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Vegetative and reproductive phenological patterns in coastal dunes in S Spain

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Abstract

Rodríguez-Gallego,C. & Navarro, T. 2015. Vegetative and reproductive phenological patterns in coastal dunes in S Spain. *Anales Jard. Bot. Madrid* 72(1): e017.

The phenology of Mediterranean plant species has been extensively studied in different types of ecosystems. However, very little research has been conducted on dune ecosystems. The aim of this research is the phenological characterization and comparison among phenological patterns in three coastal dunes areas in S Spain. For this purpose, we apply the methodology proposed by Orshan (1989) and NLPCA phenological indexes. Our results show that seasonality of species from coastal dunes in S Spain follows the pattern observed in dry and warm Mediterranean ecosystems. The maximum phenological activity occurs for a period of 7-9 months, mainly in spring and late winter, whereas summer is clearly the most inactive period of the year. Vegetative phenophases predominate over the reproductive. Flowering is mainly early (March-May), but it may extend to summer. Flowering duration has been identified as a key index in the differentiation among coastal dunes with different conditions of Mediterranean macroclimate, whereas the importance of the phenophase sequence index has been shown in order to discriminate sectors within dunes. Using the NLPCA analysis based on phenological indexes, four phenological groups of species have been determined. From a conservation perspective, the identification of these groups point out the utility of developing different strategies of management according to the high diversity of eco- and phenomorphological variability that characterize the coastal dunes.

Keywords: Coastal dunes; Mediterranean vegetation; S Spain; Phenological phases; Phenological indexes; Flowering duration.

Resumen

Rodríguez-Gallego,C. & Navarro, T. 2015. Patrones fenológicos vegetativos y reproductivos en dunas costeras Vegetative and reproductive phenological patterns in coastal dunes in S Spain. *Anales Jard. Bot. Madrid* 72(1): e017.

La fenología de las especies vegetales mediterráneas ha sido ampliamente estudiada en diferentes tipos de ecosistemas. Sin embargo, es poco lo que se conoce sobre fenología de dunas costeras. El objetivo del presente trabajo es la caracterización y comparación de patrones fenológicos en tres áreas de dunas costeras del Sur de España. Para ello, se ha aplicado la metodología propuesta por Orshan (1989) así como índices fenológicos NLPCA. Nuestros resultados muestran que la estacionalidad de las especies de dunas costeras es comparable a los patrones previamente observados en otros ecosistemas mediterráneos de tipo seco y cálido. La máxima actividad fenológica se concentra en 7-9 meses, principalmente en primavera e invierno tardío, mientras que el verano es claramente el periodo con menor actividad fenológica del año. Las fenofases vegetativas predominan sobre las reproductivas. La floración es principalmente temprana (Marzo-Mayo), aunque puede extenderse hasta elverano. La duración de la floración ha sido identificada como carácter clave en la diferenciación entre dunas costeras sometidas a distintas condiciones dentro del macroclima mediterráneo, mientras que se resalta la importancia del índice de secuenciación fenofásica para la distinción entre los sectores de la duna. El empleo del análisis NLPCA basado en los índices fenológicos ha determinado cuatro grupos fenológicos. Desde la perspectiva de la conservación, estos grupos resaltan la necesidad de desarrollar diferentes estrategias de manejo ce acuerdocon la elevada diversidad ecomorfológica y fenomorfológica que caracterizan a las dunas costeras.

Palabras clave: Dunas costeras, vegetación mediterránea, S España, fases fonológicas, índices fenológicas, duración de la floración.

INTRODUCTION

Phenology, the study of recurrent life cycle events (Nadia & al., 2012), is a decisive feature determining the plant adaptation to seasonally changing environments and their persistence in the habitats (Orshan, 1989; Castro-Díez & Montserrat-Martí, 1998). Phenophases are the life cycle events, and their distribution throughout the year constitute the plant phenological pattern (Castro-Díez & Montserrat-Martí, 1998), which is constrained by plant morphology, physiology, and more generally by the genetic and epigenetic background of each life cycle (Rathcke & Lacey, 1985).

Phenological patterns of Mediterranean species show a clear association between phenological phases and some important climate factors (Mooney & al., 1974; Reader, 1984), such as rainfall variability (Cowling & al., 2005), photoperiod (Arroyo, 1990) and summer drought (Mitrakos, 1980; Roche & al., 1997). Low winter temperatures and summer drought involve unfavourable periods (Mitakros, 1980; Castro-Díez & al., 2005). Under these conditions, plant communities reach a maximum of flowering and growth in spring, sometimes with a smaller peak in autumn (Orshan, 1989; Floret & al., 1989; Cabezudo & al., 1993), whereas the timing of other phenophases, for example fruit setting, are more variable (Orshan, 1989). However, species growing under the same climatic conditions may differ widely in the arrangement of their phenophases (Castro-Díez & Montserrat-Martí, 1998). This diversity may respond to a huge variety of structural and floristic backgrounds (Mooney & al., 1977; Kummerow, 1983).

The use of ecomorphology and phenomorphology (phenological phases) to study Mediterranean vegetation and flora was first proposed by Orshan (1989) and subsequently improved by the development of specific methodologies such as the quantification of key phenological

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indexes (Castro-Díez & Montserrat-Martí, 1998; Pérez-Latorre & Cabezudo, 2002). By using this approach, different Mediterranean communities have been characterized in phenological terms (e.g. Pérez-Latorre & Cabezudo, 2006; Pérez-Latorre & al., 2010), but this is the first time that this eco-morphological methodology has been applied to Mediterranean vegetation in coastal ecosystems.

Coastal dune systems are defined by particular environment conditions such as the wind, drought, salt spray, soil salinity, high intensity of light and temperature, or nutrient poverty (García-Mora & al., 2001; Ley Vega de Seoane & al., 2007). These features affect the composition and abundance of vegetation and functional characters (García-Mora & al., 1999; Ley Vega de Seoane, 2007), and define different environmental sectors from the sea area to the inland area (e.g. van der Maarel, 1997; Carter, 1988; Brown & McLachlan, 1994).

Coastal dunes are extremely fragile and very vulnerable to human activity, which is particularly striking in the Mediterranean (Curr & al., 2000). The current status of coastal dune ecosystems constitute a serious danger for all the ecosystem services that it develops, such as protection against sea waves, wind, floods or erosion (Kiehl & Isermann, 2007) and for the survival of the important habitats that 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 prior interest according to Red Natura 2000 (VV.AA, 2009).

Although previous studies have focused on the analysis of plant communities and on threats faced by coastal dune populations (e.g. García-Mora & al., 1999, 2000, 2001; Acosta & al., 2003, 2005; Martínez & al., 2006), very little is known regarding phenological patterns (Herrera 1986; Laguna & al., 1986; Moreno Duran & al., 1997). However, this information would be very interesting for the complete characterization of biotic and abiotic factors that has been suggested as a field of research needed in these types of ecosystem (Gracia, 2009). This novel approach would also involve important applications in terms of management, conservation and even, in studies of relationships with climatic changes and community monitoring (Beaubien & Johnson, 1994; Montserrat-Martí & al., 2004).

In addition, the selection of the study area in S Spain offers the interesting opportunity to study these ecosystems under different conditions of the Mediterranean macroclimate (Mediterranean-oceanic, Mediterranean-subtropical and Mediterranean-subdesert) and different oceanic influences (from transitional dunes between the Atlantic Ocean and the Mediterranean Sea to typical Mediterranean dunes). Consequently, the results obtained in the present work go beyond the regional scope, and could be useful at a larger scale.

The objectives of this study are (1), to assess the occurrence and intensity of phenological phases of dune plants throughout the different seasons under various conditions of the Mediterranean macroclimate (oceanic- subtropical-subdesert); (2) to compare the phenological pattern of dune plant species on fixed and mobile semi-fixed dunes; and (3) to define the main groups of species with common phenological patterns and discuss their ecological meaning in the context of coastal dunes.

MATERIAL AND METHODS

Study area and species

The study was carried out in 78 perennial species located n three Mediterranean coastal dunes in S Spain with different Mediterranean climate (DERA, 2013): P.N. del Estrecho in Cádiz (Mediterrarean-oceanic climate) (52 species), M.N. Artola-Cabopino in Málaga (Mediterranean-subtropical) (34 species) and P.N Cabo de Gata-Níjar in Almería (Mediterranean-subdesert) (24 species) (Fig. 1).

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). Temperatures are milder than those in the other two dunes (mean-minima of 13.4 °C in January and mean-minima of 23.5 °C in August) because of the effect of wind acceleration in the area. M.N. Artola-Cabopino shows an average annual rainfall of 659.2 mm, with similar rainy season to P.N. del Estrecho. January was also the coldest (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 values are observed in March and December, 40 mm). In addition, the temperatures are the harshest, with mean-minima of 10.8 °C in January and mean-maxima of 25.9 °C in August (Fig. 2).

Independently of the climatic area where the dunes were located, different sectors of dunes were identified depending on the organization of a set of environmental traits that characterize these ecosystems (e.g. Carter, 1988; van der Maarel, 1997; Brown & McLachlan, 1994). In this study, the scheme of dune sectorization was based on sands mobility (van der Maarel, 1993). This criterion was able to differentiate between fixed dunes, semi-fixed and mobile dunes. However, the two last types of dunes were unified in this work into one single type because of the low number of perennial species on mobile dunes. Fixed dunes are formed by shrubs and trees and it represents the mature stage of the ecosystem. Mobile semi-fixed dune vegetation is constituted by pioneer communities of herbs and small shrubs, which are adapted to tolerate the intense disturbances that are mainly associated to the proximity of the sea (Costa-Pérez & Valle-Tendero, 2004; Ley Vega de Seoane, 2007).

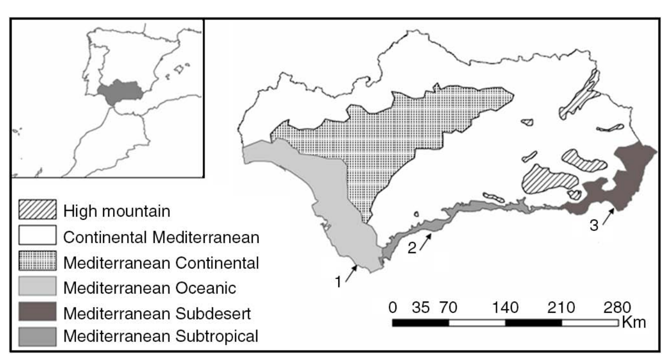

Fig. 1. Climate areas in S Spain and study areas. Black dots show the study areas: (1) P.N. del Estrecho, (2) M.N. Artola-Cabopino, (3) P.N. Cabo de Gata-Níjar. Data source: DERA ("Datos Espaciales de Referencia de Andalucía"). Junta de Andalucía. Consejería de Medio Ambiente, 2013.

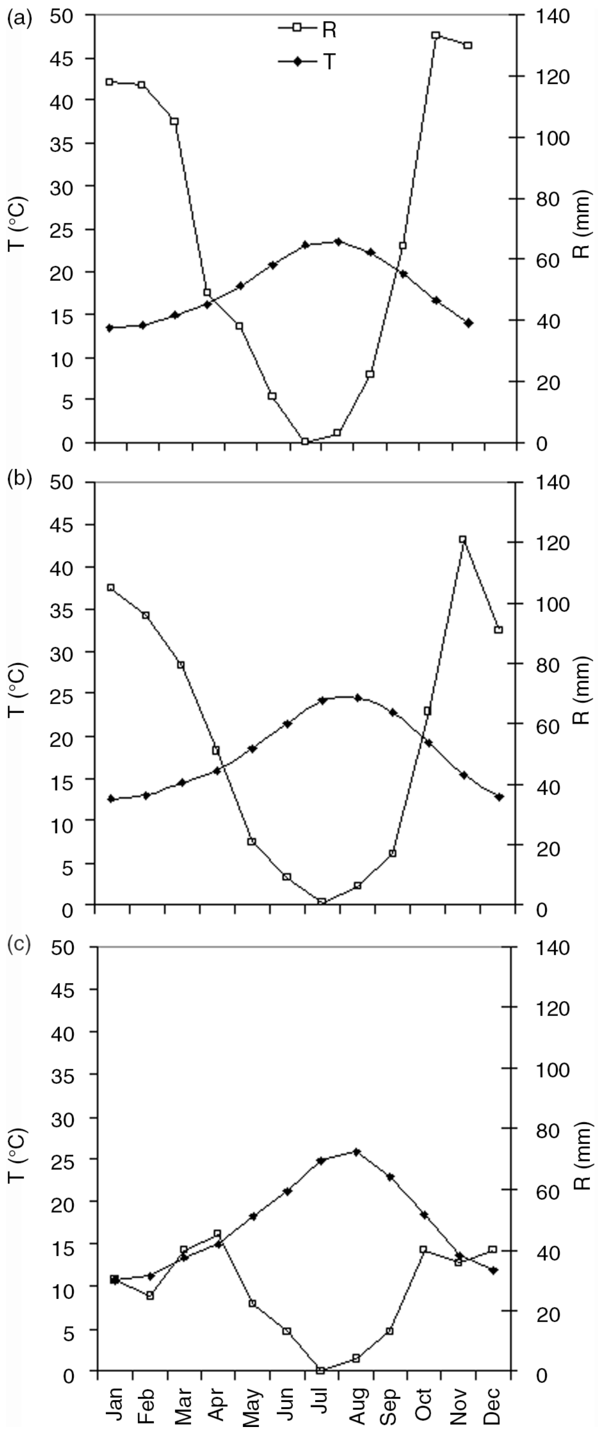

Fig. 2. Climatic diagrams (a) P.N. del Estrecho, (b) M.N. Artola-Cabopino and (c) P.N Cabo de Gata-Níjar. Data source: Rivas Martínez, 2009.

Data collection, phenological information and phenological indexes

Field sampling was carried out during the period of 2009-2012 on a minimum of 10 individuals of each species. The inventories were made following Braun Blanquet (1979) by a selection of the major representative perennial species (Van der Maarel, 1997; Navarro & al., 2006). Voucher specimens of the studied species were kept in the MGC Herbarium using botanical nomenclature accepted by Castroviejo (1986-2007). The ecomorphological traits (growth forms, leaf habit, consistence and colour) were directly determined for each species in the field (Table 1).

For the phenological study we used the methodology put forward by Orshan (1989). Data related ro vegetative and reproductive phenological phases were recorded during the period of 2007-2012. To characterize and compare the phenological patterns in S Spain coastal dunes, we studied the phenophases (Appendix A) and the phenological indexes (Appendix B) as follows.

For vegetative phases, we studied vegetative growth of dolichoblasts (DVG) and vegetative growth of brachyblasts (DVB). Brachyblast was considered to be the branches which are shorter than 3 cm in length, and dolichoblast, the longer ones (Orshan, 1989). At reproductive phases, flower bud formation (FBF), flowering (F), fruit setting (FS) and seed dispersal (SD) were tested. Phenological calendars were averaged for each species (Appendix A) and represented in diagrams (Fig. 3), which synthetically show the frequency of the occurrence of phenophases.

The length of the phenological cycle was measured using the Active Phenophasic Period of the species (APS) (Pérez-Latorre & Cabezudo, 2002). This index is defined as the number of months per year in which each species shows activity with respect to phenological phases.

$$APS=t\ (DVG+DVB+FBF+F+FS)$$

According to previous results (Pérez-Latorre & Cabezudo, 2002), it has been converted it into a qualitative scale: (1) activity all the year round; (2) long APS (10-11 months); (3) medium APS (7-9 months) and (4) short APS (<7 months).

To estimate the degree of sequencing vegetative and reproductive phenophases, the Phenophase Sequence index (PSI) (Castro-Díez & Montserrat-Martí, 1998) was calculated

$$PSI=t\ (DVG+FBF+F)/[t\ (DVG)+t\ (FBF)+t\ (F)]$$

t is the number of months needed to complete the phenophase(s) indicated between parentheses. It varies from 0.33 to 1. High index values indicate a sequential organization (PSI≥0.6), while low values are related with a greater degree of overlap (PSI<0.6).

To evaluate the relationship between reproductive and vegetative phenological phases, index of Reproductive/Vegetative Activity of the species (RVA) (Pérez-Latorre & Cabezudo, 2002) was used

$$RVA=t\ (FBF+F+FS)/t\ (DVG+DVB)$$

The predominance of vegetative phenophases is linked to RVA<1, whereas reproductive phenophases is dominant when RVA>1. In case of RVA=1, there is no predominant phase.

In relation to flowering time, two indexes were analyzed: Flowering Duration (FD) and Onset Flowering (OF) of species, which respectively indicate the length and the beginning of the phenophase, both of them measured in days.

Table 1. Some important ecomorphological traits in the studied species in coastal dunes ecosystems in S Spain

	P.N. del Estrecho				M.N. Artola-Cabopino				P.N. Cabo de Gata-Níjar			
	Fixed		Mobile-semi		Fixed		Mobile-semi		Fixed		Mobile-semi	
	N	%	N	%	N	%	N	%	N	%	N	%
Growth forms												
Herbs	1	2.56	5	38.46	1	4.17	6	54.55	0	0	3	21.43
Small shrubs	13	33.33	8	61.54	8	33.33	5	45.45	7	63.64	11	78.57
Large shmbs	19	48.72	0	0	10	41.67	0	0	4	36.36	0	0
Trees	6	15.38	0	0	5	20.83	0	0	0	0	0	0
Leaf habit												
Evergreen	17	43.59	1	7.69	10	41.67	1	9.09	5	45.45	3	21.43
Semideciuous	15	38.46	6	46.15	9	37.50	4	36.36	2	18.18	7	50
Deciduous	7	17.95	6	46.15	5	20.83	6	54.55	4	36.36	4	28.57
Leaf colour												
Green	32	82.05	7	53.85	20	83.33	3	27.27	9	81.82	6	42.86
Green-grey	3	7.69	0	0	2	8.33	1	9.09	0	0	0	0
Grey	4	10.26	6	46.15	2	8.33	7	63.64	2	18.18	8	57.14
Leaf consistence												
Sclerophyllous	17	43.59	1	7.69	12	50	1	9.09	5	45.45	1	7.14
Malacophyllous	22	56.41	12	92.31	12	50	10	90.91	6	54.55	13	92.86

$$FD=d\ (F)$$

d is the number of days needed to complete the phenophase. It has been differentiated between: (1) Short flowering duration ($FD \leq 31$); (2) medium ($31<FD<120$), which is mainly concentrated in spring; and (3) long ($120 \leq FD \leq 360$).

$$OF=i\ (F)$$

i is the number of days before the beginning of the phenophase. The OF categories are: (1) clearly early flowering ($0 \leq OF<59$), (2) early ($59 \leq OF<151$), (3) middle ($151 \leq OF<212$), (4) late ($212 \leq OF<304$) and (5) clearly late ($304 \leq OF<365$).

Statistical analysis

Continuous characters were $\log_{10}$-transformed prior to statistical analysis. All statistical analyses were performed with SPSS 15.0 (SPSS Inc). T-Tests and One-way analysis of variance ANOVA were applied after verifying the homogeneity of variance by Levene's test ($P>0.05$) to test for differences among the three coastal dunes, its dune sectors and the studied ecomorphological traits. In the case of not verifying the Levene's test, Mann-Whitney and Kruskal-Wallis analyses were done.

To identify phenological groups, a nonlinear principal component based on phenological indexes was done (NLPCA, de Leeuw, 1982) by the program CATPCA, included in the software SPSS 15.0 (SPSS Inc). NLPCA can handle variables of different types simultaneously and deal with nonlinear relationships between them. Alpha of Cronbach was calculated (Cronbach, 1951) for each extracted component. If this value is high to a specific component, it would be interpreted as an indicator of the weight of the component. Also, it serves to explain the total variance. In general, an alpha value of 0.7 or greater is considered reliable (Bland & altman, 1997).

RESULTS

Phenomorphology of coastal dunes in S Spain

The distribution of values for some relevant ecomorphological traits in the study areas are summarized in Table 1. Most of the analyzed species were shrubs with green malacophyllous leaves.

In coastal dunes from S Spain, vegetative phenophases were mainly concentrated in late winter and early spring (Jan-Mar), when the temperatures were mild and the precipitations were high (Fig. 3). In summer (Jun-Sep), when the drought is highest (Fig. 3), vegetative phenophases were overly reduced. There were some species which showed DVG throughout the year, such as *Calluna vulgaris* and *Malcolmia littorea* (Appendix A). There were those whose BVG was continued all year long (e.g. *Ononis natrix* and *Rhamnus lycioides*) (Appendix A). The shortest length of time that species took in vegetative growth was between two and three months (e.g. *Asteriscus maritimus, Sideritis arborescens* and *Stauracanthus boivinii*) (Appendix A). The maximum flower bud formation, flowering and fruit setting were consecutive, with an important drop at the beginning of summer (Jun), when seed dispersal represents the most active phenophase, until Sep (Fig. 3). Most of the studied species showed middle flowering duration, which began in late winter and was extended to early summer (Figs. 3, 4, Appendix B). The exceptions were the species with continuous flowering all year long (*Malcolmia littorea, Launea arborescens* and

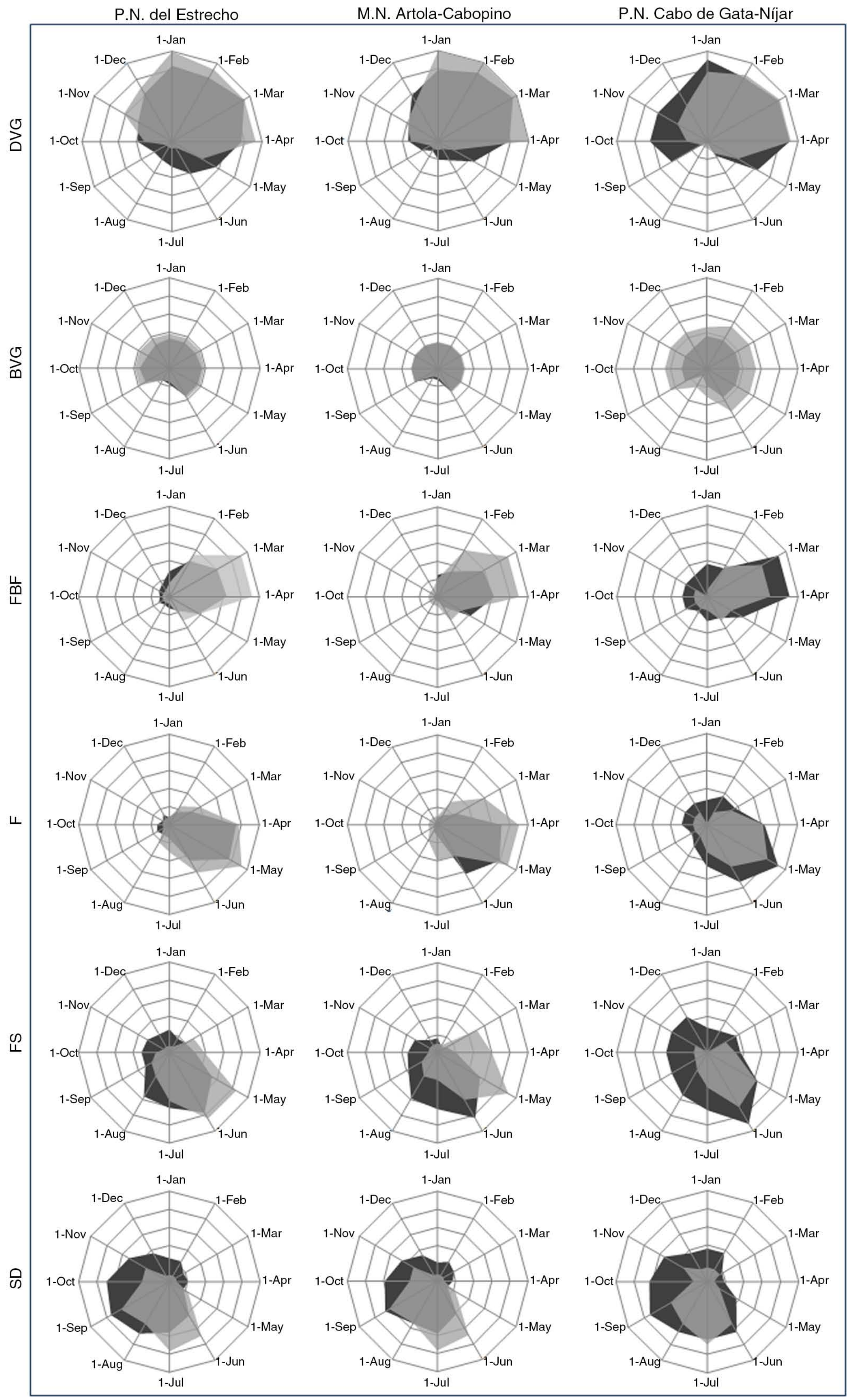

Fig. 3. Distribution of the vegetative phenological phases throughout the year in the coastal dunes, expressed as the monthly percentage of species that show each phenophase. The radius of the polar angle varies from 0, in the centre of the circle (no species developing the phenophase) to 100 (all species showing phenophase). Legend: dark-grey represents the fixed dunes; clear-grey, mobile semi-fixed dunes; and middle-grey, the overlapping of equal results in both dunes.

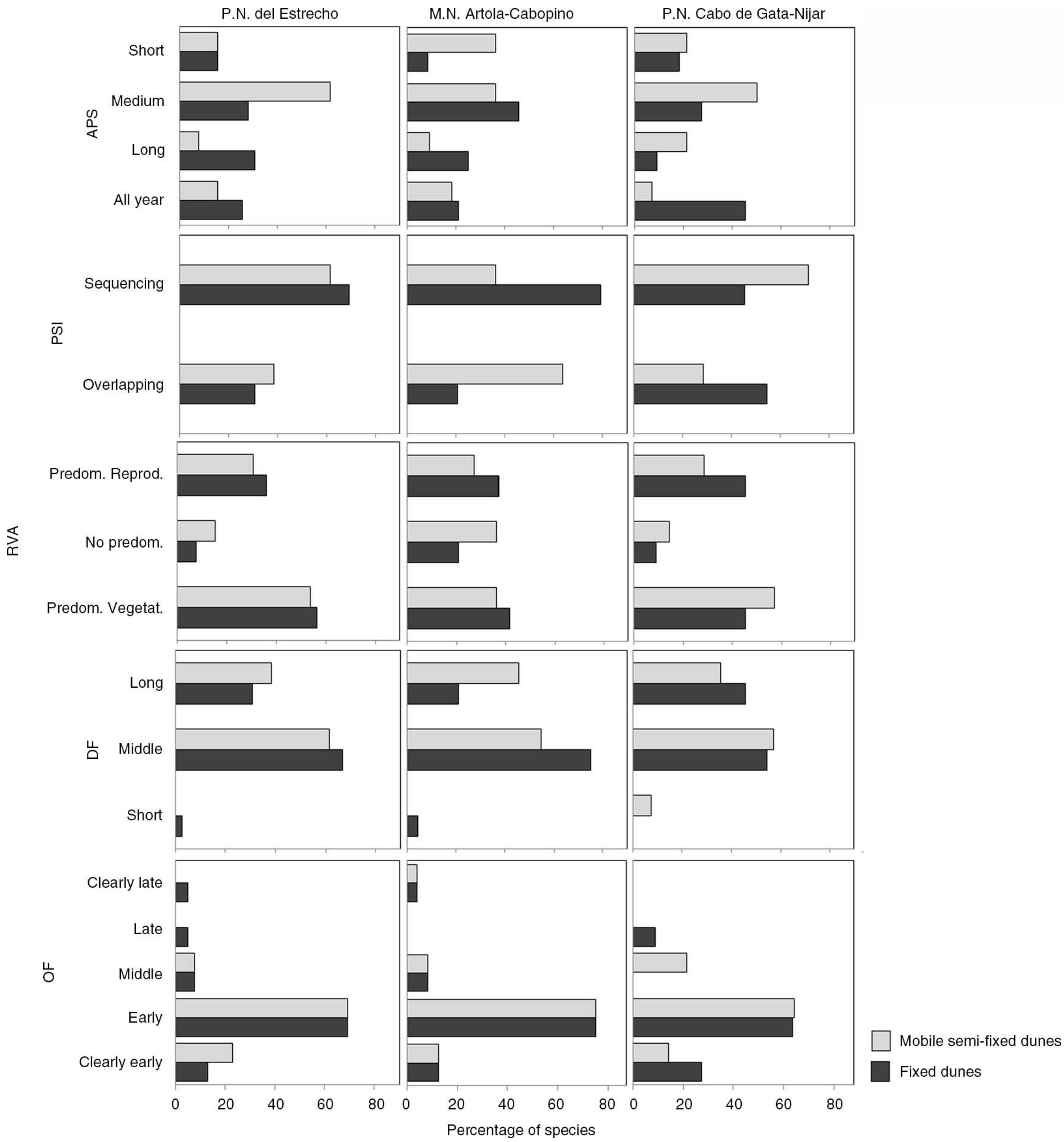

Fig. 4. Percentage of species in each of the qualitative classes defined for the different phenological indexes.

Lycium intricatum) (Appendix A) and the species that began their FBF in late summer-autumn (e.g. *Daphne gnidium* and *Calluna vulgaris*) (Appendix A). The shortest flowering duration (FD) was shown in *Juniperus phoenicea* and *Otanthus maritimus,* which only lasted one month (Appendix B).

In all studied dunes, most of the species were sequential (PSI≥0.6) with medium activity period (APS) and predominance of the vegetative phase (RVA<1) over the reproductive (RVA>1) (Fig. 4). Minimum values of APS were found in *Viola arborescens* and *Otanthus maritimus* (3-5 months), whereas APS went up to 12 months in species such as *Malcolmia littorea* and *Calluna vulgaris* (Appendix B). RVA was maximum in *Osyris lanceolata* (4) and minimum in *Plantago albicans* (0.25) (Appendix B). *Lonicera implexa* bared the maximum value of PSI (0.83) and *Malcolmia littorea,* the minimum (0.33) (Appendix B).

Comparison of phenomorphology among dunes

Among the studied ecomorphological traits, only growth forms showed significant differences among the three coastal dunes (F=2.37, P<0.1). This distinction was the result of a lower presence of large shrub and the absence of trees in P.N. Cabo de Gata.

However, significant differences of all the studied ecomorphological traits, except leaf habit (t=−0.67, P>0.1), were found between fixed and mobile semi-fixed dunes. Mobile semi-fixed dunes were differentiated to the fixed dunes by a lower presence of evergreen species, the absence of large shrubs and trees (t=−8.07, P<0.001) and the higher percentage of species with white (t=5.43, P<0.001) malacophyllous leaves (t=4.35, P<0.001).

Specific patterns within the general phenological tendency have been found in the studied coastal dunes. Among the

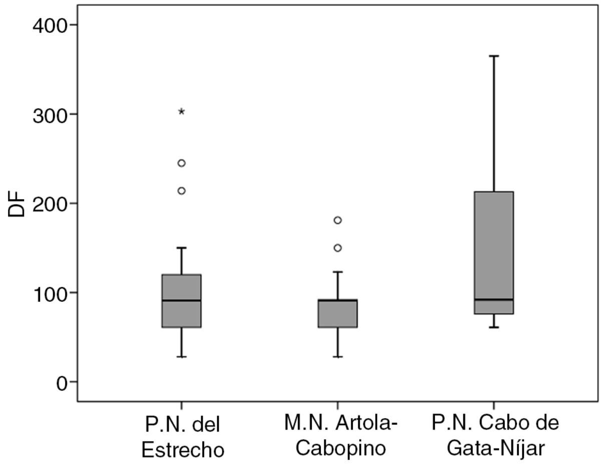

Fig. 5. Variation of FD (Flowering duration) among fixed coastal dunes in S Spain. Box plots show median, quartiles, outliers (O) and extreme (*) values of FD.

three dunes studied, ANOVA test did not show any significant difference of phenology. However, when the analysis was performed by differencing between fixed and mobile semi-fixed dunes in each studied coastal dunes, FD was shown as a good tool in the differentiation among dunes regarding Mediterranean climate types (F=3.03, P>0.1) (Fig. 5).

Only in M.N. Artola-Cabopino the t-test has confirmed significant differences of phenological indexes between dune sectors. PSI values (t=–2.05, P<0.05) (Fig. 6) meant that overlapping species were predominated on mobile semi-fixed dunes from this location, a result that contrasts with the majority of sequencing species found in fixed dunes.

Figure 3 confirms these results and it also shows some interesting differences of phenological phases. P.N. Cabo de Gata was differenced from the other two dunes by its absence of DVG in summer (especially in Jul-Aug), a pattern which was very close to that observed in mobile semi-fixed dunes from the three localities, and the higher DVG values obtained in autumn (between Sep and Nov) in its

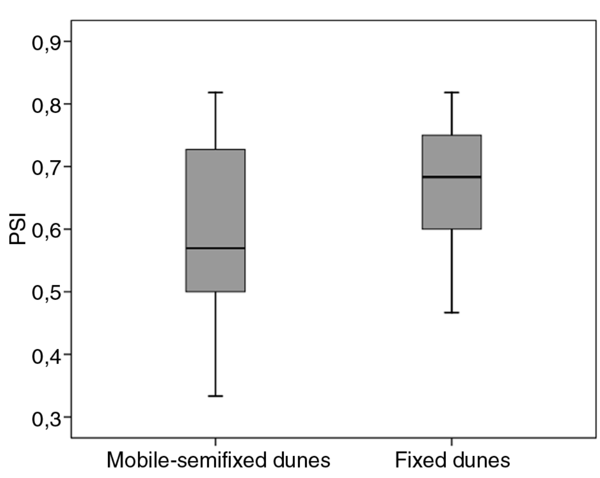

Fig. 6. Variation of PSI (Phenophase sequence index) between fixed and mobile semi-fixed dunes in M.N. Artola-Cabopino.

fixed dunes. For example, during the month of Oct, 63.64% of studied species in fixed dunes from P.N. Cabo de Gata-Níjar showed DVG, whereas this value was lower than 40% in the other two dunes (38.46% in fixed dunes in P.N. del Estrecho and 33.33% in M.N. Artola-Cabopino). Fixed dunes of P.N. Cabo de Gata-Níjar also showed differences of flowering. In this location, FBF and F were prolonged during autumn and winter, with values that are between two and six times the values obtained in P.N. del Estrecho and M.N. Artola-Cabopino, respectively. Fruit setting and seed dispersal were slightly delayed and prolonged in fixed dunes from the three locations, without a maximum peak of seed dispersal (Fig. 3).

Phenological groups

Principal component analysis identified combinations of phenological indexes (APS, PSI, RVA, FD and OF) that best summarized the data.

In Coastal dunes of P.N. del Estrecho (Fig. 7a), components extracted from the data explained 63.67% of the total trait variation (Cronbach alpha 0.86). The first principal component explained 40.79% of the total trait variation (Cronbach alpha 0.64) and it was most strongly and negatively correlated with FD but positively with PSI (–0.88 and 0.82, respectively). The second component explained a further 22.88% of variation (Cronbach alpha 0.16). This was strongly correlated with APS (0.84). In coastal dunes of M.N. Artola-Cabopino (Fig. 7b), components extracted from the data explained 68.40% of the total trait variation (Cronchach alpha 0.88). The first principal component explained 46.20% of the total trait variation (Cronchach alpha 0.71). Unlike the previous case, it was most strongly and negatively correlated with PSI (–0.89), and OF (–0.86) but positively with FD (0.87). The second component explained a further 22.20% of variation (Cronbach alpha 0.12). This was strongly correlated with APS (0.94).

In coastal dunes of P.N. Cabo de Gata (Fig. 7c), components extracted from the data explained 78.02% of the total trait variation (Cronbach alpha 0.80). The first principal component explained 56.32% of the total trait variation (Cronbach alpha 0.80) and was most strongly correlated with FD (–0.90) and OF (0.85). As in the previous coastal dunes, the second component explained a further 21.69% of variation (Cronbach alpha 0.10). This was strongly correlated with APS (0.84).

We distinguished the following four groups of species on the space defined by the two components (Fig. 7, Appendix B):

(G1) Group 1: APS ranged from 5 to 12, PSI predominantly ≥0.6 (86.25% of species) and FD showed medium values of 102.76±48.02. The majority of species in this group showed a predominance of the vegetative phenopases over the reproductive phenopases (86.25%). It was mainly formed by shrubs (82.5%) with malacophyllous leaves (71.25%). Only 25% of these species were evergreen. Some examples were *Helichrysum picardii* and *Lotus creticus*;

(G2) Group 2: maximum APS (12) and FD (>214) but low PSI (lower than 0.6). This group was formed by large shrubs (66.67%) and herbs (33.33%), with predominance of malacophyllous leaves (66.67%) and without a dominant leaf deciduousness (50% are evergreen and

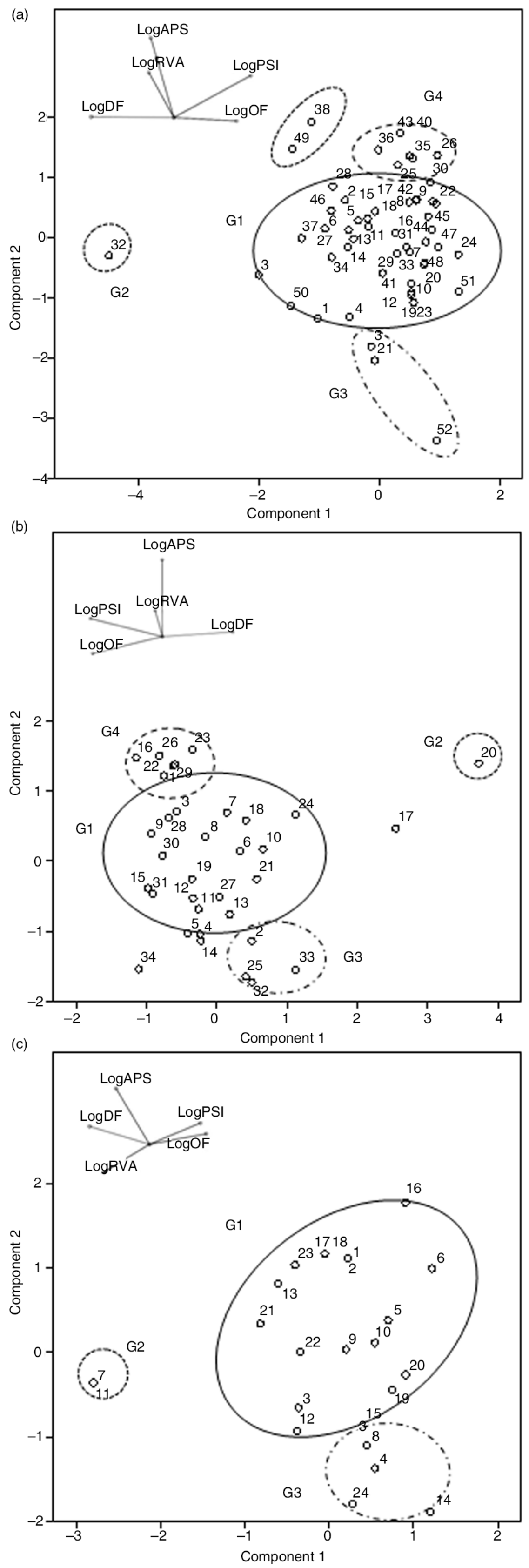

Fig. 7. Phenological groups in coastal dunes of S Spain. (a) P.N. del Estrecho, (b) M.N. Artola-Cabopino, (c) P.N. Cabo de Gata-Níjar. Legend: The numbered points represent plant species (Appendix 2); (F) Fixed dunes, (M) Mobile semi-fixed dunes; (G1) Group 1; (G2) Group 2; (G3) Group 3; (G4) Group 4.

50% are deciduous) (e.g. *Malcolmia littorea, Launea arborescens* and *Lycium intricatum*);

(G3) Group 3 was mainly formed by species of low values of APS (3-6), PSI values between 0.45-0.67 and FD lower than 120 days. This group was mainly formed by shrubs (90.91%) of semideciduous, (81.82%) and malacophyllous (81.82%) leaves, which were over represented on mobile semi-fixed dunes (63.64%) (e.g. *Viola arborescens* and *Othantus maritumus*);

(G4) Group 4: high APS (10-12) and PSI (>0.7), FD<92. These were trees (69.23%) and shrubs (30.77%) of sclerophyl leaves (84.61%) and evergreen (92.31%). This was only represented in fixed dunes of P.N. del Estrecho and M.N. Artola-Cabopino (e.g. *Juniperus phoenicea, Phyllerea angustifolia* and *Quercus coccifera*).

DISCUSSION

In this study, phenological indexes have revealed as an important tool for the complete characterization and differentiation of phenological patterns (e.g. Castro-Díez & Montserrat-Martí, 1998; Pérez-Latorre & Cabezudo, 2002; Milla, 2005) in coastal dune ecosystems.

Phenomorphological characterization of coastal dunes from S Spain

The sequence order of phenophases (PSI) plays an important role in the plant survival on coastal dunes, because it allows the species to accumulate resources through the period of development phenophase (Ratcke & Lacey, 1985) as well as makes it possible to minimize intraplant competition (Castro-Díez & Montserrat-Martí, 1998).

Similar APS values have been observed in other Mediterranean ecosystems, a result that points to the great similarity in the phenological activities of Mediterranean communities, despite the differences that exist in ecological, ecomorphological, and floristic composition aspects (Pérez-Latorre & al., 2010).

The majority of the active phenophasic period of species is occupied in vegetative growth (RVA<1), with values that ranged between 0.25 and 4. The duration and occurrence of vegetative and reproductive growth are important for the assimilation strategy and the use of carbon in Mediterranean woody plants (Mooney & al., 1977). These results match those of Mediterranean shrubland (Pérez-Latorre & Cabezudo, 2002; Pérez-Latorre & al., 2010) and contrast with the obtained in other woody Mediterranean communities, such as *Quercus suber* forest, where some species reach values of 7 (Pérez-Latorre & al., 2010).

The concentration of vegetative and reproductive phenophases observed in the studied coastal dunes coincide with patterns already described in drier and warmer Mediterranean regions, where the maximum phenological activity occurs in spring and late winter (Orshan, 1989; Navarro & al., 1993).

In coastal dunes, DVG starts in winter and it reaches its maximum when rain interval has finished and the temperature begins to increase. This result agrees with that observed on the coastal shrublands of Doñana, south Spain (Herrera, 1986), and the pattern is linked to the high demand of resources (water, carbohydrates and nutrients) necessary for the plant growth (Kummerow, 1983) and the limited storage capacity of dampness that characterized the coastal dunes (Ley Vega de Seoane & al., 2007).

According to previous studies on other coastal dune ecosystems (Cordazzo & Seeliger, 1998), middle flowering predominates in the three coastal dunes and the main flowering period occurs in early spring, just after winter rains, which is consistent with the pattern found in other Mediterranean areas of the world (Mooney & al., 1974; Kummerov, 1983; Herrera, 1986). Blooming in spring has been claimed to be optimal due to good water availability, mild temperatures and high insect activity (Baker & al., 1982; Kummerov, 1983; Herrera, 1986). Onset flowering implies how the resources allocated for maternal plant growth, seed production, germination and juvenile production will be distributed (Mazer, 1989, 1990; Bolmgren & Cowan, 2008). Therefore, an early OF is important in coastal dunes because it makes the development of the other phenophases possible and avoids summer stress. There are also species that extend F until summer and autumn (like *Calluna vulgaris* and *Stauracanthus boivinii*) or even winter (such as *Ulex australis* and *Viola arborescens*). This pattern has been observed in coastal dunes (Moreno & al., 1997) and arid ecosystems in the South East of Spain (Navarro & al., 1993), and it can be interpreted with reference to avoiding summer water stress (Castro-Díez & Montserrat-Martí, 1998; Perez-Latorre & Cabezudo, 2002) and competition for pollinators (Dafni, 1996; da Cruz & al., 2006).

Fruit setting and seed dispersal occur between late spring and early autumn, which shows the different functional strategies of the species (Navarro & Cabezudo, 1998). In the coastal dunes studied there were also species that extend their FS to late autumn or even winter. These are species with a continuous reproductive activity throughout the year (*Malcolmia littorea*, *Launea arborescens* and *Lycium intrincatum*) or species with both fleshy and heavy fruits (e.g. *Ziziphus lotus*, *Osyris lanceolata* and *Juniperus oxycedrus*) which need a longer time to mature their fruits (Milla & al., 2010). In addition, previous studies on the coastal shrublands of Doñana (Herrera, 1984, 1986) supported that this autumn ripening group is composed of species whose seeds are mainly dispersed by animals which need to match the fruiting season to the period with ample availability of avian dispersers (autumn and winter). According to Pérez-Tris & Santos (2004), at the end of the summer, many bird species leave large areas of Central and Northern Europe, and high mountains of the Mediterranean region, giving rise to a continuous movement of birds to their wintering areas, such as Strait of Gibraltar, to take advantage of the excellent ecological conditions where many trees and shrubs have begun to fruit (Tellería, 1988).

Comparison of phenomorphological patterns

Several remarkable differences of phenology have been found among the studied coastal dunes. These, are mainly related to the fixed dunes, and agree with those of the particular characteristics of mobile semi-fixed dunes. All over the world, coastal mobile semi-fixed dunes are regularly subjected to the same major types of environmental stress (García-Mora & al., 1999), and as a consequence, they show very close functional characters and diversity of species (Ley Vega de Seoane & al., 2007).

Flowering duration (FD) has been determined as a key index in the characterization and differentiation among the coastal dunes (Fig. 5), as it could be used as a functional trait related with clime (Godoy & al., 2009) and disturbance (Heinrich, 1976). Extended duration may be an advantage that allows individuals to track and accumulate resources needed for seed maturation in environments where resources are either temporally unpredictable or sparse (Rathcke & Lacey, 1985; Sánchez & al., 2012), such as subdesert (P.N. Cabo de Gata-Níjar) and mobile semi-fixed dunes.

Phenophase sequence index (PSI) has been identified as a differential index among dune sectors in M.N. Artola-Cabopino (Fig. 6). Whereas fixed dunes follow the general trend of predominating sequencing species, in mobile semi-fixed dunes there is a higher number of overlapping species, a result that is supported by the unpredictable conditions that affect this sector and the benefits of avoiding phenological activity during summer.

These harsher conditions also explain the differences of phenophases duration that have been found between dunes sectors, such as the absence of DVG in summer in mobile semi-fixed (only one species shows it, *Ononix natrix*) and the shorter FS and SD than in fixed dunes.

Phenological groups

The species tend to employ different strategies in order to complete their life cycle (Floret & al., 1989) and to reduce the interspecific competition for the resources (Navarro & Cabezudo, 1998). In the coastal dunes studied, the nonlinear principal components analysis indicate that we can differentiate among four phenological strategies.

Most of the species are included in the strategy of our group 1, and it includes the majority of the general characteristics that have been determined in this study as typical of coastal dunes. These are sequencing species, with middle APS and predominance of the vegetative phenophases, whose functional characters are adapted to the harsher environmental conditions of dunes (predominance of deciduous and semi deciduous shrubs of malacophyllous leaves). Within this general group, different phenophasic patterns previously identified in other studies in Mediterranean environments (Montenegro & al., 1989; Pérez-Latorre & Cabezudo, 2006; Pérez-Latorre & al., 2010) are included.

Group 2 is formed by species with very long phenophases (even all year long), a continuous phenological activity all year round and high overlapping. This pattern is generalized in species of tropical origin (Rathcke & Lacey, 1985), like *Launaea arborescens* (Carrión & al., 2003) that appeared in the study area during the early to mid Miocene, before the Mediterranean climate (Sánchez & al., 2012).

The species of group 3 grow and bloom when resources are abundant and remain with low phenological activity the rest of the year. Their vegetative and reproductive demands have to be supplied almost simultaneously, establishing a competition for resources (Mooney, 1983). The majority of these species (63.64%) are located on mobile semi-fixed dunes, a result which fits with Castro-Díez & Montserrat-Martí (1998), who stated that this strategy is probably more efficient to exploit environments where resources are abundant and temporally predictable.

Finally, the strategy followed by group 4 is especially relevant because it shows the most differential characteristic. This is a group constituted by species from fixed dunes, which exhibit traits similar to those known from Mediterranean forest species (e.g. Perez-Latorre & Cabezudo, 2002), such as the predominance of trees with evergreen sclerophyllous leaves and heavy fruits. These species present a long phenological activity during the year and a high phenophase sequencing index, as well as a predominance of the reproductive phenophases.

The presence of these four different patterns could be explained by the confluence of different floristic-functional elements from distinct origins and the wide ecological conditions, which permit the coexistence of different strategies (Primark, 1985; Castro-Díez & al., 2003). Their differentiation is an evidence of the high phenological diversity that is represented in Mediterranean coastal dunes, and it could be an important tool for the improvement of the management and conservation of these fragile ecosystems.

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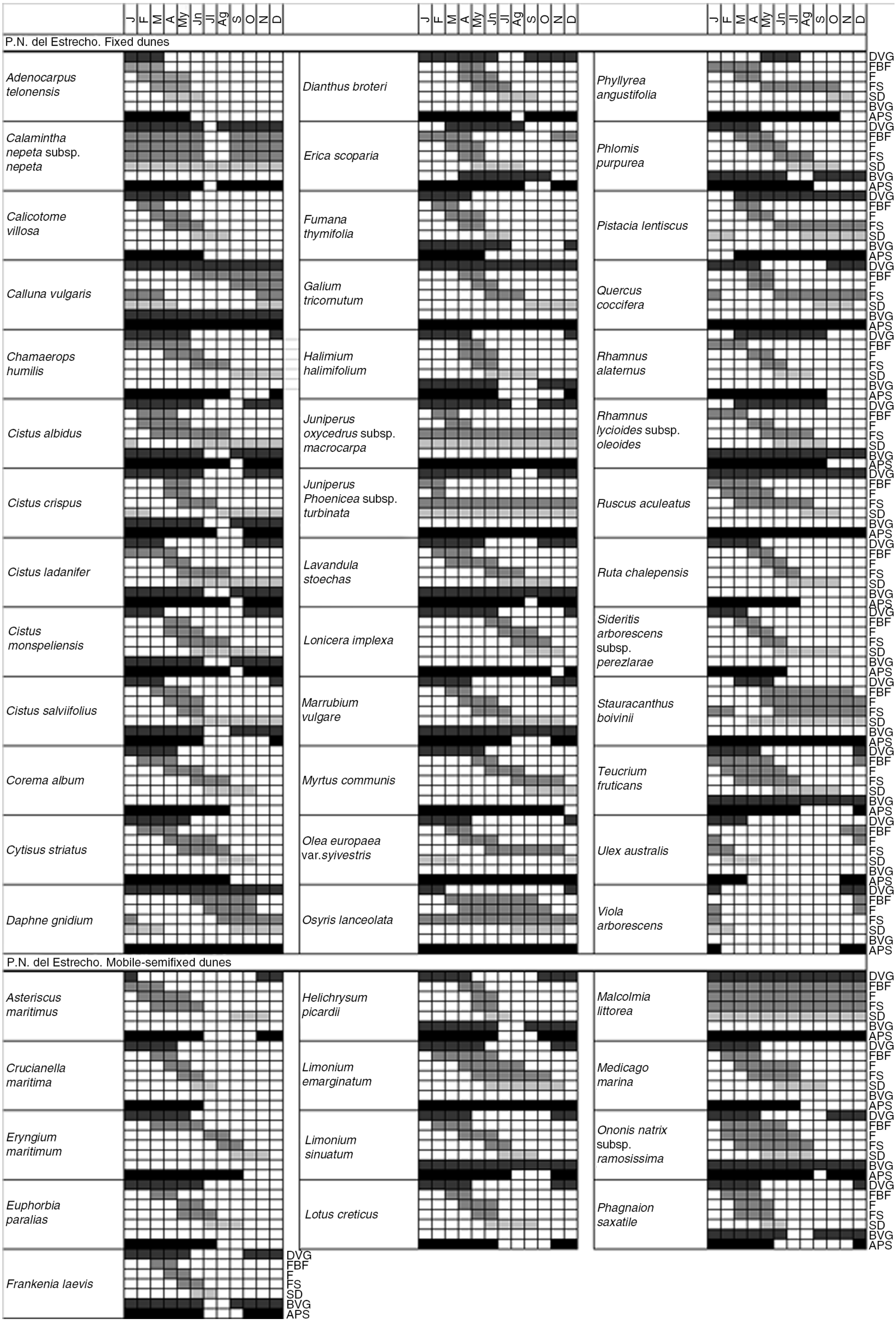
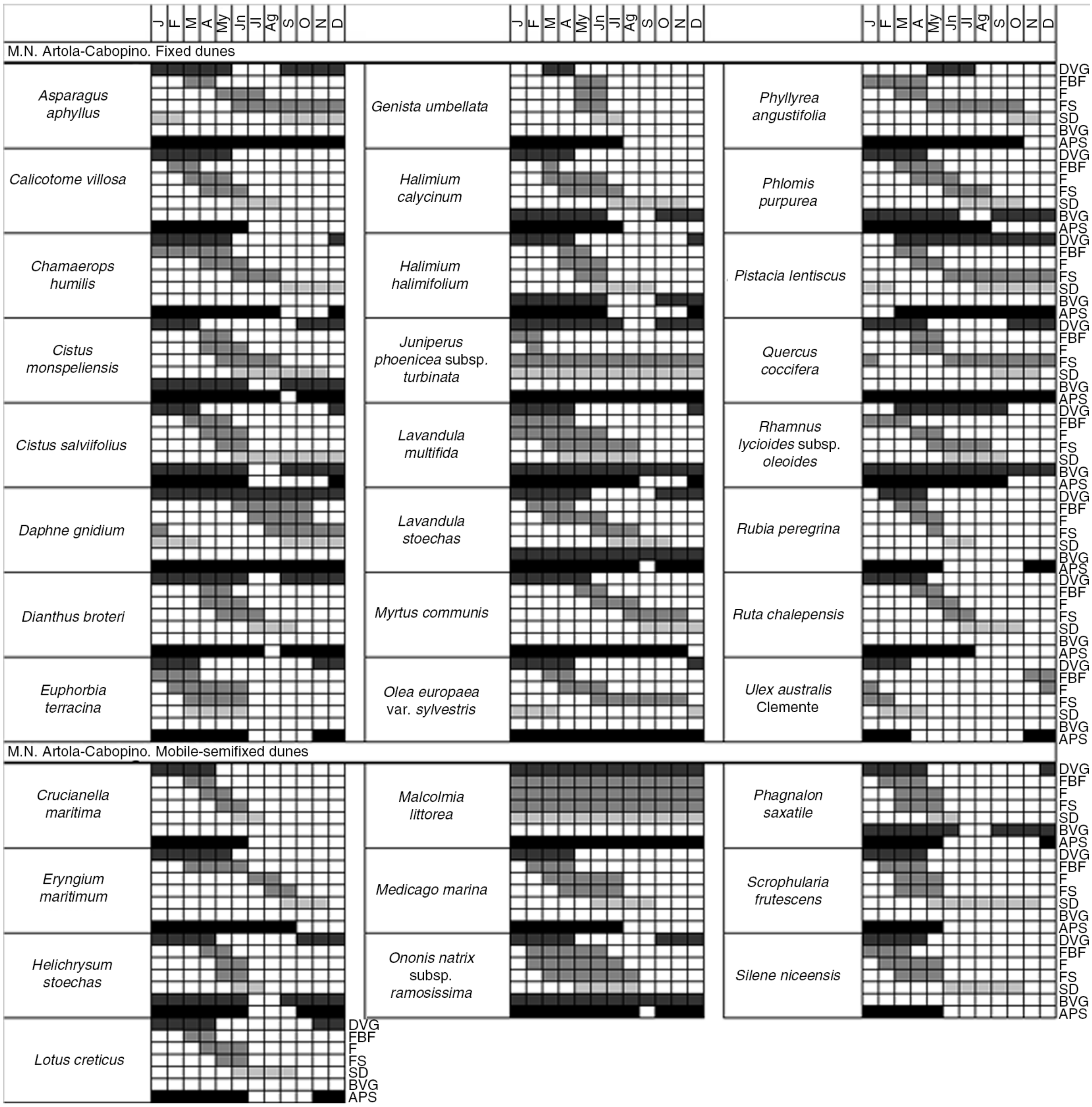
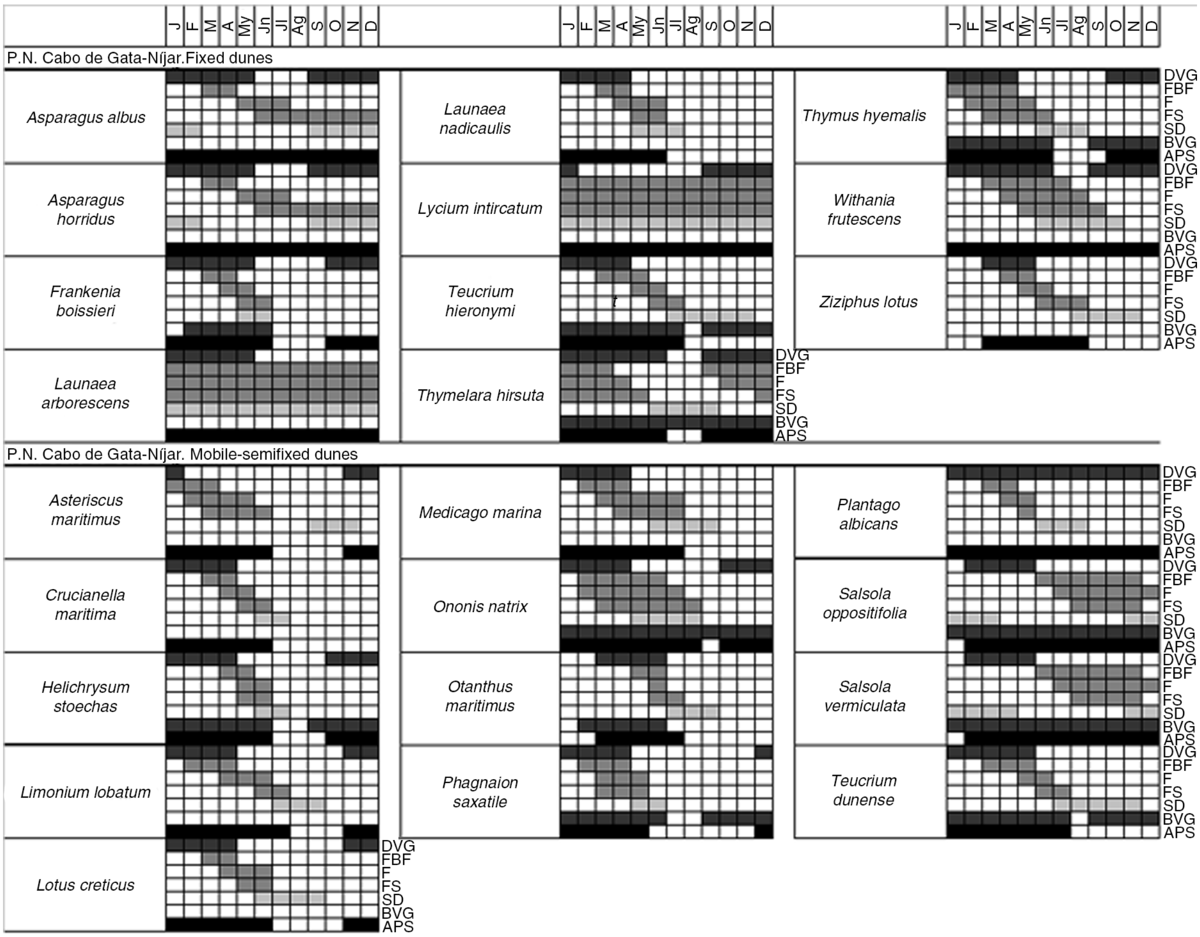
Appendix A.1


J F M A My Jn Jl Ag S O N D
P.N. del Estrecho. Fixed dunes
Adenocarpus telonensis
Calamintha nepeta subsp. nepeta
Calicotome villosa
Calluna vulgaris
Chamaerops humilis
Cistus albidus
Cistus crispus
Cistus ladanifer
Cistus monspeliensis
Cistus salviifolius
Corema album
Cytisus striatus
Daphne gnidium
Dianthus broteri
Erica scoparia
Fumana thymifolia
Galium tricornutum
Halimium halimifolium
Juniperus oxycedrus subsp. macrocarpa
Juniperus Phoenicea subsp. turbinata
Lavandula stoechas
Lonicera implexa
Marrubium vulgare
Myrtus communis
Olea europaea var.syivestris
Osyris lanceolata
Phyllyrea angustifolia
Phlomis purpurea
Pistacia lentiscus
Quercus coccifera
Rhamnus alaternus
Rhamnus lycioides subsp. oleoides
Ruscus aculeatus
Ruta chalepensis
Sideritis arborescens subsp. perezlarae
Stauracanthus boivinii
Teucrium fruticans
Ulex australis
Viola arborescens
P.N. del Estrecho. Mobile-semifixed dunes
Asteriscus maritimus
Crucianella maritima
Eryngium maritimum
Euphorbia paralias
Frankenia laevis
Helichrysum picardii
Limonium emarginatum
Limonium sinuatum
Lotus creticus
Malcolmia littorea
Medicago marina
Ononis natrix subsp. ramosissima
Phagnaion saxatile
DVG
FBF
F
FS
SD
BVG
APS

Appendix A.2


J F M A My Jn Jl Ag S O N D
M.N. Artola-Cabopino. Fixed dunes
Asparagus aphyllus
Calicotome villosa
Chamaerops humilis
Cistus monspeliensis
Cistus salviifolius
Daphne gnidium
Dianthus broteri
Euphorbia terracina
Genista umbellata
Halimium calycinum
Halimium halimifolium
Juniperus phoenicea subsp. turbinata
Lavandula multifida
Lavandula stoechas
Myrtus communis
Olea europaea var. sylvestris
Phyllyrea angustifolia
Phlomis purpurea
Pistacia lentiscus
Quercus coccifera
Rhamnus lycioides subsp. oleoides
Rubia peregrina
Ruta chalepensis
Ulex australis Clemente
M.N. Artola-Cabopino. Mobile-semifixed dunes
Crucianella maritima
Eryngium maritimum
Helichrysum stoechas
Lotus creticus
Malcolmia littorea
Medicago marina
Ononis natrix subsp. ramosissima
Phagnalon saxatile
Scrophularia frutescens
Silene niceensis
DVG
FBF
F
FS
SD
BVG
APS

Appendix A.3


J F M A My Jn Jl Ag S O N D
P.N. Cabo de Gata-Níjar.Fixed dunes
Asparagus albus
Asparagus horridus
Frankenia boissieri
Launaea arborescens
Launaea nadicaulis
Lycium intircatum
Teucrium hieronymi
Thymelara hirsuta
Thymus hyemalis
Withania frutescens
Ziziphus lotus
DVG
FBF
F
FS
SD
BVG
APS
P.N. Cabo de Gata-Níjar. Mobile-semifixed dunes
Asteriscus maritimus
Crucianella maritima
Helichrysum stoechas
Limonium lobatum
Lotus creticus
Medicago marina
Ononis natrix
Otanthus maritimus
Phagnaion saxatile
Plantago albicans
Salsola oppositifolia
Salsola vermiculata
Teucrium dunense

Appendix B

	APS	PSI	RVA	FD	OF	GF	LH	LC	PCA number	Phenological group
P.N. del Estrecho. Fixed dunes										
Adenocarpus telonensis	5	0.5	1.67	120	31	LS	D	M	1	G1
Calamintha nepeta subsp. *nepeta*	11	0.35	0.91	303	243	H	D	M	3	G1
Calicotome villosa	6	0.5	1	92	59	LS	D	M	4	G1
Chamaerops humilis	9	0.5	1.33	91	90	LS	E	S	14	G1
Calluna vulgaris	12	0.52	0.83	122	243	SS	E	S	5	G1
Cistus albidus	11	0.56	0.7	120	31	LS	SD	M	6	G1
Cistus crispus	10	0.69	0.4	61	90	SS	SD	M	7	G1
Cistus ladanifer	11	0.67	0.8	61	90	LS	SD	M	8	G1
Cistus monspeliensis	11	0.82	0.5	91	90	SS	SD	M	9	G1
Cistus salviifolius	7	0.7	0.4	91	90	LS	SD	M	10	G1
Corema album	8	0.6	1.75	91	90	SS	E	S	11	G1
Cytisus striatus	8	0.58	1.4	122	90	LS	D	M	13	G1
Daphne gnidium	12	0.57	0.67	123	181	LS	E	M	15	G1
Dianthus broteri	11	0.67	0.4	91	90	SS	D	S	16	G1
Erica scoparia	10	0.67	0.88	92	59	SS	E	S	17	G1
Fumana thymifolia	5	0.56	0.5	92	59	SS	SD	M	21	G3
Galium tricornutum	12	0.75	0.42	61	120	SS	D	S	22	G1
Halimium halimifolium	7	0.7	0.33	91	90	LS	SD	M	23	G1
Juniperus phoenicea subsp. *turbinata*	12	0.77	1.2	28	31	T	E	S	25	G4
Juniperus oxycedrus subsp. *macrocarpa*	12	0.71	1.2	61	59	T	E	S	26	G4
Lavandula stoechas subsp. *stoechas*	11	0.6	0.58	122	59	SS	SD	M	27	G1
Lonicera implexa	11	0.83	0.71	92	181	LS	E	M	30	G4
Marrubium vulgare	9	0.73	0.42	91	90	SS	SD	M	33	G1
Myrtus communis	11	0.8	1.4	92	151	LS	E	S	35	G4
Olea europaea var. *sylvestris*	12	0.7	1.8	91	90	T	E	S	36	G4
Osyris lanceolata	12	0.65	4	214	90	LS	E	S	49	G2
Phillyrea angustifolia	10	0.78	3.33	61	59	T	E	M	40	G4
Phlomis purpurea	8	0.6	0.6	91	90	LS	SD	M	41	G1
Pistacia lentiscus	10	0.71	1	61	90	T	E	S	42	G1
Quercus coccifera	12	0.73	1.43	61	90	T	E	S	43	G4
Rhamnus alaternus	9	0.75	0.86	61	90	LS	SD	M	44	G1
Rhamnus lycioides subsp. *oleoides*	9	0.75	0.67	61	90	LS	SD	S	45	G1
Ruscus aculeatus	12	0.6	0.67	120	31	LS	E	S	46	G1
Ruta chalepensis	7	0.75	1	61	120	SS	D	M	47	G1
Sideritis arborescens subsp. *perezlarae*	6	0.71	1.33	61	90	SS	SD	M	48	G1
Stauracanthus boivinii	12	0.56	3.33	245	120	LS	E	S	38	G2
Teucrium fruticans	8	0.44	0.67	150	31	LS	SD	M	50	G1
Ulex australis	5	0.71	1.33	62	334	LS	E	S	51	G1
Viola arborescens	3	0.5	0.67	62	334	SS	SD	M	52	G3
Medium value in the dune	9.41	0.65	1.10	99.05	106.56					
SD	2.50	0.11	0.82	53	72.79					
P.N. del Estrecho. Mobile-semifixed dunes										
Asteriscum maritimum	8	0.7	2	120	31	SS	SD	M	2	G1
Crucianella maritima	6	0.63	1	61	90	SS	SD	S	12	G1
Eryngium maritimum	9	0.73	1.4	62	181	H	D	M	18	G1
Euphorbia paralias	7	0.6	0.83	61	120	H	D	M	19	G1
Frankenia laevis	9	0.67	0.4	61	90	SS	D	M	20	G1
Helichrysum picardii	9	0.82	0.3	61	120	SS	SD	M	24	G1

Appendix B (*Continued*)

	APS	PSI	RVA	FD	OF	GF	LH	LC	PCA number	Phenological group
Limonium emarginatum	12	0.59	1.29	153	90	SS	SD	M	28	G1
Limonium sinuatum	9	0.67	0.5	91	90	SS	SD	M	29	G1
Lotus creticus	8	0.73	0.67	91	90	H	D	M	31	G1
Malcolmia littorea	12	0.33	1	365	1	H	D	M	32	G2
Medicago marina	7	0.58	1.5	153	59	H	D	M	34	G1
Ononis natrix subsp. *ramosissima*	11	0.56	0.58	181	31	SS	E	M	37	G1
Phagnalon saxatile	6	0.55	0.4	92	59	SS	SD	M	39	G3
Medium value in the dune	8.69	0.63	0.91	119.38	80.85					
SD	2.02	0.12	0.51	84.50	46.53					
M.N. Artola-Cabopino. Fixed dunes										
Asparagus aphyllus	12	0.79	1.11	92	120	SS	SD	S	1	G4
Calicotome villosa	6	0.5	1	92	59	LS	D	M	2	G3
Chamaerops humilis	9	0.5	1.33	91	90	LS	E	S	6	G1
Cistus monspeliensis	11	0.82	0.5	91	90	SS	SD	M	3	G1
Cistus salviifolius	7	0.7	0.4	91	90	LS	SD	M	4	G1
Daphne gnidium	12	0.57	0.67	123	181	LS	E	M	7	G1
Dianthus broteri	11	0.67	0.4	91	90	SS	D	S	8	G1
Euphorbia terracina	8	0.62	1.2	150	31	H	D	M	10	G1
Genista umbellata	7	0.64	1	61	59	SS	E	M	12	G1
Halimium calycinum	7	0.67	0.56	122	59	LS	SD	M	13	G1
Halimium halimifolium	7	0.7	0.33	91	90	LS	SD	M	14	G1
Juniperus phoenicea subsp. *turbinata*	12	0.77	1.2	28	31	T	E	S	16	G4
Lavandula multifida	9	0.47	0.67	181	1	SS	SD	M	17	G1
Lavandula stoechas subsp. *stoechas*	11	0.6	0.58	122	59	SS	SD	M	18	G1
Myrtus communis	11	0.8	1.4	92	151	LS	E	S	22	G4
Olea europaea var. *sylvestris*	12	0.7	1.8	91	90	T	E	S	23	G4
Phillyrea angustifolia	10	0.78	3.33	61	59	T	E	S	26	G4
Phlomis purpurea	8	0.6	0.6	91	90	LS	SD	M	27	G1
Pistacia lentiscus	10	0.71	1	61	90	T	E	S	28	G1
Quercus coccifera	12	0.67	1.43	61	90	T	E	S	29	G4
Rhamnus lycioides subsp. *oleoides*	9	0.75	0.67	61	90	LS	SD	S	30	G1
Rubia peregrina	7	0.57	1	61	90	SS	D	S	11	G1
Ruta chalepensis	7	0.75	1	61	120	SS	D	M	31	G1
Ulex australis	5	0.71	1.33	62	334	LS	E	S	34	G1
Medium value in the dune	9.17	0.67	1.02	88.67	93.88					
SD	2.22	0.10	0.62	33.30	63.54					
M.N. Artola-Cabopino. Mobile-semifixed dunes										
Crucianella maritima	6	0.63	1	61	90	SS	SD	S	5	G1
Eryngium maritimum	9	0.73	1.4	62	181	H	D	M	9	G1
Helichrysum stoechas	9	0.82	0.3	61	120	SS	SD	M	15	G1
Lotus creticus	8	0.73	0.67	91	90	H	D	M	19	G1
Malcolmia littorea	12	0.33	1	365	1	H	D	M	20	G2
Medicago marina	7	0.58	1.5	153	59	H	D	M	21	G1
Ononis natrix subsp. *ramosissima*	11	0.56	0.58	181	31	SS	E	M	24	G1
Phagnalon saxatile	6	0.55	0.4	92	59	SS	SD	M	25	G3
Scrophularia canina	5	0.5	1	92	59	SS	SD	M	32	G3
Silene niceensis	5	0.45	1.25	120	31	H	D	M	33	G3
Medium value in the dune	8.18	0.56	0.92	65.45	149.36					
SD	2.64	0.16	0.39	53.48	113.19					

Appendix B (*Continued*)

	APS	PSI	RVA	FD	OF	GF	LH	LC	PCA number	Phenological group
P.N. Cabo de Gata-Níjar. Fixed dunes										
Asparagus albus	12	0.79	1.11	92	120	SS	SD	S	1	G1
Asparagus horridus	12	0.79	1.11	92	120	SS	E	S	2	G1
Frankenia boissieri	9	0.67	0.44	61	90	SS	D	S	5	G1
Launea arborescens	12	0.41	2.4	365	1	LS	E	M	7	G2
Launea nadicaulis	6	0.67	1	91	90	SS	E	M	8	G3
Lycium intricatum	12	0.41	2.4	365	1	LS	D	M	11	G2
Teucrium hieronymi	7	0.67	0.45	61	120	SS	SD	M	20	G1
Thymelaea hirsuta	10	0.42	0.75	273	212	SS	E	M	21	G1
Thymus hyemalis	9	0.53	0.6	120	31	SS	D	M	22	G1
Withania frutescens	12	0.55	0.7	153	90	LS	D	S	23	G1
Ziziphus lotus	6	0.57	1.67	61	120	LS	E	S	24	G3
Medium value in the dune	9.73	0.59	1.15	157.64	90.27					
SD	2.49	0.14	0.71	119.09	61.78					
P.N. Cabo de Gata-Níjar. Mobile-semifixed dunes										
Asteriscum maritimum	8	0.7	2	120	31	SS	SD	M	3	G1
Crucianella maritima	6	0.63	1	61	90	SS	SD	S	4	G3
Helichrysum stoechas	9	0.82	0.3	61	120	SS	SD	M	6	G1
Limonium lobatum	9	0.67	1	91	90	SS	SD	M	9	G1
Lotus creticus	8	0.73	0.67	91	90	H	D	M	10	G1
Medicago marina	7	0.58	1.5	153	59	H	D	M	12	G1
Ononis natrix	11	0.56	0.58	181	31	SS	E	M	13	G1
Othantus maritima	5	0.57	0.6	30	151	SS	SD	M	14	G3
Phagnalon saxatile	6	0.55	0.4	92	59	SS	SD	M	15	G3
Plantago albicans	12	0.75	0.25	61	90	H	D	M	16	G1
Salsola oppositifolia	11	0.63	0.58	184	181	SS	E	M	17	G1
Salsola vermiculata	11	0.63	0.58	184	181	SS	E	M	18	G1
Teucrium dunense	7	0.6	0.45	61	120	SS	SD	M	19	G1
Medium value in the dune	8.36	0.64	0.80	102.21	98.79					
SD	2.21	0.08	0.50	53.02	47.95					