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Mediterranean coastal dune vegetation: Are disturbance and stress the key selective forces that drive the psammophilous succession?

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ABSTRACT

Plant communities of coastal dunes are distributed along a characteristic sea-inland gradient. Generally, there is a shift from annual and short height species with small leaves in initial successional stages to perennial tall shrubs with tough leaves in later phases. Assessing the community-weighted mean (CWM) trait values is used in plant ecology to describe ecosystem properties especially during succession. In particular, CSR (Competitive, Stress-tolerant, and Ruderal strategy) classification allows us to explore community functional shifts in terms of disturbance, stress and competition selective forces. To explore the functional basis of the psammophilous succession, we asked the following questions: (1) Can we circumscribe different functional types among plant species of Mediterranean coastal dunes? (2) How do CWM trait values vary along the environmental sea-inland gradient? (3) What is the relative importance of competition, stress and disturbance in the processes of plant community assembling? (4) Can we postulate that along primary successions there is generally a shift from ruderality to stress-tolerance? An explorative analysis of functional groups was performed by Non-Metric Multidimensional Scaling (NMDS) analysing nine morpho-functional traits measured for 45 taxa from 880 dune plots localised in Tuscany (central Italy, Europe). NMDS ordination showed a scattered distribution of psammophytes that could not be delimited in sharp plant functional types. The first NMDS axis has been interpreted as a leaf economics axis because it was correlated to leaf area (LA) and leaf dry matter content (LDMC), while the second one was a plant size axis because of its correlation with canopy height. Along the sea-inland gradient, pioneer plant communities of upper beach were dominated by ruderals (with the lowest values of LDMC and specific leaf area - SLA), well-adapted to the harsh environmental conditions of coastal dunes. More distantly from the sea, where ecological conditions were less extreme, late-successional communities of backdunes were characterised by the prevalence of stress-tolerants. This study suggested that psammophytes have evolved not a single but multiple adaptive strategies showing a high degree of functional diversity and complexity. Moreover, CSR classification supported the hypothesis of a functional shift from R-strategists in early successional stages to S-strategists in late-successional communities along a primary succession.

Key words: coastal vegetation, community-weighted mean (CWM), CSR theory, NMDS, plant adaptation, plant functional types (PFTs)

1. Introduction

Plant traits – morphological, anatomical, biochemical, physiological or phenological features measurable at the individual level (Violle et al., 2007) – reflect the outcome of evolutionary and community assembly processes responding to abiotic and biotic environmental constraints (Valladares et al., 2007). Hence, functional classification of plants (i.e. delimiting PFTs: plant functional types) is considered useful to understand ecosystem functioning and provides a promising tool for predictive ecology and global change science (Westoby, 1998; Lavorel & Garnier, 2002; Díaz et al., 2004; Wright et al., 2005; McGill et al., 2006; Kattge et al., 2011).

Plant communities of coastal dunes across various parts of the world are particularly interesting from functional studies because these ecosystems are complex and dynamic, they change along a gradient from the shoreline to the inland areas, resulting in a characteristic zonation of different plant communities (Doing, 1985; Psuty, 2004; Wiedemann and Pickart, 2004; Frederiksen et al., 2006; Acosta et al., 2007). The sequence of plant communities along coastal dunes can be classified into two broad vegetation types mainly linked to climate: one associated with temperate zones, the other to tropical regions of the world. The main differences between the two regions regard foredune vegetation: taller grasses, sedges and pioneer herbs dominate temperate zones, while low-growing creepers are predominant in tropical regions (Doody, 2013). Among temperate areas, the Mediterranean coasts show a different character from the Oceanic counterpart with higher values of water temperature and salinity, and more limited tides, waves and meteorological phenomena (compared to the oceanic storms and hurricanes). Differences between the Atlantic and the Mediterranean plant communities of costal dunes regard not only floristic, structural and ecological aspects (Feola et al., 2011; Jiménez-Alfaro et al., 2015), but also the lower effect of wind-related factors as controlling forces of Mediterranean vegetation pattern along dune systems (Fenu et al., 2013). The most important environmental factors that influence community assembly processes worldwide are salt spray, sand burial, substrate incoherence, water stress, high temperature, and nutrient scarcity (Ranwell, 1972; Hesp, 1991; Maun, 2009). In the Mediterranean basin, recent studies on coastal ecosystems have analysed geo-sedimentological aspects (Fenu et al., 2012; Angiolini et al., 2013; Bertoni et al., 2014; Ruocco et al., 2014), the influence of human pressure or coastal erosion on plant communities (Kerbiriou et al., 2008; De Luca et al., 2011; Muñoz Vallés et al., 2011; Ciccarelli et al., 2012; Santoro et al., 2012; Bertacchi and Lombardi, 2014; Ciccarelli, 2014; Malavasi et al., 2014), and the probabilistic scenario of coastal dune habitats under climate change (Prisco et al., 2013). As suggested by Maun (2009), the sea-inland zonation of coastal sand dunes is a special case of primary succession, in fact in some coastal locations zones do not exactly coincide with stages of succession because of the greater influence of several abiotic factors (such as wind velocity, salt spray and sand burial) than biotic factors (for example, the autogenic influence of plants growing in a zone). In these sites, it probably takes a longer period of time for a zone to proceed to the next stage in succession. However, the dynamic changes in vegetation of the psammophilous sequence could be more complex, thus zonation and succession often cannot be separated. For this reason, in the present paper the sea-inland zonation will be called succession.

Regarding European coastal dunes, most studies have examined several functional traits at species level to explore plant adaptation to environmental factors (García-Mora et al., 1999; Acosta et al., 2006; Ciccarelli et al., 2009, 2010; Gratani et al., 2009; Bermúdez & Retuerto, 2013, 2014; Spanò et al., 2013); others have studied functional traits at community level analysing the relationship between functional diversity and phylogenetic structure of plant communities (Ricotta et al., 2012; Carboni et al., 2013; Brunbjerg et al., 2014); few studies have analysed coastal dune vegetation adopting Grime’s (1974, 2001) CSR (Competition, Stress-tolerance, and Ruderality) strategy scheme (Macedo et al., 2010; Brunbjerg et al., 2012).

The CSR plant strategy scheme proposed by Grime (1974, 2001) is a practical method for the categorisation of plants according to a theoretical triangular scheme of competitor, stress-tolerator and ruderal plant strategies. In particular, the CSR model tries to describe vegetation processes considering the interplay of three fundamental selective forces: competition, which coincides with limitations to biomass production imposed by other species; stress, which is a suboptimal condition for metabolism imposed by the environment that results in direct limitations to biomass production; and disturbance, which causes biomass removal or tissues destruction. According to CSR theory, competitor species (C-strategists) are present in low stress and low disturbance habitats; while stress-tolerant species (S-strategists) live in high stress and low disturbance areas; lastly, ruderal species (R-strategists) are typical of low stress and high disturbance environments. Analysing seven validated functional traits, vascular plant taxa can be classified within the CSR space (Hodgson et al., 1999).

Regarding coastal dune systems, stress and disturbance are both expected to play a role along the psammophilous succession. In particular, salt spray, soil salinity, nutrient availability, water scarcity, high temperature, and high irradiance act as strong environmental stress on plants of coastal sand dunes. On the other hand, strong winds, which frequently cause sand movement and consequently sand blasting, grazing, and occasional inundation by sea water are important factors of disturbance in these ecosystems (Ranwell, 1972; Hesp, 1991; Stallins and Parker, 2003; Maun, 2009). Competition is predicted to be most important in areas with high productivity (Keddy et al., 1997). For coastal dunes, a certain degree of competition among species is expected in dune slacks and fixed dunes where the ecological conditions are less extreme and nutrient availability increases (Brunbjerg et al., 2012). Moreover, the psammophilous zonation, as a primary succession, provides an interesting example to study vegetation change and to test CSR classification along a spatial gradient. As deducted from literature (Macedo et al., 2010; Brunbjerg et al., 2012), a general shift from ruderals to stress-tolerant species is expected along the sea-inland gradient. In particular, plant communities of initial successional stages are expected to be dominated by annual species with low canopy height and small leaves, while plant assemblages of later successional phases are expected to be characterised by perennial tall shrubs with tough leaves (Acosta et al., 2006; Feagin and Wu, 2007). Moreover, an increase of functional diversity is expected along the sea-inland gradient from upper beach and embryonic dunes to transition dunes (Ricotta et al., 2012).

The principal aim of the present research is to explore the relationship between the spatial pattern of plant functional groups and the environmental sea-inland gradient along Mediterranean coastal dunes. The sea-inland psammophilous sequence is made of the following plant communities: annual vegetation of drift lines, perennial herb communities of embryonic and mobile dunes, *Crucianellion maritimae* fixed beach dunes, *Malcolmietalia* dune grasslands, and coastal dunes with *Juniperus* spp. (Vagge and Biondi, 1999; Stanisci et al., 2004; Acosta et al., 2007; Acosta and Ercole, 2015). To explore this linkage we calculated the aggregated trait values (following Garnier et al., 2004, 2007) for each herbaceous plant community across the psammophilous succession. More specifically, we asked the following questions:

1. Can we circumscribe different plant functional types among the psammophilous species of Mediterranean coastal dunes?
2. How do community-weighted mean (CWM) plant trait values vary along the environmental sea-inland gradient?
3. What is the relative importance of competition, stress and disturbance in the processes of plant community assembling?
4. Can we postulate that along primary successions there is generally a shift from ruderality to stress-tolerance?

2. Materials and methods

2.1. Study site, vegetation data and trait measurements

The present study was conducted in the coastal sand dunes of the Tuscan littoral (Italy, Fig. 1). The area is characterised by a Mediterranean climate, with a mean annual temperature >15°C and a mean annual rainfall of 700 mm (Pinna, 1985; Rapetti, 2003).

Coastal dune systems generally consist of distinct plant communities that occur along a coast-to-inland ecological gradient (Acosta and Ercole, 2015, see Appendix 1). For this study, we analysed 880 vegetation plots 1 m x 1 m in size, which were sampled in the period 2010-2011 along 20 random transects orthogonal to the seashore, starting from the annual vegetation of drift lines to the herbaceous vegetation of fixed dunes. Micro-forest vegetation with *Juniperus* spp. was excluded from this study, because CSR classification following Hodgson et al. (1999) is calibrated only to herbaceous species. For the detailed vegetation sampling and plant communities identification see Ciccarelli (2014). All the plots were classified in five community types (Appendix 2): 1) upper beach with annual vegetation of drift lines, 2) perennial herb communities of embryonic dunes, 3) mobile dunes dominated by *Ammophila arenaria*, 4a) perennial chamaephytic communities of *Crucianellion maritimae*, and 4b) *Malcolmietalia* grasslands. Both *Crucianellion maritimae* and *Malcolmietalia* communities colonise transition dunes and backdunes. Sometimes, in coastal sand dunes habitat types are distributed in a mosaic pattern because of the high environmental heterogeneity of these ecosystems. In this study, plots that were not clearly attributable to a community type were excluded from the analysis. In each plot, all vascular plant taxa were recorded and the percentage cover of each taxon was visually estimated. For each community type, all plant taxa present in at least 1% of plots (for a total of 45 taxa) were described by a set of nine functional traits. Plant nomenclature follows Conti et al. (2005, 2007).

Selected functional traits included the following quantitative variables that are related to plant size and leaf: canopy height, leaf area, leaf dry weight, leaf dry matter content, specific leaf area, and succulence index. Each trait was quantified by measuring 20 replicate samples from ten different individuals randomly selected. Leaves collected from the field were placed in labelled plastic bags in a refrigerated container at approximately 4 °C, and transported immediately to the laboratory, where they were subjected to a rehydration procedure in the dark at 4 °C for almost 6 h. Leaf measurements followed the standardised methodologies detailed by Cornelissen et al. (2003) and Pérez-Harguindeguy et al. (2013).

Canopy height (CAN-H) is the shortest distance between the upper boundary of the main photosynthetic tissues (excluding inflorescences) of a plant and the ground level, expressed in mm. This trait is generally associated with growth form, competitive vigour, and potential lifespan. Leaf area (LA) is the one-sided projected surface area of a fresh leaf, expressed in mm^2. Leaf dry weight (LDW) is the oven-dry mass of a leaf, expressed in mg. Leaf dry matter content (LDMC) is the proportion of the water-saturated fresh mass of a leaf accounted for by its oven-dry mass, expressed in %. Specific leaf area (SLA) is the one-sided area of a fresh leaf divided by its oven-dry mass, expressed in mm^2 mg^{-1}. Succulence index (SI) is the ratio of the difference between the oven-dry mass of a leaf and its water-saturated fresh mass to the leaf surface area, expressed in mg cm^{-2} (Read et al., 2005). Leaf projected area was acquired with a CanoScan LiDE 90 (Canon) and determined by CompuEye, Leaf & Symptom Area software (available at http://www.ehabsoft.com/CompuEye/LeafSArea/). LA is not only related to climatic variability, geology, altitude and latitude, but also to allometric factors and ecological strategy with respect to environmental nutrient stress and disturbances. LDMC correlates negatively with potential RGR (relative growth rate) and positively with leaf lifespan. Lastly, SLA tends to scale positively with mass-based light-saturated photosynthetic rate and with leaf nitrogen (N) concentration, and negatively with leaf longevity and C investment in quantitatively important secondary compounds such as tannins or lignin. For calculating mean and standard error, the average CAN-H, LA, LDW, LDMC, SLA, and SI for each individual plant was one statistical observation.

Plant taxa were also classified according to Grime’s (1974, 2001) CSR functional strategies as competitors, stress-tolerators and ruderals with values ranging from 0 to 100 such that C + S + R =

100. CSR classification was conducted using the method and spreadsheet calculation tool of Hodgson et al. (1999). Seven functional traits were analysed: CAN-H and lateral spread (LS) as an index of C-selection; LDMC, LDW and SLA as an index of S-selection; flowering period (FP) and flowering start (FS) as indicative of R-selection. Lateral spread was measured in the field and classified in the following six categories: 1 = plant short-lived, 2 = loosely tufted ramets (graminoids)/compactly tufted, lacking thickened rootstock (non-graminoids), 3 = compactly tufted ramets (graminoids)/compactly tufted with thickened rootstock (non-graminoids), 4 = shortly creeping (< 40 mm), 5 = creeping (40-79 mm), 6 = widely creeping (> 79 mm). Flowering period represented the normal duration of flowering (expressed in months). Flowering start was defined as the month in which flowers were first produced, and was classified in six categories from 1 to 6 that denoted March to August, respectively. FP and FS were based on field observations.

2.2. Statistical analyses

A matrix of 45 plant taxa x 9 traits (CAN-H, FP, FS, LA, LDW, LDMC, LS, SLA, and SI) were analysed using Non-metric Multidimensional scaling (NMDS). The aim of this technique is to represent samples and/or species in a low-dimensional ordination space by optimising the correspondence between original dissimilarities and distances in the ordination (Økland, 1996). The matrix was prior standardised and square-root transformed, then was subjected to the NMDS analysis using the Bray-Curtis dissimilarity index. The Spearman product-moment correlation coefficient was also calculated in order to point out which functional trait was more correlated to the NMDS axes.

For each community type, we also calculated aggregated plant traits following Garnier et al. (2004, 2007):

$$trait_{agg} = \sum_{i=1}^{n} p_i \; x \; trait_i$$

where p_i is the relative contribution of species *i* to the community (expressed as percentage coverage), and $trait_i$ is the trait value of species *i*. In order to compare the five different coastal habitats (see Appendix 2), we divided each trait aggregated value by the number of plots sampled for each community type. Aggregated plant traits were compared by the non-parametric test of Kruskal-Wallis with the Bonferroni correction for multiple comparisons to verify whether there were significant differences between plant communities.

To assess differences in CSR strategies at the community level, we calculated the community-weighted mean (CWM) CSR values at each plot as the average of single CSR values weighted by the relative abundances of each species (see Ricotta et al., in press):

$$CWM = \sum_{i=1}^{n} p_i \ x \ \sigma_i$$

where σ_i is the value of single CSR strategies for species *i*. Finally, based on the CWM values at each plot, we calculated the CWM mean value for the five community types. These values were compared by the non-parametric test of Kruskal-Wallis with the Bonferroni correction for multiple comparisons to verify whether there were significant differences between plant communities.

All statistical tests were performed using R 2.14.1 software (vegan package, Oksanen et al., 2012, http://www.r-project.org/).

3. Results

Trait mean for the 45 psammophilous taxa are presented in Appendix 3. The highest value of CAN-H was recorded in *Ammophila arenaria* (801.6 ± 27.6 mm), while the lowest one was in *Medicago littoralis* (23.6 ± 1.2 mm). *Verbascum sinuatum* showed the highest value of LA (15208.2 ± 3343.8 mm^2), while *Helichrysum stoechas* and *Vulpia fasciculata* had the lowest ones (34.4 ± 1.5 mm^2 and 34.5 ± 6.9 mm^2, respectively). LDW mean value ranged from 1.6 ± 0.2 mg in *Vulpia fasciculata* to 2426.3 ± 247.6 mg in *Echinophora spinosa*. Regarding LDMC, 40.5 ± 3.6 % was the highest mean value recorded in *Seseli tortuosum*, while 4.4 ± 0.4 % was the lowest recorded in *Cakile maritima*. The highest value of SLA was recorded in *Cerastium ligusticum* (35.9 ± 1.3 mm^2 mg^{-1}), while the lowest one was in *Echinophora spinosa* (3.0 ± 0.1 mm^2 mg^{-1}). Lastly, *Echinophora spinosa* showed the highest value of SI (166.3 ± 6.1 mg cm^{-2}), while *Phleum arenarium* had the lowest SI (10.6 ± 0.5 mg cm^{-2}).

The NMDS (Fig. 2) did not result in a clear separation of the plant taxa in distinct functional groups. The stress value of 0.07 corresponds to a good ordination with no real prospect of a misleading interpretation. Three plant traits (CAN-H, LA, and LDW) showed a high correlation with the first two NMDS axes (Spearman's coefficient > 0.9): NMDS1 was an axis of variability in size-related traits of leaf, such as LA and LDW; while NMDS2 was related to variability in whole plant size, such as CAN-H.

Aggregated trait means for the five plant communities are presented in Table 1. All the five community types differed significantly ($P < 0.001$) for the six quantitative traits (CAN-H$_{agg}$, LA$_{agg}$, LDW$_{agg}$, LDMC$_{agg}$, SLA$_{agg}$, SI$_{agg}$). Annual vegetation of upper beach showed the significantly lowest value of LDMC$_{agg}$ ($P < 0.001$); embryonic dunes had the significantly highest value of LDW$_{agg}$ ($P < 0.001$); mobile dunes showed the highest values of CAN-H$_{agg}$ and LDMC$_{agg}$, differing significantly from the other community types ($P < 0.001$). The significantly highest values of LA$_{agg}$ were recorded in embryonic dunes and mobile dunes ($P < 0.001$). *Crucianellion maritimae* vegetation and *Malcolmietalia* grasslands showed the highest values of SLA$_{agg}$ and the lowest values of SI$_{agg}$, differing significantly from upper beach and embryonic dunes ($P < 0.001$). Mobile dunes showed the significantly highest value of SLA$_{agg}$ similarly to *Crucianellion maritimae* vegetation and *Malcolmietalia* grasslands, and the significantly highest value of SI$_{agg}$ similarly to upper beach and embryonic dunes ($P < 0.001$).

Community-weighted mean (CWM) CSR values for each plant community type are showed in Table 2. All the five community types differed significantly ($P < 0.001$) for C (%), S (%), and R (%) components. Annual community of upper beach was dominated by *Cakile maritima* (C : S : R =

0% : 0% : 100%) and *Salsola kali* (0% : 0% : 100%), two true ruderals. Embryonic dunes were characterised by the dominance of *Elymus farctus* (50% : 50% : 0%, SC), *Echinophora spinosa* (75% : 0% : 25%, C/CR), and *Calystegia soldanella* (25% : 0% : 75%, R/CR). *Ammophila arenaria* (50% : 50% : 0%, SC) was the most abundant species in mobile dunes. Lastly, *Crucianellion maritimae* communities were characterised by the prevalence of *Helichrysum stoechas* (50% : 25% : 25%, C/CSR), while *Malcolmietalia* grasslands were dominated by *Vulpia fasciculata* (16% : 42 % : 42%, SR/CSR), *Medicago littoralis* (0% : 75% : 25%, S/SR), and *Silene canescens* (25% : 0% : 75%, R/CR). Hence, competitor strategists increased from 18.8% in upper beach to 46.7% in mobile dunes and decreased to 21.1% in *Malcolmietalia* grasslands. Stress-tolerators ranged from 4.1% in upper beach to 44.8% in *Malcolmietalia* grasslands. The contribution of ruderal strategists decreased from 77.1% in upper beach to 13.6% in mobile dunes and increased in *Crucianellion maritimae* communities and *Malcolmietalia* grasslands (37.3% and 34.1%, respectively). A gradient in CSR strategies, from R to S, was evident along the psammophilous succession with a predominance of C component in mobile dunes (Fig. 3).

4. Discussion

Our data suggest that plant species living in Mediterranean coastal dunes are characterised by different functional adaptations to these heterogeneous habitats. In fact, the multivariate analysis showed a scattered distribution of taxa along two main axes (Fig. 2). The first NMDS axis was related to leaf economics, showing at the right extreme plants with the highest values of LA and LDW (such as *Verbascum sinuatum* and *Echinophora spinosa*); while the second NMDS axis was inversely related to plant size, showing at the bottom extreme species with the highest value of CAN-H (such as *Ammophila arenaria*). Given that the psammophytes are randomly spread along the two NMDS axes, we can conclude that they do not share the same adaptive strategy. These data are in accordance with Ciccarelli et al. (2009) and Spanò et al. (2013) who demonstrated the ability of the psammophytes to trigger different morphological, anatomical, and physiological traits to face off the various environmental constraints of coastal dunes. Recently, Bermùdez and Retuerto (2014) argued that the spatial and temporal heterogeneity generated by disturbance factors operating in coastal dune systems may cause constantly changing scenarios. As suggested by Frenette-Dussault et al. (2012), it is therefore possible that no single evolutionary solution (i.e. primary strategy) exists for several environments, but that the community consists of a combinations of plants that are all rather poorly adapted for the existing conditions; they are able to occupy the site simply because no superior combination of traits exists. Another explanation could be that plants living in extreme habitats, such as coastal dunes, cannot develop optimal strategies for all traits because of the energetic costs. Moreover, in literature it is well-known how functional redundancy is important to ensure the persistence of ecosystem function under changing environmental conditions and to ensure resilience in response to stress or disturbance (Peterson et al., 1998).

The five plant community types differed significantly for both aggregated trait mean values and community-weighted mean (CWM) CSR values. Our data showed an increase of S-strategists and a decrease of R-strategists from the pioneer plant communities of the upper beach to the late-successional communities of the backdunes. The highest percentages of ruderals were registered in upper beach where the environmental conditions are harsher. In fact, pioneer plants of the psammophilous succession have to withstand environmental stresses such as salt spray, sand blasting, substrate movement, and occasional inundation by sea water (Ranwell, 1972; Huiskes, 1979; Stanisci et al., 2004; Acosta et al., 2006, 2007; Maun, 2009). The lowest values of $LDMC_{agg}$ and SLA_{agg} found in upper beach and embryonic dunes highlighted that foredunes are characterised by herbaceous plants, mostly annuals, with low relative growth rate (RGR) and low investments in C content.

Along the psammophilous succession, mobile dunes showed the highest values of $CAN\text{-}H_{agg}$ and $LDMC_{agg}$, which is indicative of perennial plants with high RGR and high investments in C content, with relatively tough leaves more resistant to physical hazards. Mobile dunes evidenced a peculiar behaviour with high values of competitor and stress-tolerant components. This is mainly due to *Ammophila arenaria*, the most prevalent species in mobile dunes, characterised by a SC strategy, which is explained by its vigorous and tall aerial parts and its adaptations to heavy sand deposition (Ranwell, 1972; Huiskes, 1979; Stanisci et al., 2004; Acosta et al., 2006, 2007; Maun, 2009; Ciccarelli et al., 2012; Ciccarelli, 2014).

More distant to the coastline, *Crucianellion maritimae* communities and *Malcolmietalia* grasslands evidenced quite similar values of aggregated plant traits, and confirmed the less extreme conditions of backdunes habitats, especially regarding water stress with the lowest values of SI_{agg}.

Our data are quite in accordance with the well-known sea-inland environmental gradient described for many coastal dune ecosystems, with the upper beach and embryonic dune vegetation closer to the sea and hence more exposed to salt spray, winds and sand burial than mobile dunes and especially backdunes progressively less exposed to these harsh environmental constrains (Stanisci et al., 2004; Acosta et al., 2006, 2007; Carboni et al., 2009; Fenu et al., 2012, 2013; Ciccarelli, 2014; Ruocco et al., 2014). In this study, the presence of the stress-tolerant component is not surprising in late-successional communities because water scarcity, high temperatures, and high irradiance are often limiting factors also in backdune areas. An interesting feature is the increasing of ruderality at the end of the psammophilous succession, where the disturbance component could be partly explained by the anthropogenic pressure, as evidenced by Ciccarelli (2014) in the same study area, which is quite common in backdunes in the form of trampling and paths. Brunbjerg et al. (2012) studies are in line with our data, in fact they evidenced how disturbance and stress are not uniformly distributed within Danish coastal dune systems, showing also a stronger role by human-associated disturbance than natural disturbance. Lastly, the present study showed the absence of true competitors among the 45 psammophilous taxa (see Appendix 3). A similar conclusion has been found for a primary succession along a glacier foreland, where although competition was potentially present throughout the succession, phenology and efficient resource-use were more important (Caccianiga et al., 2006).

5. Conclusions

In conclusion, we can answer the questions posed in the introduction.

1. The spatial segregation of the psammophytes in the two-dimensional plot generated by the NMDS supports the view that we cannot clearly delimit plant functional groups, but a gradient of species characterised by a specific configuration of functional traits that define different strategies. Hence, psammophytes can occupy quite different functional space suggesting a high degree of functional diversity and complexity.
2. The analysis based on community-aggregated plant trait values are in accordance with the ecological constrains along the sea-inland gradient. Upper beach and embryonic dunes are characterised by the presence of pioneer communities (with low values of $LDMC_{agg}$ and SLA_{agg}) well-adapted to the harsh environmental conditions of these habitats. More distantly from the sea, backdune vegetation is characterised by functional traits (especially low values of SI_{agg}) that confirm less extreme ecological conditions.
3. Stress and disturbance rather than competition are the most important structuring factors in Mediterranean coastal dune plant communities. Our results are partly in accordance with Macedo et al. (2010) who found stress-tolerant strategists as dominant taxa in foredune vegetation under stability conditions along the Portuguese coastline; and with Brunbjerg et al. (2012, 2015) who evidenced the principal role of disturbance as selective force in Danish dry coastal dunes. As far as we know, these are the only publications that have analysed European coastal dune vegetation adopting Grime’s CSR strategy scheme, but they were focused on Atlantic coasts. Analysing several works on factors of disturbance and stress across Mediterranean basin (De Luca et al., 2011; Attorre et al., 2013; Ciccarelli, 2014), it becomes evident that the different relative importance of disturbance and stress in

structuring plant communities could depend on the local environmental conditions, as suggested by Petrů et al. (2006).

4. CSR classification has been confirmed a useful tool to resolve a primary succession. In fact, in early successional stages pioneer plant communities are dominated by R-strategists that decrease and are replaced by S-strategists in late-successional communities. Although a certain degree of competition was present in primary successions, physical disturbance and environmental stress limit the evolution of plant communities dominated by C-strategists, as we can see in Mediterranean coastal dunes and in glacier forelands (see Caccianiga et al., 2006). Finally, we believe that CSR classification is able to elucidate the selective forces and the functional characteristics of plant communities along primary successions. Exploring other primary successions with CSR theory may refine our hypothesis.

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Abbreviations: CAN-H = canopy height, CSR = competitors/stress-tolerants/ruderals, CWM = community-weighted mean, FP = flowering period, FS = flowering start, LA = leaf area, LDMC = leaf dry matter content, LDW = leaf dry weight, LS = lateral spread, NMDS = non-metric multidimensional scaling, RGR = relative growth rate, SLA = specific leaf area, SI = succulence index

References

Acosta, A., Ercole, S. (Eds.), 2015. Gli habitat delle coste sabbiose italiane: ecologia e problematiche di conservazione. ISPRA, Serie Rapporti, 215/2015, Rome (in Italian).

Acosta, A., Ercole, S., Stanisci, A., De Patta Pillar, V., Blasi, C., 2007. Coastal vegetation zonation and dune morphology in some Mediterranean ecosystems. J. Coast. Res. 23, 1518-1524.

Acosta, A., Izzi, C.F., Stanisci A., 2006. Comparison of native and alien plant traits in Mediterranean coastal dunes. Comm. Ecol. 7, 35-41.

Angiolini, C., Landi, M., Pieroni, P., Frignani, F., Finoia, M.G., Gaggi, C., 2013. Soil chemical features as key predictors of plant community occurrence in a Mediterranean coastal ecosystem. Estuar. Coastal Shelf Sci. 119, 91-100.

Attorre, F., Maggini, A., Di Traglia, M., De Sanctis M., Vitale, M., 2013. A methodological approach for assessing the effects of disturbance factors on the conservation status of Mediterranean coastal dune systems. Applied Veg. Sci. 16, 333-342.

Bermúdez, R., Retuerto, R., 2013. Living the difference: alternative functional designs in five perennial herbs coexisting in a coastal dune environment. Func. Plant Biol. 40, 1187-1198.

Bermúdez, R., Retuerto, R., 2014. Together but different: co-occurring dune plant species differ in their water- and nitrogen-use strategies. Oecologia 174, 651-663.

Bertacchi, A., Lombardi, T., 2014. Diacronic analysis (1954-2010) of transformations of the dune habitat in a stretch of the Northern Tyrrhenian coast (Italy). Plant Biosyst. 148(2), 227-236.

Bertoni, D., Biagioni, C., Sarti, G., Ciccarelli, D., Ruocco, M., 2014. The role of sediment grain-size, mineralogy, and beach morphology on plant communities of two Mediterranean coastal dune systems. Italian J. Geosci. 133 (2), 271-281.

Brunbjerg, A.K., Borchsenius, F., Eiserhardt, W.L., et al., 2012. Disturbance drives phylogenetic community structure in coastal dune vegetation. J. Veg. Sci. 23, 1082-1094.

Brunbjerg, A.K., Cavender-Bares, J., Eiserhardt, W.L., et al., 2014. Multi-scale phylogenetic structure in coastal dune plant communities across the globe. J. Plant Ecol. **7,** 101-114.

Brunbjerg, A.K., Jørgensen, G.P., Nielsen, K.M., et al., 2015. Disturbance in dry coastal dunes in Denmark promotes diversity of plants and arthropods. Biol. Conserv. 182, 243-253.

Caccianiga, M., Luzzaro, A., Pierce, S., Ceriani, R.M., Cerabolini, B., 2006. The functional basis of a primary succession resolved by CSR classification. OIKOS 112, 10-20.

Carboni, M., Carranza, M.L., Acosta, A., 2009. Assessing conservation status on coastal dunes: A multiscale approach. Lands. Urban Plann. 91, 17-25.

Carboni, M., Acosta, A.T.R., Ricotta, C., 2013. Are differences in functional diversity among plant communities on Mediterranean coastal dunes driven by their phylogenetic history? J. Veg. Sci. 24, 932-941.

Cerabolini, B.E.L., Brusa, G., Ceriani, R.M., De Andreis, R., Luzzaro, A., Pierce, S., 2010. Can CSR classification be generally applied outside Britain? Plant Ecol. 210, 253-261.

Ciccarelli, D., 2014. Mediterranean coastal sand dune vegetation: Influence of natural and anthropogenic factors. Environ. Manage. 54, 194-204.

Ciccarelli, D., Bacaro, G., Chiarucci, A., 2012. Coastline dune vegetation dynamics: evidence of no stability. Folia Geobot. 47, 263-275.

Ciccarelli, D., Balestri, M., Pagni, A.M., Forino, L.M.C., 2010. Morpho-functional adaptations in *Cakile maritima* Scop. subsp. *maritima*: comparation of two different morphological types. Caryologia 63, 411-421.

Ciccarelli, D., Forino, L.M.C., Balestri, M., Pagni, A.M., 2009. Leaf anatomical adaptations of *Calystegia soldanella*, *Euphorbia paralias* and *Otanthus maritimus* to the ecological conditions of coastal sand dune systems. Caryologia 62, 142-151.

Conti, F., Abbate, G., Alessandrini, A., Blasi, C., (Eds.), 2005. An annotated checklist of the Italian vascular flora. Palombi Editori. Roma, Italy (in Italian).

Conti, F., Alessandrini, A., Bacchetta, G., et al., 2007. Integrazioni alla checklist della flora vascolare italiana. Natura Vicentina 10, 5-74 (in Italian).

Cornelissen, J.H.C., Lavorel, S., Garnier, E., et al., 2003. A handbook of protocols for standardized and easy measurement of plant functional traits worldwide. Austr. J. Bot. 51, 335-380.

De Luca, E., Novelli, C., Barbato, F., Menegoni, P., Iannetta, M., Nascetti, G., 2011. Coastal dune systems and disturbance factors: monitoring and analysis in central Italy. Environ. Monit. Assess. 183, 437-450.

Díaz, S., Hodgson, J.G., Thompson, K., et al., 2004. The plant traits that drive ecosystems: evidence from three continents. J. Veg. Sci. 15, 295-304.

Doing, H., 1985. Coastal fore-dune zonation and succession in various parts of the world. Vegetatio 61, 65–75.

Doody, J.P., 2013. Sand dune conservation, management and restoration. Springer-Verlag. Heidelberg, Berlin.

Feagin, R.A., Wu X.B., 2007. The spatial patterns of functional groups and successional direction in coastal dune community. Rangeland Ecol. Manage. 60, 417-425.

Fenu G., Carboni, M., Acosta, A., Bacchetta, G., 2013. Environmental factors influencing coastal vegetation pattern: new insights from the Mediterranean basin. Folia Geobot. 48, 493-508.

Fenu, G., Cogoni, D., Ferrara, C., Pinna, M.S., Bacchetta, G., 2012. Relationships between coastal sand dune properties and plant community distribution: The case of Is Arenas (Sardinia). Plant Biosyst. 146, 586-602.

Feola, S., Carranza, M.L., Schaminéè, J.H.J., Janssen, J.A.M., Acosta, A.T.R., 2011. EU habitat of interest: an insight into Atlantic and Mediterranean beach and foredunes. Biodivers. Conserv. 20, 1457-1468

Frederiksen, L., Kollmann, J., Vestergaard, P., Bruun, H.H., 2006. A multivariate approach to plant community distribution in the coastal dune zonation of NW Denmark. Phytocoenologia 36, 321–342.

Frenette-Dussault, C., Shipley, B., Léger, J.-F., et al., 2012. Functional structure of an arid steppe plant community reveals similarities with Grime's C-S-R theory. J. Veg. Sci. 23, 208-22.

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.

Garnier, E., Cortez, J., Billès, G., 2004. Plant functional markers capture ecosystem properties during secondary succession. Ecology 85, 2630-2637.

Garnier, E., Lavorel, S., Ansquer, P., et al., 2007. Assessing the effects of land-use change on plant traits, communities and ecosystem functioning in grasslands: A standardized methodology and lessons from an application to 11 European sites. Ann. Bot. 99, 967-985.

Gratani, L., Varone, L., Crescente, M.F., 2009. Photosynthetic activity and water use efficiency of dune species: the influence of air temperature on functioning. Photosynthetica 47, 575-585.

Grime, J.P., 1974. Vegetation classification by reference to strategies. Nature 250, 26-31.

Grime, J.P., 2001. Plant strategies, vegetation processes and ecosystem properties. 2nd ed. Wiley-Blackwell. Chichester, UK.

Grime, J.P., Pierce, S. 2012. The evolutionary strategies that shape ecosystems. Wiley-Blackwell. Chichester, UK.

Hesp, P.A., 1991. Ecological processes and plant adaptations on coastal dunes. J. Arid Environ. 21, 165-191.

Hodgson, J.G., Wilson, P.J., Hunt, R., Grime, J.P., Thompson, K., 1999. Allocating C-S-R plant functional types: a soft approach to a hard problem. OIKOS 85, 282-294.

Huiskes, A.H., 1979. Biological Flora of the British Isles. *Ammophila arenaria* (L.) Link. J. Ecol. 67, 363-382.

Jiménez-Alfaro, B., Marcenò, C., Guarino, R., Chytrỳ, M., 2015. Regional metacommunities in two coastal systems: spatial structure and drivers of plant assemblages. J. Biogeogr. 42, 452-462.

Kattge, J., Díaz, S., Lavorel, S., et al., 2011. TRY – a global database of plant traits. Global Change Biol. 17, 2905-2935.

Keddy, P., TwolanStrutt, L., Shipley, B., 1997. Experimental evidence that interspecific competitive asymmetry increases with soil productivity. Oikos 80, 253-256.

Kerbiriou, C., Leviol, I., Jiguet, F., Julliard, R. 2008. The impact of human frequentation on coastal vegetation in a biosphere reserve. J. Environ. Manage. 88, 715-728.

Lavorel, S., Garnier, E., 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Func. Ecol. 16, 545-556.

Macedo, J.A., Alves, P., Lomba, A., et al., 2010. On the interest of plant functional classifications to study community-level effects of increased disturbance on coastal dune vegetation. Acta Bot. Gall. 157, 305-315.

Malavasi, M., Santoro, R., Cutini, M., Acosta, A.T.R., Carranza, M.L., 2014. The impact of human pressure on landscape patterns and plant species richness in Mediterranean coastal dunes. Plant Biosyst. 29, 1541-1550.

Maun, M.A., 2009. The biology of coastal sand dunes. Oxford University Press. Oxford, UK.

McGill, B.J., Enquist, B.J., Weiher, E., Westoby, M., 2006. Rebuilding community ecology from functional traits. Trends Ecol. Evol. 21, 178-185.

Muñoz Vallés, S., Gallego Fernández, J.B., Dellafiore, C.M., 2011. Dune vulnerability in relation to tourism pressure in central Gulf of Cádiz (SW Spain), a case study. J. Coast. Res. 27, 243-251.

Økland, R.H., 1996. Are ordination and constrained ordination alternative or complementary strategies in general ecological studies? J. Veg. Sci. 7, 289-292.

Oksanen, J., Blanchet, F.G., Kindt, R., et al., 2012. Community Ecology Package. http://cran.r-project.org/. Accessed 02 Sept 2013

Perez-Harguindeguy, N., Diaz, S., Garnier, E., et al., 2013. New handbook for standardised measurement of plant functional traits worldwide. Austr. J. Bot. 61, 167-234.

Peterson, G., Allen, C.R., Holling, C.S., 1998. Ecological resilience, biodiversity and scale. Ecosystems 1, 6-18.

Petrů, M., Tielborger, K., Belkin, R., et al., 2006. Life history variation in an annual plant under two opposing environmental constraints along an aridity gradient. Ecography 29, 66-74.

Pierce, S., Brusa, G., Vagge, I., Cerabolini, B.E.L., 2013. Allocating CSR plant functional types: the use of leaf economics and size traits to classify woody and herbaceous vascular plants. Func. Ecol. 27, 1002-1010.

Pinna, M., 1985. Contributi di Climatologia. Mem. Soc. Geogr. Ital. 39, 147-167 (in Italian).

Prisco, I., Carboni, M., Acosta, A.T.R., 2013. The fate of threatened coastal dune habitats in Italy under climate change scenarios. PLOS One 8(7), e68850. doi: 10.1371/journal.pone.0068850.

Psuty, N., 2004. The coastal foredune: a morphological basis for regional coastal dune development. In: Martínez ML, Psuty N (Eds.). Coastal dunes: ecology and conservation. Springer-Verlag. Heidelberg, Germany, pp. 11–27.

R Development Core Team, 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. Available at http://cran.r-project.org/. Accessed 02 Sept 2013

Ranwell, D.S., 1972. Ecology of salt marshes and sand dunes. Chapman and Hall. London, UK.

Rapetti, F., 2003. Il clima. In: Federici, P.R. (Ed.). Atlante tematico della Provincia di Pisa. Pacini Editore. Pisa, Italy, pp. 16-17 (in Italian).

Read, J., Sanson, G.D., Lamont, B.B., 2005. Leaf mechanical properties in sclerophyll woodland and shrubland on contrasting soils. Plant Soil 276, 95-113.

Ricotta, C., Bacaro, G., Caccianiga, M., Cerabolini, B.E.L., Moretti, M. A classical measure of phylogenetic dissimilarity and its relationship with beta diversity. Basic Applied Ecol. (in press).

Ricotta, C., Pavoine, S., Bacaro, G., Acosta, A.T.R., 2012. Functional rarefaction for species abundance data. Methods Ecol. Evol. 3, 519-525.

Ruocco, M., Bertoni, D., Sarti, G., Ciccarelli, D. Mediterranean coastal dune systems: Which abiotic factors have the most influence on plant communities? Estuar. Coast. Shelf Sci. 149, 213-222.

Pignatti, S., 2002. La vegetazione delle spiagge. In: AAVV (Eds.). Dune e spiagge sabbiose. Quaderni habitat. Ministero dell'Ambiente e della Tutela del Territorio e del Mare. Museo Friulano di Storia Naturale. Udine, Italy, p. 57 (in Italian).

Santoro, R., Jucker, T., Prisco, I., Carboni, M., Battisti, C., Acosta, A.T.R., 2012. Effects of trampling limitation on coastal dune plant communities. Environ. Manage. 49, 534-542.

Spanò, C., Balestri, M., Bottega, S., Grilli, I., Forino, L.M.C., Ciccarelli, D., 2013. *Anthemis maritima* L. in different coastal habitats: A tool to explore plant plasticity. Estuar. Coast. Shelf Sci. 129, 105-111.

Stallins. J.A., Parker, A.J., 2003. The influence of complex systems interactions on barrier island dune vegetation pattern and process. Ann. Assoc. Am. Geogr. 93, 13-29.

Stanisci, A., Acosta, A., Ercole, S., Blasi, C., 2004. Plant communities on coastal dunes in Lazio (Italy). Ann. Bot. (Roma), Studi sul Territorio 48(7), 85-94.

Vagge, I., Biondi, E., 1999. La vegetazione delle coste sabbiose del Tirreno settentrionale italiano. Fitosociologia 36(2), 61-95 (in Italian).

Valladares, F., Gianoli, E., Gomez, J.M., 2007. Ecological limits to plant phenotypic plasticity. New Phytol. 176, 749-763.

Violle, C., Navas, M.-L., Vile, D., et al., 2007. Let the concept of trait be functional! OIKOS 116, 882-892.

Westoby, M., 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. Plant Soil 199, 213-227.

Wiedemann, A.M., Pickart, A., 2004. Temperate zone coastal dunes. In: Martínez, M.L., Psuty, N. (Eds.). Coastal dunes: ecology and conservation. Springer-Verlag. Heidelberg, Germany, pp. 53–65.

Wilson, J.B., Sykes, M.T., 1999. Is zonation on coastal sand dunes determined primarily by sand burial or by salt spray? A test in New Zealand dunes. Ecol. Lett. 2, 233-236.

Wright, I.J., Reich, P.B., Cornelissen, J.H.C., et al., 2005. Assessing the generality of global leaf trait relationships. New Phytol. 166, 485-496.

Fig.1. Map of Italy with Tuscany in grey. The study sites are indicated by asterisks. On the right a picture of Europe with Italy in grey.

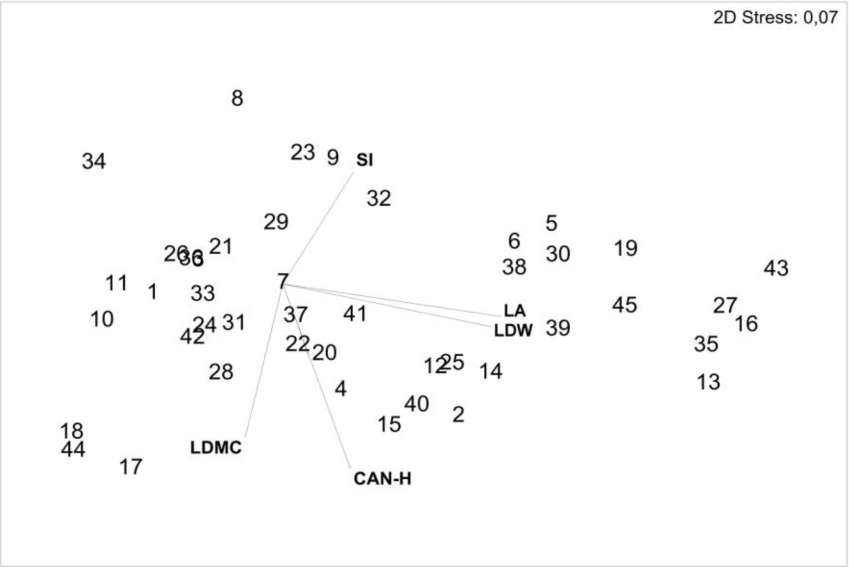


Fig. 2. NMDS diagram based on the dissimilarity (measured by the Bray-Curtis dissimilarity metric) occurring in 45 plant species measuring nine functional traits. All the traits have a Spearman correlation coefficient > 0.3 with the two axes. Trait abbreviations: CAN-H = canopy height; LA = leaf area; LDMC = leaf dry matter content; LDW = leaf dry weight; SI = succulence index. Plant codes: 1 = *Achillea maritima*; 2 = *Ammophila arenaria*; 3 = *Anthemis maritima*; 4 = *Bromus sterilis*; 5 = *Cakile maritima*; 6 = *Calystegia soldanella*; 7 = *Catapodium balearicum*; 8 = *Cerastium ligusticum*; 9 = *Chamaesyce peplis*; 10 = *Crucianella maritima*; 11 = *Cutandia maritima*; 12 = *Dittrichia viscosa*; 13 = *Echinophora spinosa*; 14 = *Elymus farctus*; 15 = *Erigeron canadensis*; 16 = *Eryngium maritimum*; 17 = *Euphorbia paralias*; 18 = *Helichrysum stoechas*; 19 = *Hypochaeris radicata*; 20 = = *Lagurus ovatus*; 21 = *Limbarda crithmoides*; 22 = *Lotus hirsutus*; 23 = *Medicago littoralis*; 24 = *Medicago marina*; 25 = *Oenothera biennis*; 26 = *Ononis variegata*; 27 = *Pancratium maritimum*; 28 = *Phleum arenarium*; 29 = *Plantago arenaria*; 30 = *Plantago coronopus*; 31 = *Polygonum maritimum*; 32 = *Pseudorlaya pumila*; 33 = *Pycnocomon rutifolium*; 34 = *Salsola kali*; 35 = *Seseli tortuosum*; 36 = *Silene canescens*; 37 = *Silene niceensis*; 38 = *Silene otites*; 39 = *Solidago litoralis*; 40 = *Spartina versicolor*; 41 = *Sporobolus virginicus*; 42 = *Teucrium polium*; 43 = *Verbascum sinuatum*; 44 = *Vulpia fasciculata*; 45 = *Xanthium orientale* subsp. *italicum*.

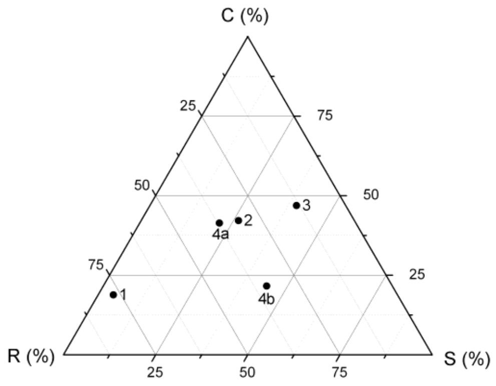
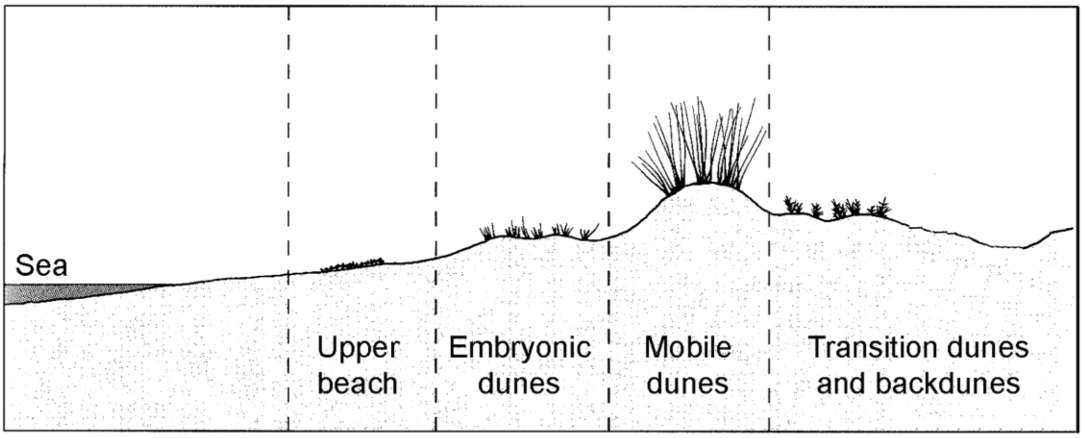


Fig. 3. The CSR plant strategy spectrum of the five plant communities. The values depicted in the triangle are the habitat mean values of community-weighted mean CSR. 1 = upper beach with annual vegetation of drift lines; 2 = embryonic dunes; 3 = mobile dunes with *Ammophila arenaria*; 4a = *Crucianellion maritimae* communities ; 4b = *Malcolmietalia* grasslands.



Appendix 1. Psammophilous sequence along the sea-inland gradient (modified from Pignatti, 2002).

Table 1 Summary of aggregated plant traits mean for each plant community type (only values for the quantitative traits are shown). The highest values are reported in bold. Abbreviations: CAN-H = canopy height; LA = leaf area; LDMC = leaf dry matter content; LDW = leaf dry weight; SLA = specific leaf area; SI = succulence index. Data are the mean ± SE. Means followed by the same letters are not significantly different at 1% according to the non-parametric Kruskal-Wallis one-way ANOVA after the Bonferroni correction for multiple comparisons.

Plant community	CAN-H$_{agg}$ (mm)	LA$_{agg}$ (mm^{2})	LDMC$_{agg}$ (%)	LDW$_{agg}$ (mg)	SLA$_{agg}$ (mm^{2} mg^{-1})	SI$_{agg}$ (mg cm^{-2})
Upper beach	2770^{a} ± 299	27940^{ab} ± 5158	187^{a} ± 23	3976^{ac} ± 994	187^{a} ± 18	1198^{a} ± 132
Embryonic dunes	6886^{bd} ± 312	**53329^{c} ± 4123**	463^{b} ± 19	**12496^{b} ± 1127**	206^{a} ± 10	1192^{a} ± 76
Mobile dunes	**23412^{c} ± 1426**	48340^{ac} ± 3665	**1136^{c} ± 61**	8098^{c} ± 781	**346^{b} ± 17**	**1246^{a}± 70**
Crucianellion maritimae shrub	8310^{d} ± 491	11896^{b} ± 1796	709^{d} ± 35	2162^{ad} ± 374	307^{b} ± 15	691^{b} ± 36
Malcolmietalia grasslands	4595^{ab} ± 370	17967^{b} ± 2092	612^{bd} ± 40	4033^{acd} ± 91	344^{b} ± 22	684^{b} ± 53

Table 2 Summary of the community-weighted mean CSR values (CWM) for each plant community type. The highest values are reported in bold. Abbreviations: C = competitors; S = stress-tolerants; R = ruderals. Data are the weighted mean ± SE. Means followed by the same letters are not significantly different at 1% according to the non-parametric Kruskal-Wallis one-way ANOVA after the Bonferroni correction for multiple comparisons.

Plant community	C (%)	S (%)	R (%)
Upper beach	18.8^{a} ± 3.4	4.1^{a} ± 0.8	**77.1^{a}** ± 7.5
Embryonic dunes	42.1^{b} ± 2.3	26.5^{b} ± 1.7	31.4^{b} ± 2.5
Mobile dunes	**46.7**^{c} ± 2.5	39.7^{c} ± 2.4	13.6^{c} ± 0.9
Crucianellion maritimae shrubs	41.1^{b} ± 2.1	21.6^{b} ± 1.2	37.3^{d} ± 1.8
Malcolmietalia grasslands	21.1^{a} ± 1.5	**44.8**^{d} ± 3.6	34.1^{bd} ± 2.4