cabopino; C, P.N. Cabo de Gata-Níjar; F, fixed dunes; M, mobile and semi-fixed dunes.

Table 2 – Soil conditions (mean±sd) and variations (two-factor ANOVA) in coastal dunes in southern Spain.
Nutrients extracted by in $AcNH_4$ pH 7 (for major nutrients: Ca, Mg, K), or with $AcNH_4$-EDTA pH 8.5 for Fe, Mn and P. Soil N was obtained by elemental analysis. Summarized results of two-factor ANOVA testing the effect of dune climate (Mediterranean-oceanic, M-subtropical and M-subdesert) and dune sector (F: fixed dunes vs. M: mobile and semi-mobile dunes) on soil nutrient content are included in the table. For each analysis, F-values are shown. N, leaf [N]; Ca, leaf [Ca]; K, leaf [K]; Mg, leaf [Mg]; P, leaf [P]; Fe, leaf [Fe]; Mn, leaf [Mn]; n.s. (not significant) $P > 0.10$; · $P \leq 0.10$; * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

	pH	N %	Ca %	K %	Mg %	P %	Fe %	Mn %
Description								
P.N. del Estrecho (Mediterranean-oceanic climate)								
F	7.5	0.15 ± 0.01	1.57 ± 1.88	0.05 ± 0.06	0.15 ± 0.20	0.004 ± 0.004	0.011 ± 0.012	0.004 ± 0.004
M	8.5	0.01 ± 0.01	1.98 ± 0.15	0.02 ± 0.01	0.04 ± 0.01	0.008 ± 0.003	0.011±0.004	0.008 ± 0.003
M.N. Artola-Cabopino (M-subtropical climate)								
F	7.0	0.20 ± 0.01	1.10 ± 0.62	0.04 ± 0.03	0.07 ± 0.04	0.015 ± 0.012	0.021 ± 0.010	0.033 ± 0.021
M	7.8	0.07 ± 0.07	1.73 ± 0.05	0.03 ± 0.01	0.04 ± 0.003	0.005 ± 0.002	0.014 ± 0.003	0.018 ± 0.003
P.N. Cabo de Gata-Níjar (M-subdesert climate)								
F	8.0	0.09 ± 0.04	1.50±1.10	0.05 ± 0.04	0.04 ± 0.02	0.008 ± 0.002	0.013 ± 0.002	0.011 ± 0.003
M	7.6	0.09 ± 0.02	4.00±0.94	0.04 ± 0.01	0.05 ± 0.003	0.014 ± 0.001	0.009 ± 0.002	0.010 ± 0.001
Variation								
Dune climate		n.s.	3.7·	n.s.	n.s.	n.s.	n.s.	6.2*
Dune sectors		n.s.	22.4 **	n.s.	n.s.	n.s.	n.s.	n.s.
Interaction effect		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

Specific leaf area (SLA) spanned 10^2 ranges (electronic appendix 1), from 10^2 (maximum in *Corema album*, 390.5 cm^2g^{-1}) to 1 cm^2g^{-1} (minimum in *Calluna vulgaris*, 4.8 cm^2g^{-1}).

Leaf [C] concentration ranged from 55.6% in *Corema album* to 29.4% in *Lycium intricatum*. It was followed by leaf [N]–[Ca] > [K] > [Mg]. Leaf [N] was maximum in *Cytisus striatus* (4%) and minimum in *Thymus hyemalis* (0.7%). However, the other nutrients were even more variable among species, with the highest concentration being between 17–32 times the lowest (0.07–1.2% [Mg], 0.2–4% [K] and 0.2–6.1% [Ca]) (electronic appendix 1).

Leaf [P], [Fe] and [Mn] were shown in smaller concentrations than 10^{-1}%. Leaf [P] ranged from 0.04% (*Calluna vulgaris, Erica scoparia* and *Stauracanthus boivinii*) to 0.4% (*Frankenia laevis*), whereas [Mn] and above all, [Fe] were more variable among species. Mn showed differences of 20 times between the lowest and the highest values (from 0.001% in *Teucrium* sp. to 0.030% in *Phagnalon saxatile*) and Fe, even reach differences of 75 times (from 0.004% in *Rhamnus alaternus* and *Lonicera implexa* to 0.3% in *Silene niceensis* and *Phlomis purpurea*) (electronic appendix 1).

Correlations among leaf traits

The correlations explaining most variation were found in fixed dunes in M.N. Artola-Cabopino (electronic appendix 2). Leaf nutrients were mainly positively correlated among them and with SLA, but negatively with LS. The exception was leaf [C], which showed the contrary tendency in all the cases.

Particularly, in relation to the leaf economic spectrum, SLA and leaf [N] were positively correlated in P.N. del Estrecho and in M.N. Artola-Cabopino (fig. 3a). Leaf [N] and [P] were significantly correlated only in fixed dunes in P.N. del Estrecho (fig. 3b). Specific leaf area and leaf [P] were positively associated in fixed dunes in P.N. del Estrecho and M.N. Artola-Cabopino (fig. 3c). P.N. Cabo de Gata did not confirm any of these relationships, result which could be related to the low number of species in this study area and which may be analyze in future studies.

Variation of leaf traits among major functional groups

MANOVA showed that there were significant effects of growth forms (Wilk's $\lambda = 0.40$, $F = 2.20$; $df = 30, 180$; $P < 0.01$) and deciduousness (Wilk's $\lambda = 0.56$, $F = 2.03$; $df = 20, 122$; $P < 0.01$) on leaf traits, but that leaf consistence did not affect leaf traits (Wilk's $\lambda = 0.90$, $F = 0.67$; $df = 10, 61$; $P > 0.1$). In addition, there was also a significant growth form-by-deciduousness interaction (Wilk's $\lambda = 0.60$, $F = 1.77$; $df = 20, 122$; $P < 0.05$) as well as a significant leaf consistence-by-deciduousness interaction (Wilk's $\lambda = 0.48$, $F = 2.72$; $df = 20, 122$; $P < 0.0001$).

Subsequent univariate ANOVAs showed that leaf [C] and leaf size significantly increased from herbs to trees, whereas leaf [Ca] and specific leaf area significantly decreased (table 3). Deciduousness only showed significant effects on leaf [Ca], that significantly decreased from deciduous to evergreen (table 4). Leaves showing contrasting leaf consistence also showed significantly different nutrient content. The percentage of leaf [C] was higher in sclerophyll species, whereas other nutrient content, such as [N], [Ca], [K], [Mg] and [P], showed higher values in malacophyll species (table 4).

Variation of leaf traits among studied coastal dunes

Two-way ANOVA showed that comparing dunes with different climate, SLA, [Mg] and [Fe] were significantly higher in P.N. Cabo de Gata-Níjar, whereas M.N. Artola-Cabopino included the highest values of [Mn] (table 3, fig. 4). Between dune sectors, fixed dunes showed significantly higher

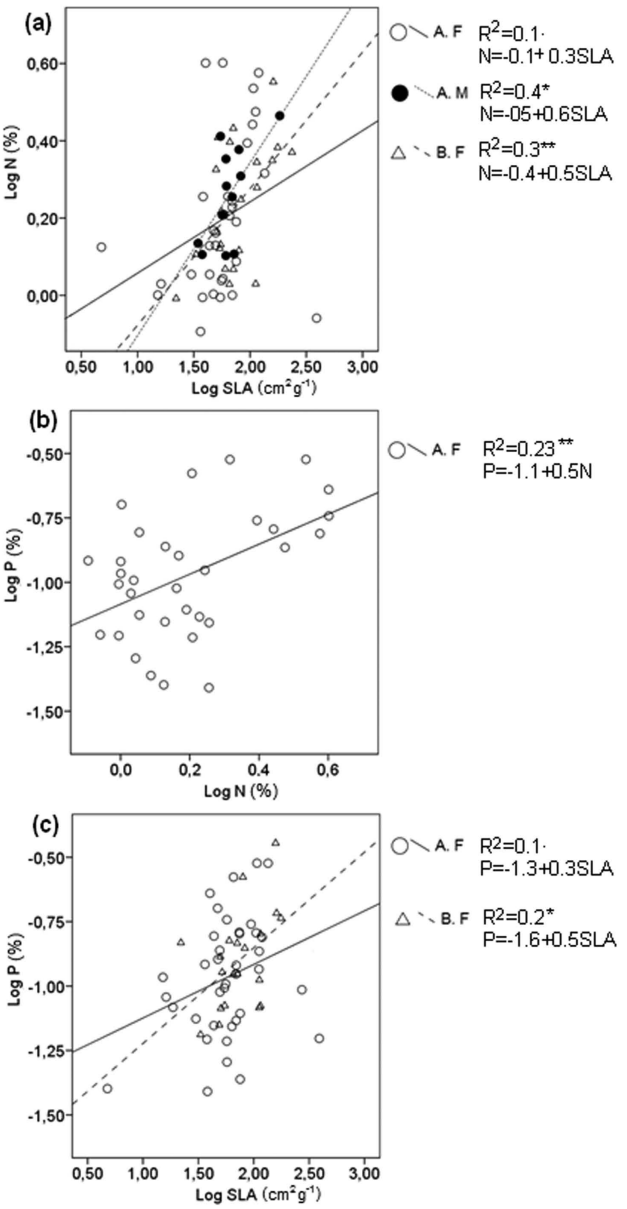


Figure 3 – Relationships between leaf [N], [P] and SLA in coastal dunes. r^2 are calculated for a linear dependence. Lines provide a regression equation fitted to the data from each analysed dunes. Only significant correlations are included. A, P.N. del Estrecho; B, M.N. Artola-Cabopino; F, fixed dunes; M, mobile and semi-fixed dunes. · $P \leq 0.10$, * $P \leq 0.05$, ** $P \leq 0.001$, *** $P \leq 0.0001$.

Table 3 – Summarized results of two-factor ANOVA testing the effect of dune climate (Mediterranean-oceanic, M-subtropical and M-subdesert) and dune sector (fixed dunes vs. mobile and semi-mobile dunes) on soil nutrient content.
For each analysis, F-values are shown. LS, leaf size; SLA, specific leaf area; C, leaf [C]; N, leaf [N]; Ca, leaf [Ca]; K, leaf [K]; Mg, leaf [Mg]; P, leaf [P]; Fe, leaf [Fe]; Mn, leaf [Mn]; n.s. (not significant) $P > 0.10$; · $P \leq 0.10$; * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

	Dune climate	Dune sector	Interaction effect
LS	1.1 n.s.	0.0001 n.s.	0.63 n.s.
SLA	6.01**	1.05 n.s.	0.20 n.s.
C	0.05 n.s.	21.61***	0.37 n.s.
N	0.86 n.s.	1.53 n.s.	0.04 n.s.
Ca	0.56 n.s.	9.99**	0.93 n.s.
K	0.69 n.s.	0.005 n.s.	0.89 n.s.
Mg	3.70*	15.88***	0.19 n.s.
P	0.87 n.s.	5.63*	0.98 n.s.
Fe	27.39***	0.46 n.s.	0.34 n.s.
Mn	5.51**	3.59·	0.01 n.s.

[C], while mobile and semi-fixed dunes were richer in [Ca], [Mg], [P] and [Mn] (table 3, fig. 4).

Leaf patterns of specialization in coastal dunes

A NLPCA was performed on all the species using the ten studied leaf traits and the major functional groups.

The first two axes accounted for 59% of the variation. The positive direction of axis 1 pointed towards sclerophyllous evergreen large shrubs and trees with high leaf [C] and low [Ca]. Axis 2 showed in its positive direction species of high LS and low leaf [Fe], [Mg] and [Mn] (electronic appendix 3).

This analysis separated among studied dunes (fig. 5). Inter-dunes analysis showed that P.N. Cabo de Gata-Níjar dunes were over represented in the bottom left corner of the figure (predominance of malacophyll and deciduous herbs and small shrubs, with small leaves size and high nutrient concentrations), whereas the other two dunes showed a wider pattern.

Intra-dunes analysis demonstrated that mobile semi-fixed dunes were mainly found in the left area of the figure showing negative values of axis 1 (predominance of small growth forms showing malacophyll deciduous and semi-deciduous leaves with higher nutrient content and higher SLA values), whereas fixed dunes species showed a wider distribution in the figure.

DISCUSSION

Although Mediterranean-type ecosystems provide an excellent system in which to examine leaf traits relationships (Ackerly et al. 2002), this is the first study where co-variation patterns of leaf traits have been analysed in Mediterranean vegetation on coastal dunes under different environmental conditions. New leaf trait values have been obtained for many species, especially on mobile semi-fixed dunes. Additionally, for the first time, leaf trait differences among different types of dunes (in terms of climate or mobility) have been highlighted.

Leaf functional traits in coastal dunes

The results of this study confirm that coastal dunes could be differentiated from other habitats in terms of the leaf economic spectrum. In coastal dunes, leaf traits values are close to the ones obtained in previous studies performed in harsher Mediterranean ecosystems, such as halophytic vegetation in open xerophytic shublands (e.g. Foulds 1993, Díaz & Cabido 1997, Navarro et al. 2010) and calcareous alkaline soils (e.g. Hobbie & Gough 2002). Leaf area spanned four orders of magnitude, ranging from sub-lepto- to micro-mesophyll leaf classes and SLA values (49–360 cm^2g^{-1}) are in the same range as in previous studies in other sand dunes (86–282 cm^2g^{-1}, e.g. Yulin et al. 2005). Leaf nutrient content showed lower values of leaf [N] (1.61–2%), compared to the range obtained in previous studies (1–4%N, e.g. Thompson et al.

Table 4 – Results from univariate ANOVAs on individual plant traits after MANOVAs.
For each analysis, F-values are shown. GF, growth forms; D, deciduousness; LC, leaf consistence; LS, leaf size; SLA, specific leaf area; C, leaf [C]; N, leaf [N]; Ca, leaf [Ca]; K, leaf [K]; Mg, leaf [Mg]; P, leaf [P]; Fe, leaf [Fe]; Mn, leaf [Mn]; n.s. (not significant) $P > 0.10$; · $P \leq 0.10$; * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

	GF	D	LC	GF × D	GF × LC	D × LC	GF × D × LC	Error
LS	8.09***	0.07 n.s.	0.77 n.s.	1.72 n.s.	0.77 n.s.	5.50**	0.07 n.s.	
SLA	2.72*	0.84 n.s.	0.29 n.s.	0.30 n.s.	0.59 n.s.	5.46**	0.49 n.s.	
C	2.2 ·	0.54 n.s.	5.64**	6.92**	0.47 n.s.	2.18n.s.	1.61 n.s.	
N	1.46 n.s.	0.61 n.s.	3.82*	2.40 n.s.	0.71 n.s.	1.19 n.s.	2.07 n.s.	
Ca	3.17*	3.08·	5.03**	2.49·	1.83 n.s.	4.44**	1.06 n.s.	
K	0.38 n.s.	0.89 n.s.	6.46**	0.86 n.s.	1.49 n.s.	4.21*	0.76 n.s.	
Mg	0.82 n.s.	0.004 n.s.	3.85*	0.36 n.s.	1.54 n.s.	3.87*	0.16 n.s.	
P	0.51 n.s.	0.50 n.s.	4.10*	1.23 n.s.	2.07 n.s.	1.66 n.s.	2.74·	
Fe	1.24 n.s.	1.06 n.s.	1.04 n.s.	0.60 n.s.	0.93 n.s.	0.75 n.s.	0.13 n.s.	
Mn	1.45 n.s.	0.17 n.s.	1.29 n.s.	0.08 n.s.	0.84 n.s.	0.30 n.s.	2.88·	
df	3	2	1	2	2	2	2	70

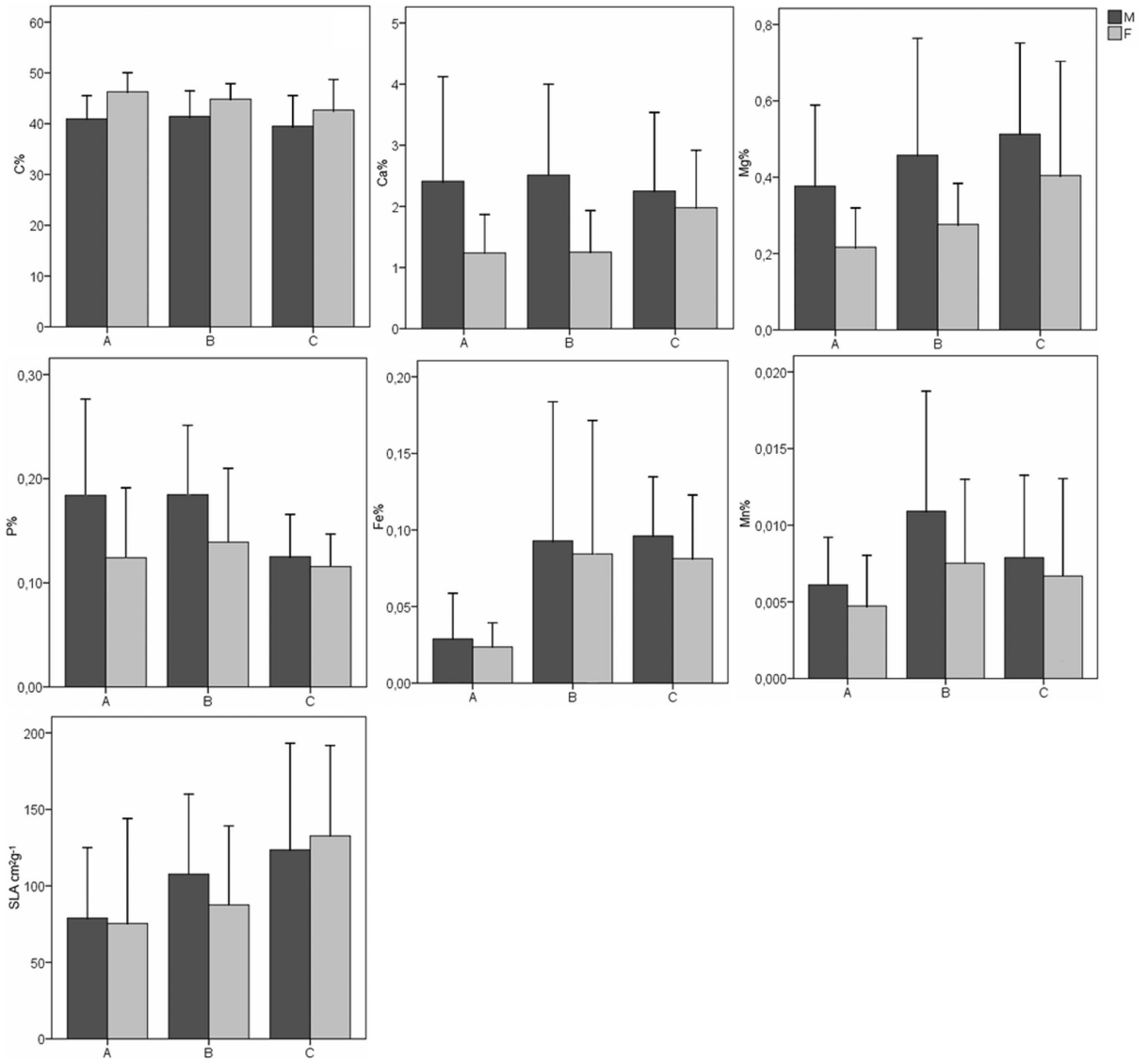


Figure 4 – Measurements of leaf traits in coastal dunes under different climates. Darker bars represent means (±SE) for plants in mobile and semi-fixed dunes (M) whereas lighter bars are plants in fixed dunes (F). A, Mediterranean-oceanic climate (P.N. del Estrecho); B, Mediterranean-subtropical climate (M.N. Artola-Cabopino); C, Mediterranean-subdesert climate (P.N. Cabo de Gata-Níjar).

1997, Niinemets & Kull 2003), and higher leaf [Ca] (from 6.1 to 0.3% *vs*. 0.02–3.9% obtained by Foulds 1993, Glew et al. 1997, Thompson et al. 1997, Niinemets & Kull 2003) and [Fe] (from 0.004 to 0.3 *vs.* 0.001–0.06 % obtained by Glew et al. 1997, Hänsch & Mendel 2009). According to Bakker et al. (2005), the higher leaf [Ca] and [Fe] in the study area may be related to the seepage. Depending on the origin of the water and the mineral composition of the layers that it passed though, seepage water may contain high concentrations of Ca^{2+}, HCO^{3-} and Fe^{2+} (Stuyfzand 1993, Bakker et al. 2005), which is reflected in higher leaf nutrients concentration. Additionally, previous studies (e.g. Hobbie & Gough 2002) have shown that alkaline soils, such as the soils analysed in this study, shows higher amount of exchangeable Ca, situation that involved a high leaf [Ca]. However, the high variability of leaf nutrient concentration obtained among species may suggest that foliar nutrient concentration is as much a species-level trait as it is reflective of soil nutrient availability. Leaf [P], [K], [Mg] and [Mn] could not be used as differential leaf traits of coastal dunes (e.g. Foulds 1993, Thompson et al. 1997, Niinemets & Kull 2003, Hu & Schmidhalter 2005, Hänsch & Mendel 2009)

Relationships among leaf traits in coastal dune also showed differentiated results that characterized this type of ecosystem. The co-variations of the leaf economic spectrum (Wright et al. 2004) have been confirmed in the studied coastal dunes. Specific leaf area, leaf [N] and [P] are broadly correlated (e.g. Güsewell & Koerselman 2002, Güsewell 2004). However, these relationships are highly variable among the studied coastal dunes and specially reduced in all mobile semi-fixed dunes, and in fixed dunes from P.N. Cabo de Gata-Níjar. This evidence suggests that the correlation between leaf traits may vary depending on environmental con-

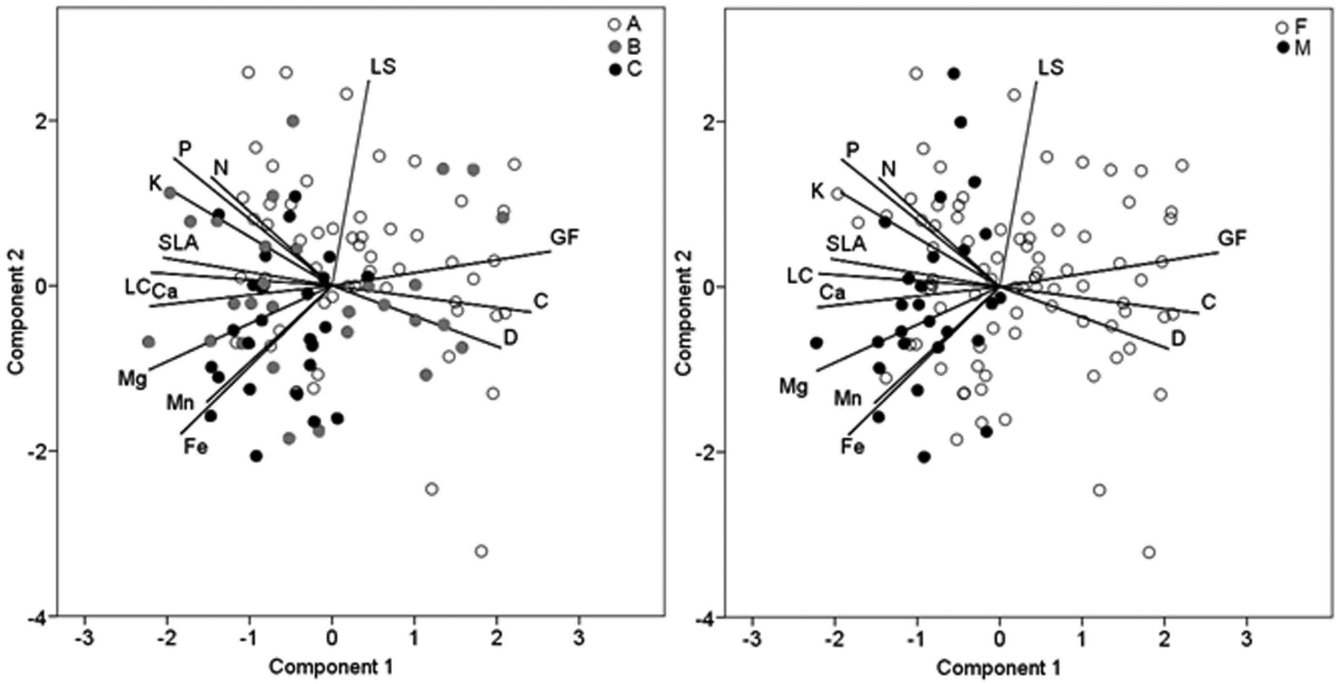


Figure 5 – Non-linear principal components analysis of species in coastal dunes, ordinated according to leaf functional traits. A, P.N. del Estrecho; B, M.N. Artola-Cabopino; C, P.N. Cabo de Gata-Níjar; F, fixed dunes; M, mobile and semi-fixed dunes; D, deciduousness; GF, growth forms; LC, leaf consistence; LS, leaf size; SLA, specific leaf area; C, leaf [C]; Ca, leaf [Ca]; Fe, leaf [Fe]; K, leaf [K]; Mg, leaf [Mg]; Mn, leaf [Mn]; N, leaf [N]; P, leaf [P].

ditions (Wilson et al. 1999). Interestingly, K apparently also follows the same pattern in our result.

Most comparisons of how leaf economic spectrum is affected by functional groups have been focused on growth forms and deciduousness (e.g. Wright et al. 2004, 2005). However, we examined whether leaf consistence could also concern the relationships among leaf traits, and our results show that the differentiation of species by this functional group involve the most significant differences in leaf traits. We also found that the effects of deciduousness over leaf traits include effects of growth forms and leaf consistence, because malacophyll leaves are associated to deciduous and semi-deciduous small growth forms, such as herbs, whereas sclerophyll leaves are mainly represented in evergreen large growth forms, such as trees. Consequently, we suggest that species in coastal dunes with short leaf turnover times (malacophyll deciduous herbs and shrubs) generally had higher leaf nutrient concentrations and SLA than species with long leaf turnover times (sclerophyll evergreen shrubs and trees) (Ackerly et al. 2002, Hobbie & Gough 2002), whose leaves show the greatest carbon gain profits over transpirational losses (Turner 1994).

According to the leaf economics spectrum (Wright et al. 2004), leaf relationship patterns obtained in coastal dunes involve that this vegetation is mainly formed by species with slow potential rate of return, low rates of photosynthesis and respiration, which need a higher investment per unit leaf area. This strategy has been identified as a higher nutrient use-efficiency in habitats experiencing high light, low nutrient, or low moisture availability (Niinemets & Kull 1994, Ackerly & Reich 1999), such as coastal dunes.

Different leaf patterns of specialization among the three dunes with contrasting climates

Climate-related variations of leaf traits have been observed in previous researches (e.g. Wright et al. 2004). In the present work, it has been shown how coastal dunes under variations into the Mediterranean climate could show differences of leaf functional traits.

Mediterranean-subdesert dunes (P.N. Cabo de Gata-Níjar) are characterized by small growth forms (perennial herbs and small shrubs) of deciduous and semi-deciduous leaves, which are the most adapted to avoid the strong summer drought (Mooney & Dunn 1970, Quezada 1981).

Traditionally, dry-site species have been associated to low SLA (Reich et al. 1999, Wright & Westoby 2003). A new perspective has been shown in this study. The relationship between dry-conditions and low SLA has been based on the drought tolerance strategy selected in these places. Dry-placed species are expected to be evergreen showing leaf thickness and sclerophylly (Mooney & Dunn 1970, Parsons 1976), characteristics which are linked to low SLA (Wilson et al. 1999, Ackerly et al. 2002). Low SLA contributes to long leaf-life span, high nutrient retention and protection from desiccation (Mooney & Dunn 1970, Ackerly et al. 2002), strategy which is extended in resource-poor environments, such as coastal dunes (Van der Valk 1974). However, most of the species in these dunes use a contrasting strategy, they are xerophytic malacophyllous, which has been determined as of high interest in plants on semi-deserts in warm temperate regions (Blanca 1990, Grubb 1998) and in disturbed environments where the human activity has involved

an increase of the aridity (Castro-Díez et al. 2001). These species are mainly herbs and small shrubs showing relatively soft leaves that live only a short time, often a few months. Consequently, the higher value of SLA is also supported by the absence of trees in coastal dunes in P.N. Cabo de Gata-Níjar. The loss of leaves during the drought time has been seen as of value in cutting down transpiration and respiration during periods when plants are rarely able to achieve positive net assimilation (Mooney et al. 1975).

Leaf nutrient content also showed significant differences among dunes, showing the most Atlantic dunes (M-oceanic dunes in P.N. del Estrecho) had the poorest leaves (the lowest values of leaf [Fe], [Mg] and [Mn] have been found in these dunes). This difference is explained by the distribution of major functional groups, because the majority of evergreen sclerophyll species, which are expected to show lower leaf N and other nutrients content (Westoby et al. 2002, He et al. 2006), are located on P.N. del Estrecho. However, soil composition is also relevant in this result, because soil conditions exert an important and direct influence on nutrients concentration in leaves (e.g. Rode et al. 1992, Thompson et al. 1997), and these soils are indeed the poorest in [Mn].

Different leaf patterns of specialization among the dune sectors

This study has demonstrated that dune sectors show distinct leaf traits. The exception was P.N. Cabo de Gata-Níjar, where no significant difference was found between fixed and mobile semi-fixed dunes. Fixed dunes are closer to the result obtained in previous studies in Mediterranean ecosystems (e.g. Ackerly et al. 2002). These are the typically stress-tolerant species which are predominant in coastal dunes.

However, mobile semi-fixed dunes show closer leaf patterns to those found in M-subdesert dunes (P.N. Cabo de Gata-Níjar). They are dominated by xerophytic malacophyllous species of small size (herbs and small shrubs). The high leaf nutrient content in this dune sector may be related to the dominance of deciduous/semi-deciduous species (He et al. 2006). Particularly relevant is the leaf Ca content, even higher than leaf [N], and whose enrichment could be explained by the higher Ca content in these soils. Coastal soils are known to receive large annual inputs of nutrients in the form of salt spray (Clayton 1972, Van der Valk 1974), rich in [K], [Mg] and [Ca] (Riley & Tongudai 1967, Clayton 1972).

CONCLUSIONS

This is the first study where co-variation patterns of leaf traits have been analysed in Mediterranean vegetation on coastal dunes under different environmental conditions. New leaf trait values have been obtained for many species, and for the first time, leaf trait differences among different types of dunes (in terms of climate and mobility) have been highlighted.

Coastal dunes are characterized by lower values of leaf [N] and higher values of leaf [Ca] and [Fe] than in other ecosystems and by a broad correlation among specific leaf area, leaf [N], [P] and [K].

Within the studied coastal dunes, leaf traits have been shown to be affected by climate and sea proximity as well as by the distribution of functional groups. Mediterranean-subdesert dunes showed a predominance of xerophytic malacophyllous strategy, whereas M-oceanic dunes are dominated by stress tolerant species. These two strategies based on leaf traits also differs among dune sectors. Mobile and semi-fixed dunes showed a leaf strategy closer to the observed on M-subdesert dunes but with a relevantly higher leaf Ca content, whereas fixed dunes are characterized by the stress tolerant strategy.

SUPPLEMENTARY DATA

Supplementary data are available in pdf at Plant Ecology and Evolution, Supplementary Data Site (http://www.ingentaconnect.com/content/botbel/plecevo/supp-data), and consist of (1) leaf trait values in coastal dunes in southern Spain; (2) correlations among leaf traits in coastal dunes in southern Spain; and (3) loading of the leaf traits on the first two components from Nonlinear Principal Components Analysis (NLPCA).

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