



Carmen M. Rodríguez Gallego

Caracteres Funcionales de Dunas del Sur de España



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Universidad de Málaga
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Departamento de Biología Vegetal
(Área de Botánica)

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Caracteres Funcionales de Dunas Costeras del Sur de España

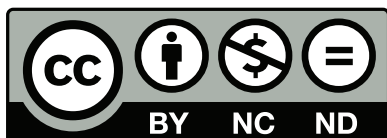
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Caracteres Funcionales de Dunas Costeras del Sur de España

Memoria presentada por la Lda. Carmen M. Rodríguez Gallego para optar al grado de Doctor en Biología.

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INFORMA:

Que el mencionado trabajo de investigación ha sido realizado bajo mi supervisión en el Departamento de Biología Vegetal (Área de Botánica) de la Universidad de Málaga, que se considera finalizado y puede ser presentado para su exposición y defensa como Tesis Doctoral, habiéndose alcanzado los objetivos propuestos.

Y para que así conste, a efectos administrativos para la obtención del grado de Doctor, firmo el presente informe en Málaga, a 28 de octubre de 2013.

Fdo. Teresa Navarro del Águila

D. Miguel Ángel Quesada Felice, Director del Departamento de Biología Vegetal de la Universidad de Málaga,

INFORMA:

Que el trabajo de investigación titulado “Caracteres Funcionales de Dunas Costeras del Sur de España”, llevado a cabo por la Lda Carmen M. Rodríguez Gallego ha sido realizado en este Departamento.

Y para que así conste, firmo el presente informe en Málaga, a 28 de octubre de 2013.

Fdo. Miguel Ángel Quesada Felice

*Caminante, son tus huellas
el camino y nada más;
Caminante, no hay camino,
se hace camino al andar.
Al andar se hace el camino,
y al volver la vista atrás
se ve la senda que nunca
se ha de volver a pisar.
Caminante no hay camino
Sino estelas en la mar.*

Antonio Machado.

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Resumen	1
Introducción general	3
Introducción	5
1. Los sistemas dunares costeros	5
1.1. Interés del estudio de los sistemas de dunas costeras	7
2. Una aproximación funcional al estudio de los sistemas costeros de duna	8
3. Los caracteres funcionales	8
3.1. Aplicaciones de los caracteres funcionales	9
3.2. Selección de los caracteres funcionales	11
3.2.1. Fenología	11
3.2.2. Caracteres funcionales regenerativos y de dispersión	13
3.2.3. Caracteres funcionales vegetativos. El espectro foliar	15
Objetivos e hipótesis	17
Estructura de la memoria	19
Áreas y especies de estudio	21
References	33
Capítulo 1. Vegetative and reproductive phenological patterns in coastal dunes	43
Abstract	45
1. Introduction	47
2. Material and methods	48
2.1. Study area	48
2.2. Data collection, phenological information and phenological indexes	49

2.3. Statistical analysis	51
3. Results	51
3.1. Phenology of coastal dunes in S Spain	51
3.2. Variation of phenology among dunes	52
3.3. Phenological patterns	53
4. Discussion	56
4.1. Phenological characterization of coastal dunes in S Spain	56
4.2. Variation of phenology among dunes	59
4.3. Phenological patterns	60
5. Acknowledgements	62
6. References	62
Capítulo 2. Dispersal traits and patterns in coastal dunes from S Spain	75
Abstract	77
1. Introduction	79
2. Material and methods	80
2.1. Study area and species	80
2.2. Samples and measurements	81
2.3. Statistical analysis	83
3. Results	83
3.1. Dispersal traits in coastal dunes in S Spain	83
3.2. Comparison of dispersal traits among coastal dunes	84
3.3. Comparison of dispersal traits among growth forms	87
3.4. Dispersal patterns	87
4. Discussion	89
4.1. Dispersal characterization in coastal dunes	89
4.2. Comparison of dispersal traits among dunes and growth forms	90
4.3. Dispersal patterns	91

5. Acknowledgements	93
6. References	94
Capítulo 3. A comparative study of leaf traits relationships in coastal dunes in S Spain	103
Abstract	105
1. Introduction	107
2. Material and methods	108
2.1. Study area	108
2.2. Samples and measurements	109
2.3. Data analyses	110
3. Results	110
3.1. Leaf functional traits in coastal dunes in S Spain	111
3.2. Correlations among leaf traits	112
3.3. Variation of leaf traits among taxonomic families and major functional groups	113
3.4. Variation of leaf traits among studied coastal dunes	113
3.5. Leaf patterns of specialization in coastal dunes in S Spain	113
4. Discussion	115
4.1. Leaf functional traits in coastal dunes	115
4.2. Correlation patterns among leaf traits	117
4.3. Taxonomic families and leaf traits	118
4.4. Major functional groups and leaf traits	119
4.5. Different leaf patterns of specialization among the three dunes with contrasting climates	119
4.6. Different leaf patterns of specialization among the dune sectors	121
5. Acknowledgements	121
6. References	121
Conclusiones	133

Índice de tablas

Introducción

1. Factores ambientales y adaptaciones de las plantas en sistemas de dunas costeras 6
2. Caracteres funcionales más relevantes 12

Área y especies de estudio

1. Listado de especies seleccionadas para su estudio en cada una de dunas analizadas 29

Capítulo 1

1. Some important ecomorphological traits in the studied species in coastal dunes ecosystems in S Spain 52

Capítulo 2

1. Traits recorded on 78 species in Coastal dunes in S Spain, and used for analysis 83
2. Dispersal spectrum of qualitative traits in Mediterranean coastal dunes 85
3. Dispersal and persistence traits among growth forms 88
4. Loading of the dispersal traits on the first two components from Nonlinear Principal Components Analysis (NLPCA) 90

Capítulo 3

1. Major functional groups for the studied species in coastal dunes in S Spain 111
2. Soil conditions (mean \pm sd) of coastal dunes in S Spain 112
3. Correlations among leaf traits in coastal dunes in S Spain 114
4. Leaf functional traits of perennial species in coastal dunes in S Spain grouped by families and major functional groups 115

5. Variations of leaf functional traits among major functional groups 116
6. Variations of leaf traits among the three coastal dunes in S Spain with different Mediterranean climate and between sectors of dunes 117

Índice de figuras

Introducción

1. Sectorización vegetal transversal de un sistema dunar 6
2. Biodiversidad composicional, estructural y funcional representadas como esferas interconectadas 8
3. Estrategias adaptativas basadas en caracteres foliares 16

Área y especies de estudio

1. Mapa de regiones climáticas en Andalucía. Las áreas de estudio se señalan con flechas 21
2. Dunas costeras seleccionadas en el Sur de España para el estudio 23
3. Mapas de valores normales anuales de variables climatológicas en Andalucía en la serie histórica 1961-1990 24
4. Sectorización vegetal transversal analizada en los sistemas de dunas costeras del sur de España 26
5. Distribución de la diversidad de especies en las dunas estudiadas 27
6. Índice de similitud de Jaccard entre dunas 28

Capítulo 1

1. Different climates in S Spain and study areas. 49
2. Climatic diagrams 49
3. Distribution of the vegetative phenological phases throughout the year in the coastal dunes 54
4. Percentage of species in each of the qualitative classes defined for the different phenological indexes 58
5. Variation of FD (Flowering duration) among fixed dunes. 59
6. Variation PSI (Phenophase sequence index) between fixed and mobile semi-fixed dunes in M.N. Artola-Cabopino 59

7. Phenological groups in coastal dunes of S Spain	61
--	----

Capítulo 2

1. Different climates in S Spain and study areas	81
2. Climatic diagrams	81
3. Diaspore mass distribution of perennial species in coastal dunes from S Spain	84
4. Diaspore mass grouped by growth forms in box plots	86
5. Ordination plot of perennial species from coastal dunes using NLPCA	92

Capítulo 3

1. Different climates in S Spain and study areas	109
2. Climatic diagrams	109
3. Leaf size classes	112
4. Relationships between leaf traits in coastal dunes	118
5. Principal components analysis of species in coastal dunes, ordinated according to leaf functional traits.	120

Índice de Anexos

Área y especies de estudio

Flora y vegetación en las dunas costeras del sur de España	30
--	----

Capítulo 1

A. Phenophasic calendar of species in Mediterranean coastal dunes in S Spain	67
B. Phenological indexes of the species, some important ecomorphological characters and phenological groups in coastal dunes of S Spain.	71

Capítulo 2

Dispersal traits in species in Mediterranean coastal dunes from S Spain.	100
--	-----

Capítulo 3

Leaf traits of perennial species in coastal dunes in S Spain	129
--	-----

Lista de abreviaciones

APS	Index of Active Phenophasic Period of the species
PSI	Phenophase Sequence index
RVA	Index of Reproductive/Vegetative Activity of the species
FD	Index of Flowering Duration
OF	Index of Onset Flowering
LS	Leaf size
SLA	Specific leaf area
[C]	Leaf carbon content
[N]	Leaf nitrogen content
[Ca]	Leaf calcium content
[K]	Leaf potassium content
[Fe]	Leaf iron content
[Mg]	Leaf magnesium content
[Mn]	Leaf manganese content
[P]	Leaf phosphorous content
D	Deciduousness
GF	Growth forms
H	Perennial herbs
SS	Small shrubs
LS	Large shrubs
T	Trees
LC	Leaf consistence
D.M	Diaspore mass
D.S	Diaspore size
D.Mr	Diaspore morphology
D.Md	Dispersal mode
B	Bradyspory
M	Myxospermy
S	Synaptospermy
C.R	Clonality and resprouting ability
NLPCA	Nonlinear principal components analysis

Resumen

Los sistemas dunares costeros son ecosistemas terrestres únicos, situados en la transición entre ambientes continentales y marinos. Sin embargo, la fuerte presión humana a la que han estado sometidos, especialmente en las últimas décadas, ha dado lugar a un nivel de deterioro, en ocasiones irreversible, con nefastas consecuencias para su funcionalidad. Cabe destacar la pérdida de los importantes servicios ecosistémicos que estos aportan así como la destrucción de los vulnerables hábitats que albergan. Ante dicha problemática, se hace fundamental el desarrollo de estudios que sirvan como base científica de conocimientos que avalen y contribuyan a mejorar las medidas de conservación y restauración de estos sistemas.

En este contexto surge la presente memoria de doctorado, la cual pretende colaborar a este fin a través de la caracterización funcional de especies vegetales perennes en dunas costeras del Sur de España. Para ello, se han analizado caracteres fenológicos, foliares, de dispersión y de regeneración en tres sistemas de dunas del Sur de España. Esta región ofrece la oportunidad de estudiar dunas costeras bajo tres variantes del macroclima Mediterráneo: Mediterráneo-oceánico (en las dunas del P.N. del Estrecho, Cádiz), M-subtropical (en el M.N. de Artola-Cabopino, Málaga) y M-subdesértico (en el P.N. Cabo de Gata-Níjar, Almería). Además, dentro de cada sistema dunar se ha distinguido entre dunas fijas y dunas móviles y semi-fijas, en base a la existencia de un gradiente ambiental desde la franja intermareal hacia el interior.

El estudio comprende información de 78 especies perennes, 34 de ellas representadas en más de un sistema dunar. Para cada una de estas especies se ha realizado su respectivo calendario fenológico (112 calendarios en total) y se han obtenido las medidas y observaciones directas en el campo necesarias para la elaboración de una completa base de datos que incluye información sobre índices fenológicos, caracteres foliares (ej. área específica de la hoja, el tamaño foliar y la concentración de nutrientes) y caracteres de dispersión y regenerativos (ej. peso, tamaño y tipo de diáspora, modo de dispersión en el espacio, existencia de mecanismos de supervivencia, etc.).

El análisis de estos caracteres funcionales ha puesto de manifiesto cómo los sistemas de dunas costeras están mayoritariamente formados por especies secuenciadoras, con ciclo fenológico activo de duración media (7-9 meses) y predominio de las fases vegetativas sobre las reproductivas. La floración dura 3-4 meses y es principalmente temprana (febrero-Mayo). El crecimiento vegetativo tiene lugar en los meses más favorables, alcanzándose los máximos valores cuando las lluvias han pasado y las temperaturas empiezan a subir. El verano es el periodo de máxima inactividad, siendo entonces cuando tiene lugar la dispersión de las semillas.

La dispersión es llevada a cabo por diásporas de pequeño tamaño (2-4 mm, 10^{-5} -1 g), en muchos casos desprovistas de estructuras que faciliten su desplazamiento a larga distancia (ej. alas, envolturas carnosas, etc.). Estas se quedan próximas a la planta madre, situación que se ve favorecida por la abundante presencia de mecanismos de supervivencia *in situ* (antitelecóricos). La regeneración de los sistemas de dunas costeros estudiados se lleva a cabo mayoritariamente por el papel de la dispersión, siendo minoritarias las especies con la habilidad de rebrotar y/o con clonalidad.

El verano es también un periodo de inactividad foliar en el área de estudio, dónde el 61.3% de las especies son deciduas o semi-deciduas. Las hojas de sistemas de dunas costeras son principalmente nanófilas (0.25-2.25 cm²), con bajos valores de SLA (4.77-390.5 cm²g⁻¹) y bajos porcentajes de nutrientes (N-Ca > K > Mg > P > Fe > Mn).

Se han analizado los patrones de co-variación entre los caracteres foliares, confirmándose las relaciones determinadas por el espectro económico foliar en otros ecosistemas. Sin embargo, en el área de estudio la concentración de K foliar se revela como un importante carácter funcional de la hoja, con potencialidad para ser incluido entre los caracteres funcionales que componen el espectro económico foliar.

La variación de los caracteres funcionales entre grupos funcionales ha sido confirmada en sistemas de dunas costeras. Árboles y arbustos de hoja perenne y esclerófila presentan, en comparación a las hierbas perennes y pequeños arbustos, menores valores de caracteres funcionales foliares (a excepción de la concentración de carbono), ciclos fenológicos más largos, mayor predominio de la fase reproductiva sobre la vegetativa y mayores tamaños de diáspora.

En base a todas estas características funcionales se han determinado diferentes patrones de especialización funcional en sistemas de dunas costeras, los cuales ponen de manifiesto las variadas estrategias funcionales de estos interesantes ecosistemas, tanto en términos de fenología, como de patrones de funcionamiento foliar y de dispersión. A grandes rasgos, los ecosistemas costeros de dunas presentan estrategias típicas de ambientes secos y cálidos, dónde priman las especies tolerantes al estrés y cuyas estrategias de dispersión van dirigidas al mantenimiento de la comunidad *in situ*.

El análisis de variación entre los tres tipos de dunas de estos patrones funcionales generales denota como los sistemas dunares de clima M-oceánico y M-subtropical son más similares entre sí que respecto al subdesértico. Así mismo, la diferenciación entre dunas fijas y dunas móviles más semi-fijas ha sido confirmada, poniendo de relevancia la necesidad de que los futuros planes de gestión de sistemas de dunas costeras contemplen diferentes medidas para los distintos sectores.

Palabras clave: dunas costeras, vegetación mediterránea, fenología, índices fenológicos, peso de la diáspora, modos de dispersión, área específica de la hoja, nutrientes foliares.



Monumento
Natural

Duna de Bolonia

Introducción General

Introducción

1. Los sistemas de dunas costeras

Los sistemas de dunas costeras son ecosistemas terrestres únicos, situados en la transición entre ambientes continentales y marinos. Según Van der Maarel (1993), estos pueden definirse en base a tres criterios clave:

- Son formaciones sólidas en su conjunto, próximas al mar, pero nunca, o sólo muy de vez en cuando, inundadas por agua de mar
- Están sometidas a la influencia de la niebla salina y de vientos aún más fuertes que los de sistemas continentales, lo cual conlleva efectos de acumulación, movilidad y erosión de arenas
- Tienen clima marítimo, presentando por lo tanto temperaturas suaves a lo largo del año y mayor humedad del aire que en tierra adentro

Otros autores añaden a esta definición un cuarto punto, especialmente referido al tipo de sustrato,

- Presentan sustratos arenosos de grano grueso, pobres en nutrientes y ricos en sales, con una elevada permeabilidad y baja capacidad de campo (Barbour et al., 1985; Clark, 1986; Hesp, 1991; Kumler, 1997; Ley Vega de Seoane et al., 2007)

Estas características actúan con diferente intensidad desde la zona intermareal, hacia las áreas interiores (García-Mora et al., 2001; Ley Vega de Seoane et al., 2007; Fenu et al., 2012), resultando un gradiente ambiental que va asociado a la sucesión de unidades geográficas con diferencias fisiográficas y ecológicas (Van der Maarel et al. 1985; Carter 1990) (Fig. 1). En general, la velocidad del viento, salinidad, movilidad y tamaño de las arenas, radiación y contenido en carbonato cálcico y pH del suelo decrecen hacia el interior, mientras que el contenido en materia orgánica y nutrientes se incrementa (Brown & McLachlan, 1994; Martínez & Psuty, 2004) (Fig. 1). Las perturbaciones (impactos del oleaje, inundaciones de agua de mar, erosión o sedimentación de arenas), sin embargo, ocurren predominantemente en la zona más próxima al mar, donde actúan con intensidad variable, espacial y temporalmente (Hesp & Martínez, 2007).

Tanto las citadas características definitorias de estos sistemas como la existencia de sectores diferentes dentro de las dunas son patrones comunes a todos los sistemas dunares costeros, independientemente de la zona geográfica o climática donde se desarrollen, situación tal que conlleva una gran similitud entre estos ecosistemas a lo largo de todo el mundo (Ley-Vega de Seoane, 2007).

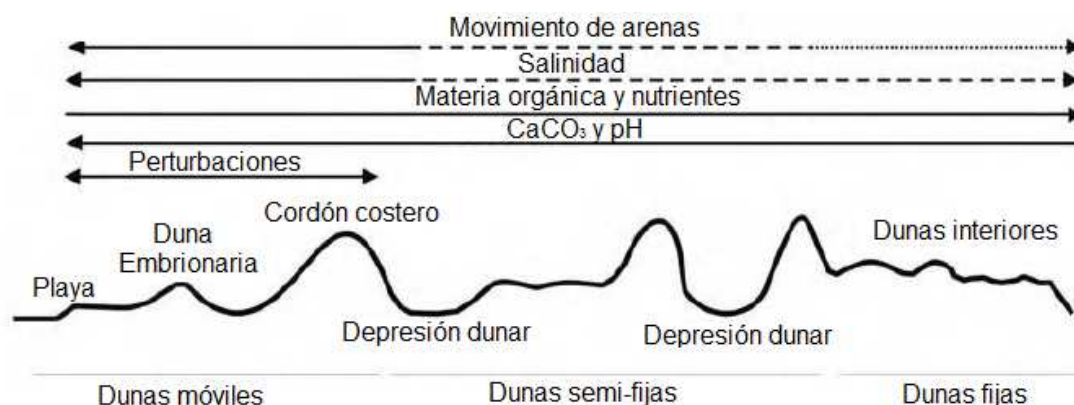


Fig. 1. Sectorización vegetal transversal de un sistema dunar (Ley Vega de Seoane, 2007).

En todos ellos, la vegetación presenta adaptaciones características para su supervivencia (Tabla 1), así como una particular composición y abundancia. Está fundamentalmente representada por unas pocas especies de amplia distribución geográfica, eventualmente acompañadas de otras especies de distribución limitada, sobre todo en el oeste y sur de Europa (Van der Maarel & Van der Maarel-Versluys, 1996).

Tabla 1. Factores ambientales y adaptaciones de las plantas en sistemas de dunas costeras (Modificada de Hesp, 1991; Ley Vega de Seoane et al., 2007).

Factor ambiental	Adaptación
Inundación por agua de mar	Resistencia a la inundación, dispersión de semillas por agua
Espray salino	Resistencia/tolerancia/preferencia por la sal
Sequía	Pérdida de hojas, eficiencia en el uso del agua, succulencia
Alta intensidad de luz y altas temperaturas	Colores claros, pubescencia
Exposición al viento	Formas aerodinámicas
Erosión marina	Dispersión de semillas por agua/viento
Suelos salinos	Resistencia/acumulación de sal, succulencia
Suelos pobres en nutrientes	Fijación de nitrógeno, relaciones micorrízicas

1.1. Interés del estudio de los sistemas de dunas costeras

Los sistemas de dunas costeras, como el resto de hábitats litorales, son extremadamente frágiles, ajustados en su formación, desarrollo y evolución a procesos naturales, y fácilmente vulnerables frente a la acción humana (Ley Vega de Seoane et al., 2007). Desafortunadamente, en las últimas décadas se han multiplicado e intensificado las actividades que acarrearán el deterioro, a veces irreversible, de estos ecosistemas. A modo de ejemplo, a nivel europeo sólo el 45% de estas formaciones se encuentran conservadas en estado natural, cifra que en la región mediterránea queda reducida a un 25% (Gallego-Fernández et al., 2003).

La alteración o interrupción de la dinámica sedimentaria costera debido a la construcción de infraestructuras y urbanizaciones se considera como el factor clave de la situación actual de los sistemas costeros. En menor medida, pero no por ello carente de importancia, el cultivo y el pastoreo desmedido constituyen también una fuente de peligro para las dunas costeras. Por otro lado, estos ecosistemas costeros soportan la presión de miles de personas que anualmente ven en las playas un lugar de ocio y esparcimiento (García-Mora et al., 1998).

Dichas actividades conllevan una pérdida directa de la cubierta vegetal que atrapa y mantiene la arena sobre las dunas, promoviendo una mayor susceptibilidad de las dunas frente a la erosión eólica e hídrica que finalmente conduce a la pérdida de los numerosos y valiosos bienes y servicios ecosistémicos que las dunas ofrecen en estado natural (MEA, 2005; Ley Vega de Seoane et al., 2007). Entre estos, cabe destacar la protección de regiones costeras frente a la inundación y la erosión, así como el establecimiento de hábitats particulares que posibilitan la supervivencia de especies vegetales y animales con adaptaciones específicas frente a las severas condiciones ambientales que caracterizan a estos ecosistemas (Kiehl & Isermann, 2007). A nivel de vegetación, cabe destacar la presencia de importantes hábitats naturales en sistemas de dunas costeras, entre los cuales destacan los catalogados por la Red Natura 2000 (Directiva 92/43/CEE) como hábitats naturales de interés prioritario, tales y como son las dunas fijas descalcificadas atlánticas (*Calluno-Ulicetea*) (código 2150*) y las dunas litorales con *Juniperus* spp. (código 2250*). Dentro de este último, se incluye el *J. oxycedrus* subsp. *macrocarpa*, en peligro de extinción en Andalucía según el libro rojo de la flora amenazada de la región (Blanca et al., 1999).

En consecuencia, la mayoría de las dunas costeras presentan actualmente un alto grado de deterioro, y las zonas aun conservadas se enfrentan a un grave riesgo por la disyuntiva entre conservación y desarrollo turístico (García-Mora et al., 1998; Gómez-Pina et al., 2002).

En este contexto surge la necesidad de desarrollar estudios que posibiliten el establecimiento de una base de conocimientos científicos que sirva de fundamento para la elaboración de medidas de gestión eficientes que garanticen la conservación de estos ecosistemas, aseguren su plena funcionalidad y posibiliten la recuperación de aquellos que han desaparecido o han sido gravemente dañados. En esta dirección, el estudio de las características funcionales del ecosistema ofrece nuevas posibilidades.

2. Una aproximación funcional al estudio de los sistemas costeros de dunas

Son numerosos los trabajos que han sido desarrollados sobre diversidad estructural (ej. Moreno-Casasola, 1986; Gómez-Pina et al., 2002; Feagin et al., 2005; Navarro-Pons et al., 2010) y composicional (ej. Babour et al., 1985; Acosta, 2003, 2005; Vallés et al., 2009) en sistemas costeros. Sin embargo, son pocos los que se han centrado en el estudio de la diversidad desde la perspectiva de la ecología funcional en estos espacios (Fig. 2).

Los cambios ambientales influyen de forma indirecta en las propiedades y el funcionamiento de los ecosistemas a través de su impacto sobre la biodiversidad, y se manifiestan a través de cambios en la diversidad funcional. Según Díaz et al. (2007), la diversidad funcional puede definirse como "el tipo, nivel y abundancia relativa de las características funcionales que están presentes en una comunidad".

Consecuentemente, el estudio de los caracteres funcionales se perfila como una herramienta clave para conocer y cuantificar la diversidad funcional en sistemas costeros de dunas (Grime, 1974; Díaz et al., 2001, 2004, 2007; Lavorel & Garnier, 2002; Mayfield et al., 2005, 2006), así como para predecir la distribución, diversidad y vulnerabilidad de estas frágiles comunidades (Keddy, 1992; Grime, 1998; Mittelbach et al., 2001). Además, la valoración de dichos caracteres haría factible ensayar en dunas costeras el enfoque integral que Noss (1990) propone (Fig.2) cómo esencial para la evaluación del estado de conservación de la biodiversidad.

3. Los caracteres funcionales

Los caracteres funcionales de las plantas son aquellos que se refieren a las características morfológicas, fisiológicas y fenológicas que se puede medir en un organismo (Martín-López et al., 2007), y que tienen una influencia potencialmente significativa en el establecimiento y la supervivencia de las plantas (Reich et al., 2003). Todos estos caracteres deben cumplir una serie de requisitos:

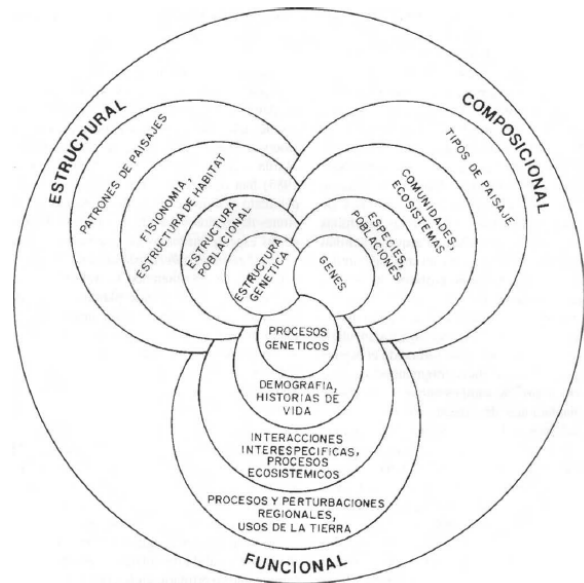


Fig. 2. Biodiversidad composicional, estructural y funcional representadas como esferas interconectadas, incluyendo cada una diversos niveles de organización (Noss, 1990).

- Representar conjuntamente las respuestas de los efectos de la vegetación a varios niveles: comunidades, ecosistemas, biomas y continentes (Cornelissen et al., 2003)
- Poder ser usados para elaborar una clasificación funcional satisfactoria que pueda servir como herramienta modelo a nivel regional y global (Cornelissen et al., 2003)
- Contribuir a responder cuestiones adicionales de teoría ecológica, de conservación de la naturaleza y de gestión del territorio (Wheier et al., 1999)
- Ser fácilmente observables (medibles y/o cuantificables), estar estandarizados y que sus correlaciones expresen patrones consistentes de asociación con caracteres medioambientales, pudiendo ser extrapolados o exportados a otros ecosistemas del mundo (Leishman & Westoby, 1992; Grime et al., 1996).

Además, la gran variedad de trade-offs (patrones recurrentes de correlación) entre variables hacen posible el conocimiento de las habilidades funcionales de las especies a través del análisis de un pequeño número de caracteres (Wheier et al., 1999).

3.1. Aplicaciones de los caracteres funcionales

Las muchas ventajas que ofrece el estudio de los caracteres funcionales han conllevado que a lo largo de los últimos años se hayan desarrollado numerosos trabajos que ponen de manifiesto sus variadas aplicaciones. Cabe destacar su uso en:

- Modelos de dinámica global de la vegetación (ej. Woodward et al., 1995; Neilson & Running, 1996)
- Modelos empíricos de paisaje (ej. Box, 1981; Woodward, 1987)
- Ecología comparativa (ej. Grime et al., 1988; Keddy, 1992)
- Ecofisiología y mecanismos de respuesta de las plantas al medio (ej. Lambers & Porter, 1992; Reich et al., 1997; Porter & Garnier, 1999)
- Predicción de los cambios en la composición de la comunidad y en el funcionamiento del ecosistema (Ej. Lavorel & Garnier, 2002)
- Conocimiento y predicción de la abundancia y distribución de las especies a lo largo de gradientes ambientales (Ej. Lavorel & Garnier, 2002; Ackerly, 2004)
- Análisis de las relaciones entre el clima y la vegetación (Ej. Niinemets, 2001)

- Análisis de las relaciones evolutivas y filogenéticas entre las plantas (Ej. Silvertown et al., 1997; Ackerly & Reich, 1999)
- Predicción de la dinámica de las comunidades vegetales en paisajes regularmente alterados (Noble & Gitay, 1996; Díaz & Cabido, 1997)
- Evaluación de los impactos ecológicos y la respuesta a los problemas actuales en la gestión del territorio (Ej. Noble & Gitay, 1996; Díaz et al., 2002)
- Estudio de los servicios ecosistémicos (Díaz et al., 2007; Martín-López, 2007).
- Clasificación funcional de las especies en patrones recurrentes de especialización ecológica (grupos funcionales) (Ej. Díaz & Cabido, 1997; Grime et al., 1997; Wheier et al., 1999; Díaz et al., 2004) que presentan respuestas similares a las condiciones ambientales y con efectos análogos sobre los procesos dominantes del ecosistema (Walker, 1992; Noble & Gitay, 1996; Díaz & Cabido, 1997), como resultado de la similitud entre un conjunto de caracteres funcionales clave (Lavorel et al., 1997, 1999; McIntyre & Lavorel, 2001).

Dichas aplicaciones adquieren un papel especialmente relevante en los sistemas de dunas costeras donde, de acuerdo con García-Mora et al. (1999), el estudio de los grupos funcionales permite el establecimiento de comparaciones ecológicas entre los tipos de vegetación de dunas litorales a una escala mucho mayor de lo que sería posible a través de los enfoques tradicionales florísticos.

Además, el estado habitualmente alterado que exhibe la mayoría de estos ecosistemas como consecuencia de las presiones e impactos a los que se encuentran expuestos, hace del estudio de los caracteres funcionales una valiosa herramienta en el conocimiento de su funcionamiento y el pronóstico de su evolución frente a factores clave tal y como son el estrés o las perturbaciones. De hecho, es en esta línea donde se ha profundizado en mayor medida en los últimos años (Ej. Silander & Antonovics, 1982; García Mora, 1999, 2000, 2001).

En este sentido, estudios previos desarrollados en sistemas dunares españoles ya han puesto de manifiesto la necesidad de realizar una caracterización que integre componentes activos, bióticos y abióticos (Gracia, 2009), constituyendo la valoración de los caracteres funcionales en estos sistemas un pilar fundamental con importantes aplicaciones dentro de la evaluación del estado de las dunas litorales y su gestión.

3.2. Selección de los caracteres funcionales

La selección de los caracteres funcionales constituye el marco en el cual se desarrolla la investigación. Estos deben ser ecológicamente significativos para las relaciones de las plantas con su entorno biótico y abiótico, de modo que sean capaces de expresar la respuesta de la vegetación al cambio ambiental (Grime, 1979; Schulze & Money, 1994; Box, 1996; Lavorel et al., 1997; Díaz et al., 1999; Westoby et al., 2002; Reich et al., 2003).

De acuerdo con esta premisa, los caracteres funcionales más relevantes (Tabla 2) serían aquellos relacionados con la fenología de la planta, los regenerativos y de dispersión así como los vegetativos que integran el espectro económico foliar (Díaz & Cabido, 1997; Grime et al., 1997; Lavorel et al., 1997; Westoby et al., 2002; Díaz et al., 2002; Cornelissen, 2003).

3.2.1. Fenología

Desde una perspectiva funcional, se considera a la fenología como un carácter adaptativo fundamental, ya que la duración y distribución en el tiempo del crecimiento vegetativo y de la actividad reproductiva tienen gran importancia para determinar las estrategias de asimilación y uso del carbono en las plantas mediterráneas, posibilitando la persistencia de las especies en los habitats (Mooney et al., 1977; Orshan, 1989; Castro-Díez and Montserrat-Martí, 1998; Montserrat-Martí et al., 2004).

La adaptación fenológica tiene lugar como respuesta a variaciones del clima, de los recursos básicos (luz, agua y nutrientes) o de factores bióticos, dando lugar a respuestas integradas de la planta, dependientes del modelo de organización básico de la especie (Montserrat-Martí et al., 2004).

El ajuste fenológico a la estacionalidad del clima presenta una gran importancia adaptativa, especialmente en el caso de un clima tan difícil para el crecimiento vegetal como es el mediterráneo (Orshan, 1989; Castro-Díez & Montserrat-Martí, 1998). El ajuste fenológico de una especie al clima implica el desarrollo de sus órganos durante cada ciclo fenológico, de modo que las estructuras en desarrollo no sean dañadas por el estrés climático. Esto puede conseguirse evadiendo el estrés o bien tolerándolo para poder crecer en condiciones desfavorables (Castro-Díez & Montserrat-Martí, 1998). La máxima expresión de evasión del estrés tiene lugar durante los meses de sequía en ecosistemas áridos, periodo en el cual las plantas pueden llegar a perder todas sus hojas y cesar su crecimiento, a la espera de la llegada de las lluvias de otoño (Grubb, 1998; Navarro & Cabezudo, 1998).

La adaptación fenológica a los recursos básicos es fundamental en sistemas de dunas costeras dada la baja concentración de nutrientes y limitada capacidad hídrica de sus suelos (Ley vega de Seoane et al., 2007). En ecosistemas áridos, cuyas características a nivel de recursos se aproximan a las de dunas costeras, la comunidad puede mostrar asincronía entre estrategias fenológicas, de acuerdo con la

Table 2. Caracteres funcionales más relevantes. Asociación con los factores abióticos y bióticos del ecosistema.

Carácter funcional	Relación con factores bióticos y abióticos
<i>Fenológicos</i>	
Fenología del fruto y tiempo de dispersión	Relacionado con la (1) dispersión en el espacio y el tiempo, (2) el tamaño de la diáspora, (3) la regeneración
Fenología foliar (Deciduidad)	Relacionado con factores climáticos
Inicio y duración de la floración	Relacionado con (1) el estrés, (2) la perturbación y (3) la regeneración
<i>Vegetativos de la planta completa</i>	
Forma de crecimiento	Relacionado con (1) la estrategia de la planta, (2) factores climáticos y (3) usos del suelo. (4) En varios estudios se ha puesto de manifiesto las relaciones que existen entre la forma de crecimiento y el patrón fenológico de las plantas superiores
Clonalidad	Relacionado con (1) el vigor competitivo y la habilidad de explorar nuevos territorios más ricos en recursos, (2) la persistencia después de una perturbación medioambiental, y (3) con la reproducción vegetativa.
<i>Vegetativos foliares</i>	
Consistencia de la hoja	Relacionado con (1) la perturbación y (2) el clima
Área específica de la hoja	Relacionado de forma positiva con (1) tasa potencial de crecimiento relativo, (2) masa basada en la tasa fotosintética máxima, (3) ambientes ricos en recursos, (4) tasa de capacidad fotosintética por unidad de masa foliar, (5) tolerancia a la sombra y (6) área de la hoja. Relacionado de forma negativa con (7) inversión relativamente alta en la defensa de la hoja, (8) longevidad de la hoja, (9) tasa de asimilación, (10) hojas esclerófilas, (11) tiempo de residencia de los nutrientes y (12) altura de la planta. También se correlaciona con las (13) condiciones ambientales y la (14) deciduidad de las especies.
Área de la hoja	Relacionado con (1) el balance de agua y energía, (2) variación climática, (3) geología, (4) factores alométricos, (5) factores filogenéticos, (6) bajo contenido en nitrógeno, (7) intercepción de la luz, (8) penetración de la luz a través de la copa, (9) bajo contenido en nitrógeno, (10) baja tasa de fotosíntesis, (11) altura de la planta, (12) morfología reproductiva y (13) forma de vida. Relacionado de forma negativa con (14) la edad de la planta, (15) estrés por calor y frío, (16) precipitación media anual, (17) incremento de la altitud o la latitud, (18) estrés por sequía, (19) estrés por alta radiación, (20) ambientes áridos, (21) soleados o (22) pobres en nutrientes.
Contenido de P y N foliar	Relacionado con (1) la producción primaria y (2) el ciclo de los nutrientes
Contenido de nutrientes de la hoja	Relacionado con la respuesta frente a la (1) disponibilidad de recursos en el suelo, (2) el control del crecimiento relativo de la planta y (3) la eficiencia de uso de los nutrientes.
<i>Dispersión y Regenerativos</i>	
Modo de dispersión	Relacionado con (1) la dispersión en el espacio y el tiempo. Es muy importante en los procesos de regeneración de la mayoría de las plantas.
Dispersión en el espacio	Relacionado con (1) la capacidad de colonizar nuevos espacios
Peso de la diáspora	Relacionado con (1) la dispersión en el espacio, (2) la longevidad del banco de semillas, (3) el éxito en el establecimiento y (4) la fecundidad. Correlación negativa con el número de semillas. Correlación positiva con la longevidad de la planta y el tamaño de reservas nutritivas. Es un carácter usado como indicador de persistencia.
Tamaño de la diáspora	Relacionado con la persistencia del banco de semillas en el suelo
Capacidad de rebrotar	Relacionado con la persistencia en ecosistemas con grandes episodios de perturbación

potencialidad de cada una para explorar el agua y los nutrientes almacenados en el suelo (Bertiller et al., 1991; Navarro & Cabezudo, 1998).

La relación de la fenología con los factores bióticos ha sido estudiada desde diferentes perspectivas, destacándose la relación de fenofases con la fauna del ecosistema. La primavera se considera el periodo óptimo para la floración, no sólo por las condiciones ambientales abióticas, sino también por el papel que parecen jugar los polinizadores en la determinación del inicio de la floración a lo largo del año (ej. Mosquin, 1971; Herrera, 1986; Elzinga et al., 2007). En el mismo sentido, la relación entre la maduración y dispersión de la semilla con la actividad de animales frugívoros, especialmente con las aves, ha sido objeto de numerosos estudios (Herrera, 1984, 1994; Tellería, 1988; Willson, 1986).

Sin embargo, en el caso concreto de los sistemas de dunas costeras, donde la adaptación fenológica es clave para la supervivencia de las especies, estos aspectos no han recibido la atención pertinente, con la excepción de algunas referencias ya alejadas en el tiempo (p. ej. Herrera, 1986; Cordazzo & Seeliger, 1988; Mazer, 1989) cuyo interés estaba fundamentalmente dirigido al estudio de la floración y fructificación como fenofases directamente relacionadas ya sea con las características del fruto, la germinación de la semilla o los factores bióticos del ecosistema (Herrera, 1986; Tellería, 1988; Mazer, 1989), recibiendo menos atención aún el análisis de las fenofases vegetativas.

Desde una perspectiva funcional, el crecimiento vegetativo es la fenofase que requiere mayor inversión de recursos (Kummerow, 1983; Montserrat Martí et al., 2004), los cuales tal y como se ha comentado con anterioridad, escasean en dunas costeras (Ley Vega de Seane, 2007). Consecuentemente, su distribución en el tiempo, así como la relación de esta con otras fenofases constituyen adaptaciones fundamentales, que posibilitarán la supervivencia de la planta en este tipo de ecosistemas.

3.3.3. *Caracteres funcionales dispersivos y de regenerativos*

La dispersión es el factor más importante en el control de la composición y riqueza de especies de las comunidades vegetales (Pärtel et al., 1996; Zobel et al., 1998), estableciendo los límites de la diversidad y su dinámica (Cain et al., 2000). Además, su estrecha relación con la supervivencia de la comunidad frente a cambios ambientales (Cain et al., 2000), fragmentación y perturbación (Chapin et al., 1993; Jauffret & Lavorel, 2003) ha dado lugar a que la dispersión sea considerada como un factor clave para la conservación (Haddad et al., 2003; Trakhtenbrot et al., 2005) y la restauración ecológica (Palmer et al., 1997).

La dispersión tiene dos componentes principales, la dispersión en el tiempo y en el espacio. La dispersión en el tiempo se puede medir como la longevidad de la diáspora y la longevidad del banco de semillas (Thompson et al., 1997), siendo el peso y la forma de la semilla dos importantes indicadores de la dicha longevidad (Thompson 1987, 1992, 1993; Trabaud, 2000). La dispersión en el espacio determina

el potencial de migración de la especie (Higgins & Richardson, 1999). El modo de dispersión tiene consecuencias sobre la distancia que puede ser recorrida, las rutas por las que puede viajar y los lugares donde puede terminar (Cornelissen et al., 2003). Esta se relaciona con el peso de la semilla (Thompson et al., 1993; Leishman et al., 1995) y la presencia de estructuras que favorecen la dispersión (ej. alas, estructuras nutritivas, ganchos) a través de diferentes medios (ej. anemocoría, zoocoría, hidrocoría) (Van der Pijl, 1982; Cornelissen et al., 2003).

Las plantas necesitan dispersarse para asegurar su supervivencia específica hacia nuevos enclaves (Weiher et al., 1999). Sin embargo, investigaciones realizadas en zonas áridas han puesto de manifiesto como en estas áreas se favorece la dispersión a corta distancia (restringida) (Ellner & Schmida, 1981; Jurado, 1991, 2001; Navarro et al., 2008, 2009). Este modo de dispersión propicia que las semillas se depositen en las proximidades de la planta madre, asegurando así la supervivencia *in situ* (Ellner & Schmida, 1981; Van Rheede van Oudtshoorn & Van Rooyen, 1990; Navarro et al., 2009). Esta se ve potenciada por el desarrollo de mecanismos antitelecóricos (Ellner & Schmida, 1981; Van Rheede van Oudtshoorn & Van Rooyen, 1990; Ehrman & Cocks, 1996), mecanismos que además posibilitan la sincronización estacional de la dispersión y germinación con el período climáticamente más favorable (Van Rheede van Oudtshoorn & Van Rooyen, 1990). Esta estrategia podría ser clave en sistemas costeros dunares, cuyas condiciones ambientales se asemejan en gran medida a la de entornos donde predomina dicha dispersión restringida. Sin embargo, no existen trabajos previos sobre el tema.

La relación entre caracteres de la diáspora, mecanismos de dispersión y capacidad de la planta para rebrotar y/o presentar clonalidad determinan la regeneración del ecosistema (Cornelissen et al., 2003; Kleyer et al., 2008). Estos dos últimos son especialmente significativos en comunidades sometidas a eventos de perturbación (Díaz & Cabido, 1997; Puigdefabregas & Pugnaire, 1999; Navarro et al., 2008).

A pesar de la importancia del conocimiento acerca de cómo se regeneran y dispersan los sistemas costeros de dunas para la aplicación de medidas de gestión, es poco lo que se conoce al respecto (e.g. Mazer, 1989; García-Mora et al., 1999; Nzunda et al., 2007; Guja et al., 2010; Yang et al., 2012). Además, las escasas publicaciones existentes están dirigidas al estudio de la dispersión por mar, haciéndose necesario el desarrollo de estudios integrales que posibiliten el conocimiento para comprender no sólo cómo se mantienen las poblaciones vegetales de dunas costeras *in situ* y *ex situ*, sino también qué relación guardan estas estrategias con la supervivencia de otros niveles del ecosistema, ya que como ha sido demostrado en trabajos anteriores, existe una relación muy estrecha entre dispersión y fauna (ej. Bond & Slingsby, 1983; Herrera, 1984, 1995; Zedler & Black, 1992).

3.2.2. Caracteres funcionales vegetativos. El espectro económico foliar

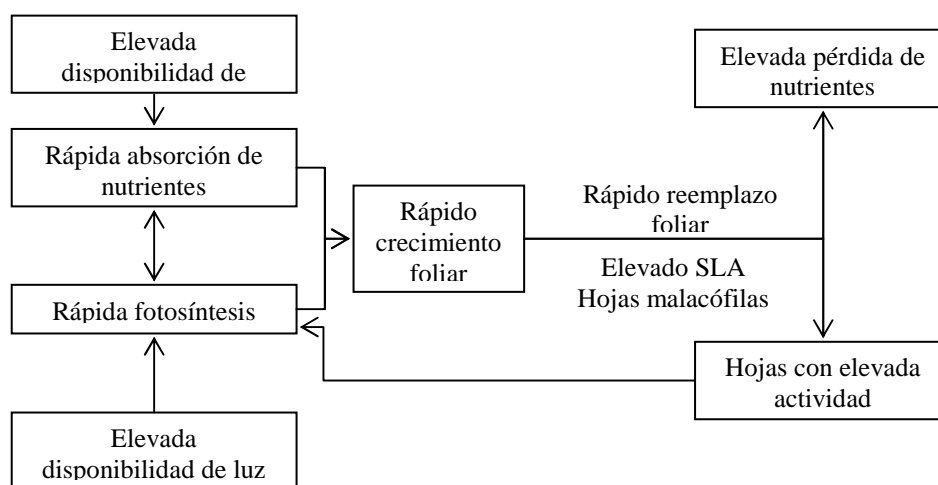
Entre los caracteres funcionales vegetativos, los relativos a la hoja están considerados como los más relevantes en base a su valor ecológico y ecofisiológico. Los diferentes caracteres de la hoja desempeñan un papel particularmente importante en relación con la asimilación de carbono, las relaciones de equilibrio de agua y energía (Ackerly et al., 2002) y la eficiencia de las estrategias de las plantas (Westoby et al., 2002), siendo por tanto estos caracteres un elemento de gran importancia en el conocimiento y predicción del funcionamiento de los ecosistemas (Ehleringer & Field, 1993; Garnier et al., 2001; Cornelissen et al., 2003; Norby & Luo, 2004; He et al., 2006; Díaz et al., 2007).

En consecuencia, a lo largo de los últimos años se han desarrollado numerosas investigaciones en el marco del estudio comparativo sobre las características de la hoja (Grubb, 1977; Woodward, 1987), dando lugar incluso, a la elaboración de importantes bases de datos sobre caracteres funcionales foliares (BIOPOP, Poschlod et al., 2003; GLOPNET, Reich et al. 2007). En estas bases de datos se incluye información a nivel mundial procedente de los más variados ecosistemas, pero son escasas las provenientes de sistemas de dunas costeras (e.g. Van der Valk, 1974; Li et al., 2005).

La importancia de las co-variaciones entre caracteres de la hoja afloró a partir de los estudios de Wright et al. (2004). El análisis del espectro económico de la hoja posibilita el conocimiento del funcionamiento del ecosistema mediante la valoración de unos pocos caracteres funcionales de la hoja de sencilla medición. El espectro foliar distingue estrategias adaptativas que van desde aquellas plantas con una económica formación de hojas poco duraderas (estrategia asociada a elevados valores de área específica de la hoja (SLA) que co-varían de forma positiva con el contenido foliar de nitrógeno y fósforo) hasta las que presentan hojas duraderas cuya formación es costosa en términos de energía y biomasa. Estas estrategias se asocian además a diferentes tipos de hábitats (Lavorel & Garnier, 2002) y grupos funcionales (He et al., 2006; Westoby & Wright, 2006), proporcionando por tanto información integral del ecosistema. Chapin (1980) describe dos grandes estrategias funcionales que reflejan lo recogido por el espectro económico foliar (Fig. 3). Estas diferencian entre plantas de *estrategia competitiva* (equivalente a los valores bajos del espectro) y las de *estrategia tolerante al estrés* (altos valores del espectro).

Estas variaciones no han sido nunca estudiada en especies de sistemas costeros de dunas, a pesar de la luz que pueden arrojar acerca de las estrategias predominantes en estos sistemas, la gestión que hacen las plantas de los escasos recursos, del ciclo de los nutrientes (alterado por la pobreza de los suelos y el efecto del spray salino) e incluso, de la capacidad de respuesta del ecosistema ante impactos como es el caso de la herbivoría (Hobbie & Gough, 2002; Reich et al., 2007).

ESTRATEGIA COMPETIDORA



ESTRATEGIA TOLERANTE AL ESTRÉS

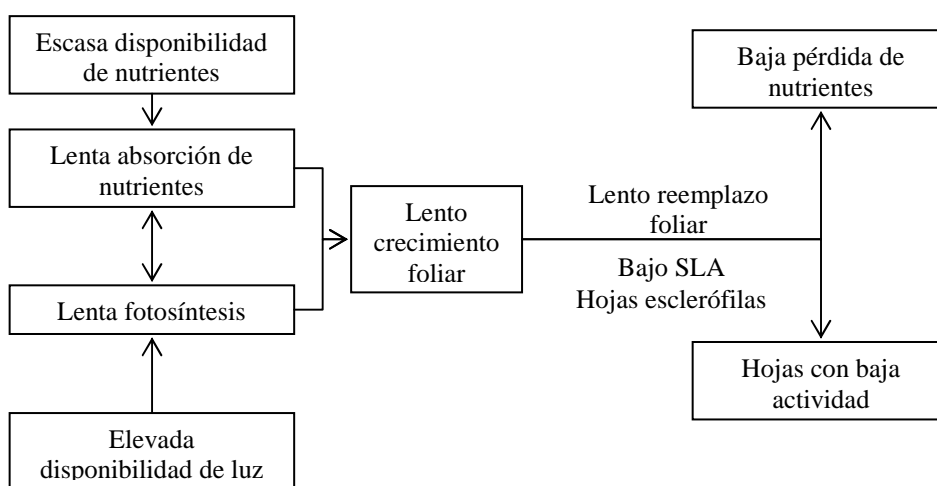


Fig. 3. Estrategias adaptativas basadas en caracteres foliares (Modificado de Chapin, 1980)

Objetivos e hipótesis

El objetivo general de esta memoria de doctorado es la caracterización funcional de especies vegetales perennes en dunas costeras del sur de España.

Para ello, se han planteado cinco objetivos específicos, los cuales se desarrollan a lo largo de los diferentes capítulos en los que se enmarca este estudio:

1. *Relacionado con los caracteres funcionales fenológicos.* Describir la distribución anual e intensidad de las fenofases de las especies vegetales perennes en sistemas de dunas costeras del sur de España. Se comprueba la hipótesis de que los sistemas dunares presentan características fenológicas similares a las encontradas previamente en regiones mediterráneas cálidas y secas (Orshan, 1989; Navarro et al., 1993). Además, se examina el papel de los índices fenológicos como herramientas de caracterización fenológica en sistemas costeros de dunas, tal y como se ha realizado ya en otros sistemas mediterráneos (Ej. Castro-Díez & Montserrat-Martí, 1998; Pérez-Latorre & Cabezudo, 2002).

2. *Relacionado con la dispersión y regeneración.* Definir los principales caracteres de dispersión en sistemas de dunas costeras del sur de España y estudiar su variación entre formas de crecimiento. Se examina la hipótesis de que en dunas costeras predominan las diásporas de pequeño tamaño con adaptaciones para la dispersión restringida en el espacio, como forma de favorecer el mantenimiento *in situ* del sistema costero frente a las duras condiciones de estrés ambiental (Ley Vega de Seoane et al., 2007). Estas características han sido previamente observadas en trabajos realizados en ecosistemas áridos (Ellner & Schimida, 1981; Jurado et al., 1991, 2001; Navarro et al., 2008, 2009).

3. *Relacionado con los caracteres funcionales de la hoja.* Comprobar en sistemas de dunas costeras del sur de España, los patrones de co-variación entre caracteres foliares que han sido previamente publicados en otros ecosistemas, así como las variaciones de estos entre familias taxonómicas y grupos funcionales (formas de crecimiento, deciduidad y consistencia de la hoja). Se analiza la hipótesis de que estos sistemas siguen los patrones de variación propuestos por el espectro económico foliar (Wright et al., 2004).

4. *Relacionado con la variación de los caracteres funcionales en el área de estudio.* Analizar la variación de caracteres funcionales vegetales entre dunas con variaciones dentro del macroclima Mediterráneo (Mediterráneo-oceánico, M-subtropical, M-subdesértico) y entre sectores de duna (duna móvil, semi-fija, fija). Se ensaya la hipótesis de que los sistemas de dunas costeras son muy similares, independientemente de la zona geográfica o climática donde se desarrollen (Ley Vega de Seoane et al., 2007). Además, en base a la existencia de un gradiente ambiental desde la zona intermareal, hasta las áreas interiores (García-Mora et al., 2001; Ley Vega de Seoane et al., 2007; Fenu et al., 2012), se analiza

la hipótesis de que la caracterización funcional de los sistemas dunares costeros debe diferenciar, al menos, entre dunas fijas, y dunas móviles y semi-fijas.

5. *Relacionado con los patrones recurrentes de especialización ecológica.* Determinar los patrones de especialización funcional en sistemas de dunas costeras en el sur de España. Se chequea la hipótesis de que los sistemas de dunas costeras incluyen particulares estrategias fenológicas, funcionales foliares y de dispersión, que determinan el funcionamiento y regeneración de estos sistemas dunares.

Estructura de la memoria

La memoria de doctorado se desarrolla en el contexto del proyecto nacional de investigación «*Los caracteres funcionales como herramienta para la conservación de las comunidades vegetales y la predicción de sus cambios*» (CGL 2010 16880, Ministerio de Economía y Competitividad). Esta se estructura en una descripción general de las áreas y especies de estudio, tres capítulos en los que se desarrollan los objetivos planteados, y una síntesis final en la cual se resumen las principales conclusiones del estudio.

El primer objetivo se desarrolla en el capítulo uno, “*Vegetative and reproductive phenological patterns in coastal dunes in S Spain*”. Para ello se determinan los calendarios fenológicos de cada una de 78 especies estudiadas (112 calendarios, dada la repetición de especies entre dunas) y se lleva a cabo la representación en diagramas circulares del desarrollo de las fenofases a lo largo del año en las diferentes dunas y sectores dunares analizados. Además, se establecen los valores de importantes índices fenológicos (APS, PSI, RVA) a nivel de especies y de sectores de duna.

El segundo objetivo se desarrolla en el capítulo dos, “*Dispersal traits and patterns in coastal dunes in S Spain*”. Se estudian los caracteres de dispersión y regeneración en sistemas de dunas costeras, destacándose la medida del peso de las diásporas y la determinación de importantes caracteres nominales, tales y como son la morfología y el tipo de diáspora, el modo de dispersión en el espacio, o la existencia de mecanismos de supervivencia (mecanismos antiteleocóricos). Además, se analiza la variación de estos caracteres funcionales entre formas de crecimiento.

Finalmente, el tercer objetivo se desarrolla en el tercer y último capítulo, “*A comparative study of leaf traits relationships in coastal dunes in S Spain*”. Con este fin, se lleva a cabo la elaboración una importante base de datos en la cual se engloban valores de área específica de la hoja (SLA), tamaño de la hoja (LS) y contenido en nutrientes de la hoja (N, P, Ca, K, Mg, Mn y Fe). Se analiza cómo co-varían dichos caracteres foliares y se determina la variación de estos entre familias y grupos funcionales.

Los objetivos 4 y 5 son transversales a los tres capítulos, conformando el hilo conductor que cohesiona la memoria. A lo largo de los tres capítulos se determinan patrones funcionales de especialización de carácter fenológico, de dispersión y regeneración, y foliar, determinándose además cómo estos varían entre las tres dunas analizadas con diferente clima (Mediterráneo-oceánico, M-subtropical, M-subdesértico) y entre sectores de dunas (dunas fijas y dunas móviles y semifijas).

Los tres capítulos han sido escritos en inglés, con el fin de facilitar su publicación en revistas internacionales, y se encuentran actualmente enviados a las revistas *Anales del Jardín Botánico de Madrid*, *Plant Biosystems* y *Plant Ecology and Evolution*, respectivamente. En cuanto a la autoría, los capítulos 1 y 2 están firmados por la doctoranda Carmen Rodríguez-Gallego y la directora, la Dra. Teresa Navarro, mientras que en el tercero ha colaborado también el Dr. Pierre Meerts¹.

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Áreas y especies de estudio

1. Selección de las áreas de Estudio

El sur de España proporciona la oportunidad única de estudiar dunas costeras sometidas a diferente climatología e influencia oceánica, desde las dunas de transición entre el océano Atlántico y el mar Mediterráneo, hasta las típicamente mediterráneas.

De acuerdo con los datos recopilados por la Consejería de Agricultura, Pesca y Medio ambiente de la Junta de Andalucía (DERA, 2013), las costas andaluzas se dividen climatológicamente en litoral atlántico (clima Mediterráneo oceánico), litoral mediterráneo (clima Mediterráneo subtropical) y litoral mediterráneo y sureste (clima Mediterráneo subdesértico) (Fig. 1).

Dentro de cada una de estas regiones climáticas costeras se ha seleccionado un sistema de dunas como área de estudio. En el litoral atlántico se estudiaron las dunas del Parque Natural del Estrecho, en el litoral mediterráneo se analizaron las que conforman el Monumento Natural de Artola-Cabopino, y en el litoral mediterráneo y sureste, las dunas del Parque Natural del Cabo de Gata-Níjar (Fig. 1).

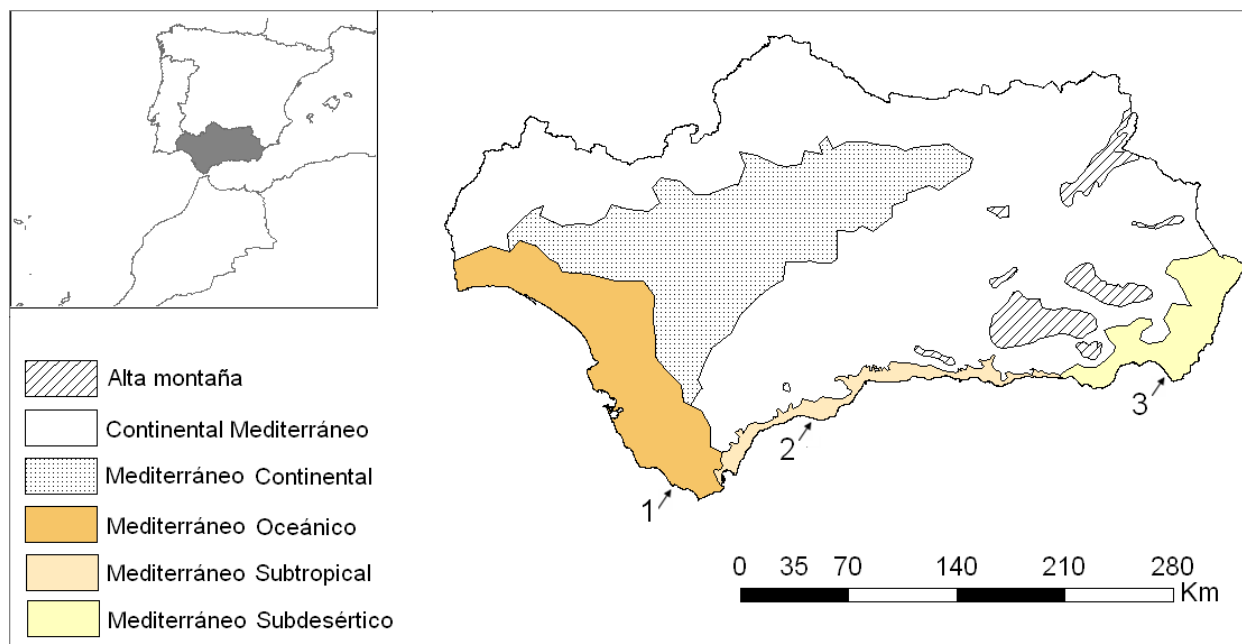


Fig. 1. Mapa de regiones climáticas en Andalucía. Las áreas de estudio se señalan con flechas: 1 (P.N. del Estrecho), 2 (M.N. Artola-Cabopino), 3 (P.N. Cabo de Gata-Níjar). Datos tomados de DERA, 2013.

1.1. Litoral atlántico: dunas del P.N. del Estrecho

Geográficamente, la región litoral atlántica se localiza en el océano Atlántico, pero la proximidad del mar Mediterráneo y el Magreb tienen una fuerte influencia sobre la composición de especies en esta zona. Consecuentemente, estas costas se consideran como un espacio de transición entre el mar Mediterráneo y el océano Atlántico, así como entre Europa y el Norte de África.

La región litoral atlántica se caracteriza por presentar una variante oceánica del macroclima Mediterráneo. En esta zona se determinó la selección de las dunas pertenecientes exclusivamente al Parque Natural del Estrecho (Cádiz) (Fig. 2A) en razón a la mayor influencia Mediterránea a la que están expuestas estas dunas y al mucho menor interés y conocimiento que de ellas se tiene frente a la atención recibida por las dunas del Parque Nacional de Doñana, que forman parte de la mayor reserva natural de Europa y que, como tal, han generado un bagaje de información y publicaciones enorme. Por el contrario, como ya se ha mencionado, los estudios desarrollados en las dunas del P.N. del Estrecho son muy escasos, siendo este el primero que se centra en aspectos de ecología funcional. Finalmente, el valor de las dunas del P.N. del Estrecho ha sido puesto de manifiesto en los últimos años a través de la catalogación de la duna de Bolonia como Monumento Natural en 2001.

Estas dunas presentan las temperaturas más suaves de entre las tres localidades analizadas. En ellas se observa una reducción de la amplitud térmica anual (17-19°C) debido a la proximidad del estrecho de Gibraltar, el cual determina y condiciona el fenómeno de entubamiento y aceleración del viento (Fig. 3A). Las precipitaciones (500-700 mm anuales) (Fig. 2b) son predominantemente invernales y ausentes en verano.

Sobre estas dunas se asienta vegetación perteneciente a la *geoserie edafoxerófila litoral termomediterránea Mediterráneo-iberoatlántica psammofila* (Psa) (Anexo), dentro de la cual destacan las dunas fijas descalcificadas atlánticas (*Calluno-Ulicetea*) (Código 2150*) así como las formaciones de *Juniperus phoenicea* subsp. *turbinata* y *J. oxycedrus* subsp. *macrocarpa* (EN, UICN) (Código 2550*), ambas contempladas como hábitat de interés comunitario y prioritario según la Red Natura 2000 (VV.AA., 2009). En estas dunas se encuentran además otras especies incluidas en el libro rojo de la flora silvestre amenazada de Andalucía (Blanca et al. 1999, 2000), como son *Sideritis perezlarae* (VU Junta de Andalucía; EN, UICN) o *Corema album* (VU Junta de Andalucía; LR, dc;UICN).

1.2. Litoral mediterráneo: dunas del M.N. Artola-Cabopino

Dentro del litoral típicamente mediterráneo se han estudiado las dunas que integran el Monumento Natural de Artola-Cabopino, en Málaga (declaradas bajo tal categoría de protección en 2003) (Fig. 2B). Desafortunadamente, en la actualidad este reducido enclave es el único testigo de lo que fue el cordón dunar existente en esta área de la costa malagueña. De acuerdo con Asensi-Marfil & Diez-Garretas (1993), las dunas de Artola-Cabopino conforman la única zona con desarrollo de dunas extensas en esta

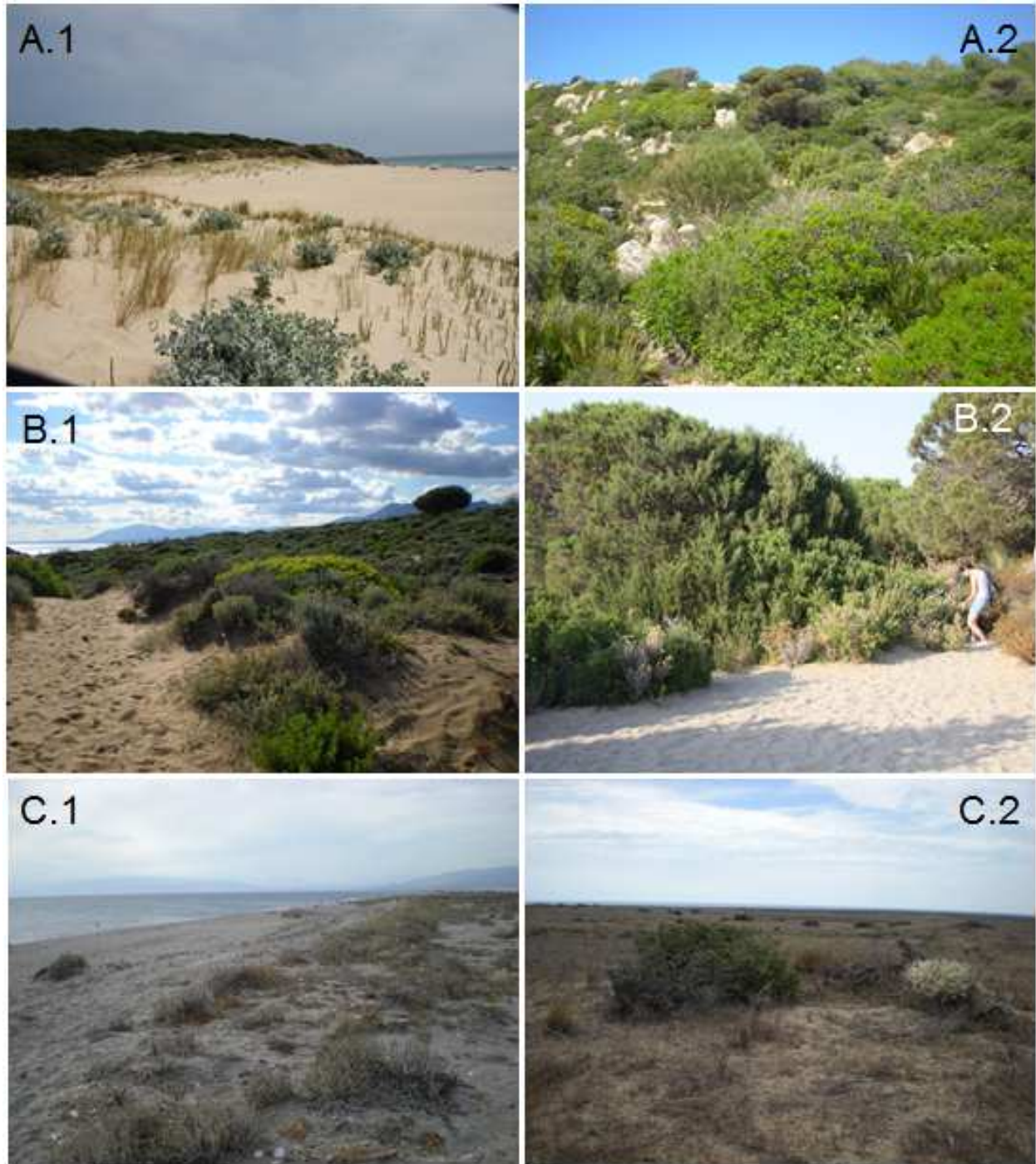


Fig. 2. Dunas costeras seleccionadas en el sur de España para el estudio. (A) P.N. del Estrecho, (B) M.N. de Artola-Cabopino, (C) P.N. del Cabo de Gata-Níjar; (1) Duna móvil y semifija, (2) Duna fija.

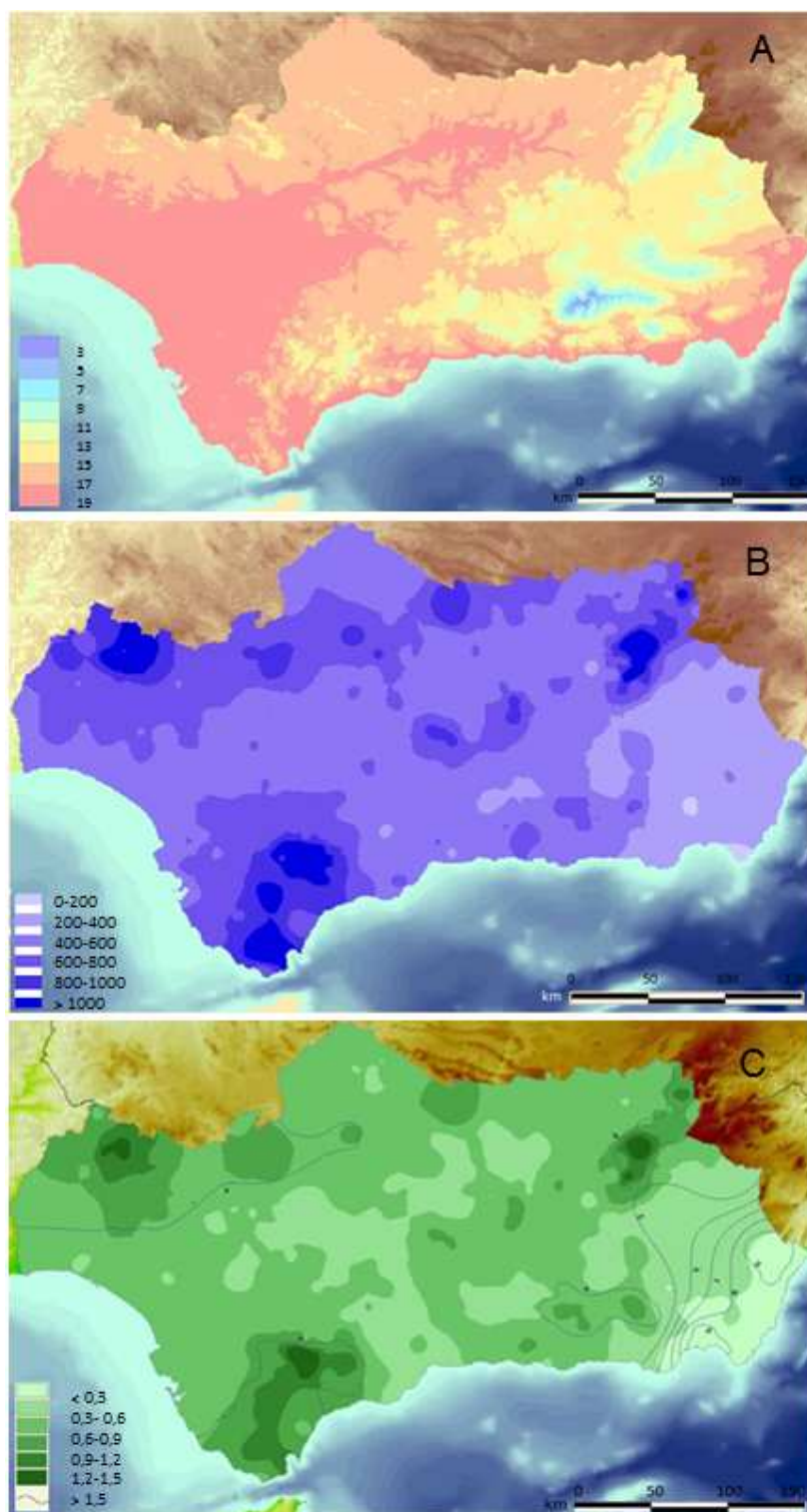


Fig. 3. Mapas de valores normales anuales de variables climatológicas en Andalucía en la serie histórica 1961-1990. (a) Temperatura anual media (b) Precipitación, (c) Índice de humedad. Fuente original: Junta de Andalucía, Consejería de Agricultura, Pesca y Medio Ambiente.

región litoral. La posibilidad de expansión de este reducto dunar es nula, dado que se encuentra completamente rodeado de urbanizaciones. Además, la problemática con las especies exóticas en estas dunas podría agravarse en pocos años, debido a la rápida expansión de alóctonas invasoras como son *Lantana cámara* y *Acacia saligna*, ampliamente utilizadas en el ajardinamiento de las parcelas privadas y medianas de las carreteras que rodean a la vegetación natural.

El clima mediterráneo subtropical es el que caracteriza a la mayor parte de la costa mediterránea andaluza. El hecho más característico de este ámbito son las suaves temperaturas invernales, que se generan como consecuencia de la intervención de tres mecanismos básicos: la influencia suavizadora del mar, la orientación sur de la costa y la protección frente a las coladas septentrionales que le otorgan las cadenas Béticas. Sin embargo, durante el verano se pueden registrar episodios muy cálidos como resultado de los vientos terrales, pudiendo entonces llegar a alcanzarse los 40°C. Las precipitaciones son muy variables de unos enclaves a otros (400-900 mm anuales) (Fig. 3B) y, en general, muestran un gradiente de disminución oeste-este.

La vegetación que conforma estas dunas se encuadra en la *geoserie edafoxerófila litoral termomediterránea mediterráneo-iberolevantina psammofila* (Ps1) (Anexo). Esta duna incluye formaciones de *Juniperus phoenicea* subsp. *turbinata* (Código 2550*) (VV.AA, 2009).

1.3. Litoral mediterráneo y sureste: dunas del P.N. Cabo de Gata-Níjar

Las dunas del litoral mediterráneo y sureste se encuentran en la actualidad profundamente alteradas como consecuencia de la devastadora extracción de arena que se produjo hasta la década de los ochenta del siglo pasado para su empleo en la incipiente agricultura intensiva (Viciano Martínez-Lage, 1999). Los muestreos en esta región se llevaron a cabo en las dunas del P.N. del Cabo de Gata-Níjar, en Almería (Fig. 2C).

El clima mediterráneo subdesértico define a todo el sector sureste de la provincia de Almería. El hecho distintivo es la escasez de precipitaciones, que hace de esta zona una de las áreas más secas de toda Europa (<200 mm anuales) (Fig. 3B). Las escasas precipitaciones se producen además con una fuerte torrencialidad, situación que junto a la elevada evapotranspiración (Fig. 3C), conlleva la acentuación de la aridez en la zona.

En estas dunas se encuentra vegetación de la *geoserie edafoxerófila litoral termomediterránea mediterráneo-iberolevantina psammofila* (Ps1) (Anexo) así como matorrales arborescentes de *Ziziphus* (5220*) (VV.AA, 2009) sobre las dunas fijas más interiores, tal y como son los situados en la zona de las Amoladeras (Ferre-Bueno & Sencales-González 2001).

1.4. Sectores de duna

Dentro de cada localidad de estudio se ha diferenciado entre dos grandes sectores de duna. Tal y como se mencionaba en la introducción general, la conexión con el mar determina que los sistemas costeros de dunas se vean sometidos a una serie de características ambientales (viento, sequía, espray salino, intensidad lumínica o escasez de nutrientes) que actúan con diferente intensidad desde la orilla del mar hasta las áreas interiores (García-Mora et al., 2001; Ley Vega de Seoane et al., 2007; Fenu et al., 2012). El resultado es el establecimiento de unidades geográficas con diferencias fisiográficas y ecológicas (Carter, 1990) que han sido caracterizados en base a diferentes criterios.

En el presente estudio, la terminología empleada es la basada en la movilidad del sustrato (Van der Maarel, 1993), diferenciándose entre duna fija y duna móvil y semi-fija (Fig. 4).

Las dunas fijas están formadas por árboles y arbustos que representan la etapa madura del ecosistema, mientras que dunas móviles y semi-fijas están constituidas por comunidades pioneras de hierbas y pequeños arbustos adaptados a la intensa perturbación que está asociada a la proximidad del mar (Costa-Pérez & Valle-Tendero, 2004; Ley Vega de Seoane et al., 2007). La vegetación que se encuentran sobre cada uno de estos sectores en las dunas estudiadas puede consultarse en el Anexo.

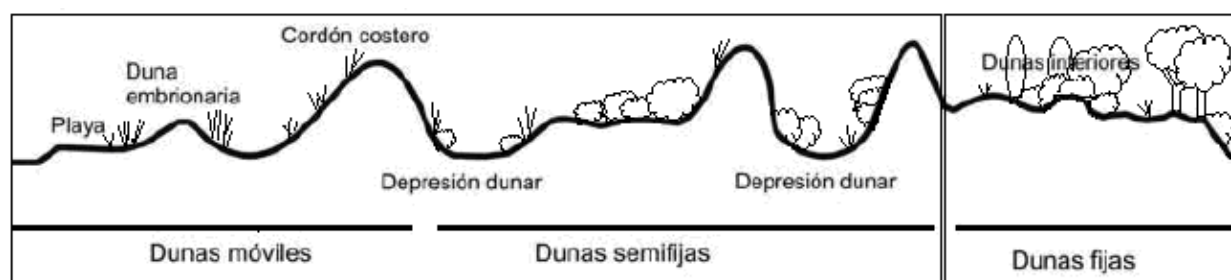


Fig. 4. Sectorización vegetal transversal analizada en los sistemas de dunas costeras del sur de España (modificado de van der Maarel, 1993; Ley Vega de Seoane, 2007).

2. Selección de las especies de estudio

Con la finalidad de obtener resultados homogéneos y comparables, la información de campo recogida en cada una de las localidades y los datos que conforman este trabajo, son referentes exclusivamente a las especies perennes con mayor representación y cobertura, aunque excluyendo de este grupo a aquellas pertenecientes al orden Poales (APG III, 2009).

Hierbas anuales y Poales en general, tienen un papel muy interesante en dunas costeras, tanto en relación a su densidad y diversidad, como a los servicios ecosistémicos que estas procuran (ej. Ley Vega

de Seane et al., 2007), pero conforman grupos funcionales particulares, que deben estudiarse de forma independiente (Lavorel et al., 1999). De acuerdo con McIntyre et al. (1999), existen tres determinantes clave para la diferenciación de estos dos grupos funcionales: (1) La selección de caracteres a estudiar debe realizarse de forma distinta en estos dos grupos, dado que en ellos se hace irrelevante el estudio de determinados caracteres funcionales, tales como la esclerofilia o la deciduidad; (2) el rango de variación de dichos atributos variaría, y (3) la significación de las variaciones encontradas en los análisis de comparación podría verse alterada.

Consecuentemente, el estudio se centró en un total de 78 especies a lo largo de las tres dunas analizadas (Tabla 1): 52 especies en P.N. del Estrecho, 34 especies en M.N. Artola-Cabopino y 24 especies en P.N. Cabo de Gata-Níjar (Fig. 5).

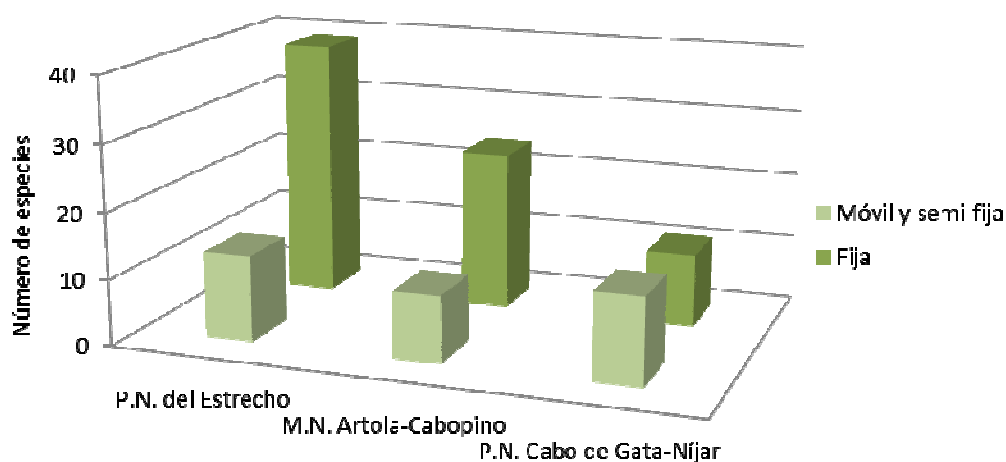


Fig. 5. Distribución de la diversidad de especies en las dunas estudiadas.

La figura 6 muestra los resultados de un análisis de similitud (índice de Jaccard) entre las dunas y sectores dunares de las tres localidades en base a las especies comunes y no comunes en los sistemas considerados. Los resultados ponen de manifiesto la escasa similitud entre las dunas fijas del P.N. del Estrecho y M.N. Artola-Cabopino ($\approx 30\%$), aunque estos valores se incrementan hasta algo más del 50% en el caso de las móviles y semifijas. No obstante, la observación más destacable es la constatación de la singularidad de las dunas del P.N. Cabo de Gata-Níjar, especialmente las fijas, que muestran una similitud nula con las correspondientes a Cádiz y Málaga, incrementándose dicha similitud hasta superar el 20% en el caso de las móviles.

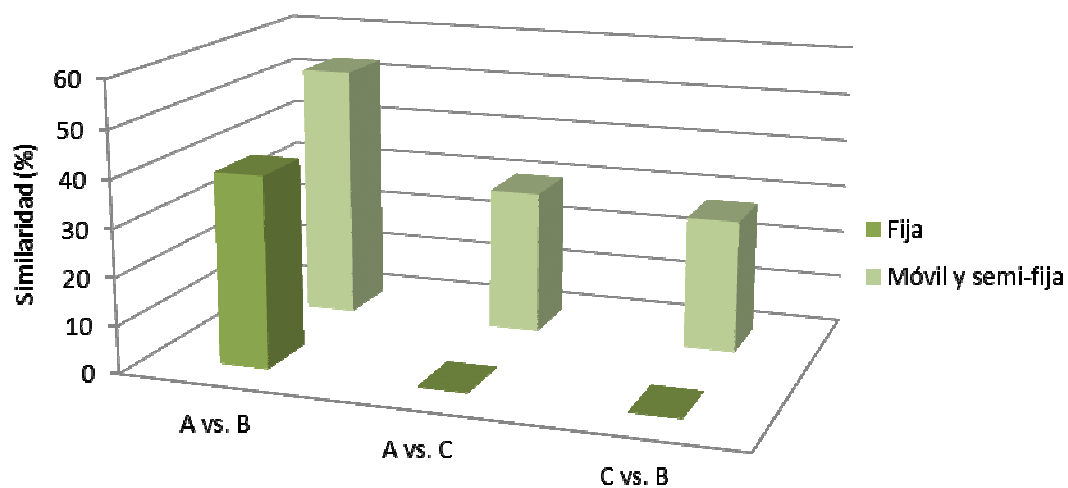


Fig.6. Análisis de similaridad entre dunas utilizando el índice de Jaccard ($I = \frac{xy}{x+y-xy}$, donde x : nº especies presentes en la localidad X; y : nº especies presentes en la localidad Y; xy : nº de especies presentes en las localidades X e Y). Leyenda: A (P.N. del Estrecho), B (M.N. Artola-Cabopino), C (P.N. Cabo de Gata-Níjar).

Tabla 1. Listado de especies seleccionadas para su estudio en cada una de dunas analizadas. Leyenda: (F) Duna fija, (M) Duna móvil semi-fija.

	P.N. del Estrecho		M.N. Artola-Cabopino		P.N. Cabo de Gata-Níjar			P.N. del Estrecho		M.N. Artola-Cabopino		P.N. Cabo de Gata-Níjar	
	F	M	F	M	F	M		F	M	F	M	F	M
<i>Adenocarpus telonensis</i>	X						<i>Limonium lobatum</i>						X
<i>Asparagus albus</i>					X		<i>Limonium sinuatum</i>		X				
<i>Asparagus aphyllus</i>			X				<i>Lonicera implexa</i>	x					
<i>Asparagus horridus</i>					X		<i>Lotus creticus</i>		X		X		X
<i>Asteriscus maritimus</i>		X				X	<i>Lycium intricatum</i>						X
<i>Calamintha nepeta</i> subsp. <i>nepeta</i>	X						<i>Malcolmia littorea</i>		X		X		
<i>Calicotome villosa</i>	X		X				<i>Marrubium vulgare</i>	X					
<i>Calluna vulgaris</i>	X						<i>Medicago marina</i>		X		X		X
<i>Cistus albidus</i>	X						<i>Myrtus communis</i>	X		X			
<i>Cistus crispus</i>	X						<i>Olea europaea</i> var. <i>sylvestris</i>	X		X			
<i>Cistus ladanifer</i>	X						<i>Ononis natrix</i> subsp. <i>ramosissima</i>		X		X		X
<i>Cistus monspeliensis</i>	X		X				<i>Osyris lanceolata</i>	X					
<i>Cistus salviifolius</i>	X		X				<i>Othantus maritima</i>						X
<i>Corema album</i>	X						<i>Phagnalon saxatile</i>		X		X		X
<i>Crucianella maritima</i>	X	X		X		X	<i>Phillyrea angustifolia</i>	X		X			
<i>Cytisus striatus</i>	X						<i>Phlomis purpurea</i>	X		X			
<i>Chamaerops humilis</i>	X		X				<i>Pistacia lentiscus</i>	X		X			
<i>Daphne gnidium</i>	X		X				<i>Plantago albicans</i>						X
<i>Dianthus broteri</i>	X		X				<i>Quercus coccifera</i>	X		X			
<i>Erica scoparia</i>	X						<i>Rhamnus alaternus</i>	X					
<i>Eryngium maritimum</i>		X		X			<i>Rhamnus lycioides</i> subsp. <i>oleoides</i>	X		X			
<i>Euphorbia paralias</i>		X					<i>Rubia peregrina</i>			X			
<i>Euphorbia terracina</i>			X				<i>Ruscus aculeatus</i>	X					
<i>Frankenia boissieri</i>	X						<i>Ruta chalepensis</i>	X		X			
<i>Frankenia laevis</i>		X					<i>Salsola oppositifolia</i>						X
<i>Fumana thymifolia</i>	X						<i>Salsola vermiculata</i>						X
<i>Galium tricornutum</i>	X						<i>Scrophularia canina</i>				X		
<i>Genista umbellata</i>			X				<i>Sideritis arborescens</i> subsp. <i>perezlarae</i>	X					
<i>Halimium commutatum</i>			X				<i>Silene niceensis</i>			X			
<i>Halimium halimifolium</i>	X		X				<i>Stauracanthus boivinii</i>	X					
<i>Helichrysum picardii</i>		X					<i>Teucrium dunense</i>						X
<i>Helichrysum stoechas</i>				X		X	<i>Teucrium fruticans</i>	X					
<i>Juniperus oxycedrus</i> subsp. <i>macrocarpa</i>	X						<i>Teucrium hieronymi</i>						X
<i>Juniperus phoenicea</i> subsp. <i>turbinata</i>	X	X					<i>Thymelaea hirsuta</i>						X
<i>Launaea arborescens</i>					X		<i>Thymus hyemalis</i>						X
<i>Launaea nudicaulis</i>					X		<i>Ulex australis</i>	X		X			
<i>Lavandula multifida</i>			X				<i>Viola arborescens</i>	X					
<i>Lavandula stoechas</i> subsp. <i>stoechas</i>	X		X				<i>Withania frutescens</i>						X
<i>Limonium emarginatum</i>		X					<i>Ziziphus lotus</i>						X

Anexo. Flora y vegetación en las dunas costeras del sur de España (Costa-Pérez & Valle-Tendero, 2004).

Sectorización vegetal		Vegetación en Psa. Comunidad de especies.	Descripción
Dunas móviles	Dunas embrionarias	Comunidad de dunas primarias (<i>Euphorbia paraliae</i> – <i>Agropyretum junceiformis</i>) Especies características: <i>Elymus farctus subsp. boreali-atlanticus</i> , <i>Eryngium maritimum</i> , <i>Euphorbia paralias</i> . Especies acompañantes: <i>Cakile maritima</i> .	Asociación pionera de las dunas embrionarias o de los pequeños montículos arenosos próximos al mar.
	Cordón costero	Lastonar psammofilo (<i>Loto cretici-Ammophiletum australis</i>) Especies características: <i>Ammophila arenaria subsp. australis</i> , <i>Lotus creticus</i> , <i>Montagnites candollei</i> , <i>Othantus maritimus</i> . Especies acompañantes: <i>Helichrysum picardii</i> , <i>Pancratium maritimum</i> .	Vegetación vivaz que coloniza las crestas de las dunas móviles.
	Dunas semi-fijas	Matorral sobre dunas (<i>Artemisia crithmifoliae</i> – <i>Amerietum pungentis</i>) Especies características: <i>Armeria pungens</i> , <i>Artemisia crithmifolia</i> , <i>Helichrysum picardii</i> , <i>Crucianella maritima</i> , <i>Scrophularia frutescens</i> , <i>Thymus carnosus</i> . Especies acompañantes: <i>Corynephorus canescens</i> , <i>Cyperus mucronatus</i> , <i>vulpia alopecuros</i> .	Vegetación vivaz en la que dominan los pequeños arbustos de talla media que se desarrollan en las dunas litorales semifijas contribuyendo a su fijación. Representan una etapa previa a la aparición de las plantas leñosas de gran talla que forman un tipo de vegetación estable y madura.
Dunas fijas		Enebral sobre dunas (<i>Rhamno oleoides</i> - <i>Juniperetum macrocarpae</i>) Especies características: <i>Daphne gnidium</i> , <i>Juniperus oxcedrus subsp. macrocarpa</i> , <i>Juniperus turbinata</i> , <i>Phillyrea angustifolia</i> , <i>Pistacia lentiscus</i> , <i>Rhamnus oleoides</i> , <i>Rubia peregrina subsp. longifolia</i> . Especies acompañantes: <i>Ammophila arenaria</i> , <i>Armeria pungens</i> , <i>Corema album</i> .	Asociación constituida por árboles y grandes arbustos a los que acompañan algunos caméfitos e hierbas. Esta comunidad sólo se conoce en las costas gaditanas y onubenses. Representa la comunidad permanente de las dunas fijas externas.
		Matorral de camarinas (<i>Rubio longifoliaceae</i> – <i>Coremetum albi</i>) Especies características: <i>Antirrhinum majus subsp. cirrhigerum</i> , <i>Corema album</i> , <i>Pistacia lentiscus</i> , <i>Rhamnus oleoides</i> , <i>Rubia peregrina subsp. longifolia</i> . Especies acompañantes: <i>Helichrysum picardii</i> , <i>Lotus creticus</i> , <i>Malcomia littorea</i> .	Comunidad arbustiva de pequeña talla. Representa una etapa avanzada en la fijación de los sistemas dunares siendo la orla natural de los sabinares y enebrales sobre las dunas.
		Sabinar sobre dunas (<i>Osyrio quadripartitae</i> – <i>Juniperetum turbinatae</i>) Especies características: <i>Asparagus acutifolius</i> , <i>A. aphyllus</i> , <i>Daphne gnidium</i> , <i>osyris quadripartita</i> , <i>phillyrea angustifolia</i> , <i>Pistacea lentiscus</i> , <i>Rhamnus alaternus</i> , <i>Rubia longifolia</i> . Especies acompañantes: <i>Cistus salviifolius</i> , <i>Geranium purpureum</i> , <i>Lagurus ovatus</i> , <i>Rosmarinus officinalis</i> .	Comunidad que representa la etapa madura del ecosistema litoral fuera de la influencia de los vientos marinos cargados de sales. Formada por pequeños árboles que prosperan en dunas fijas.
		Jaguarzal o monte blanco (<i>Halimio halimifolii</i> - <i>Stauracanthetum genistoidis</i>) Especies características: <i>Armeria velutina</i> , <i>Cistus bourgaeanus</i> , <i>Halimium commutatum</i> , <i>h. halimifolium</i> , <i>Helichrysum picardii var. Virescens</i> , <i>Stauracanthus genistoides</i> , <i>Thymus masticina subsp. tomentosus</i> . Especies acompañantes: <i>Asparagus aphyllus</i> , <i>Centaurea exarata</i> , <i>Scirpus holoschoenus</i> , <i>Stipa gigantea</i> .	Comunidad constituida por pequeños arbustos xerófilos que colonizan las dunas fijas del distrito Onubense. La destrucción de los sabinares propicia la aparición de esta asociación.

Sectorización vegetal		Vegetación en PsI. Comunidad de especies.	Descripción
Dunas móviles	Playa	Comunidad de especies nitrohalófilas (<i>Salsola kali-Cakiletum maritima</i>) Especies características: <i>Salsola kali</i> y <i>Crucianella maritima</i> . Especies acompañantes: <i>Suaeda maritima</i> , <i>Lobularia maritima</i> , <i>Pancratium maritimum</i> .	Comunidad pionera, halonitrófila a causa de desechos arrojados por el oleaje, que se asientan sobre suelos arenosos. Su presencia está ligada siempre a condiciones de inestabilidad del sustrato, aparece como una primera banda de vegetación a veces incluso muy próxima a la zona de influencia de la pleamar.
	Dunas embrionarias	Comunidad de dunas primarias (<i>Cypero mucronati - Elymetum maritae</i>) Especies características: <i>Elymus farctus subsp. farctus</i> , <i>Cyperus capitatus</i> , <i>Otanthus maritimus</i> , <i>Sporobolus pungens</i> . Especies acompañantes: <i>Salsola kali</i> , <i>Glaucium flavum</i> , <i>Polyogum maritimum</i> .	Comunidad pionera que coloniza dunas embrionarias. Esta comunidad y la siguiente cuentan con especies adaptadas para soportar la intensa insolación y el hálito marino, ya que presentan órganos suculentos, densos tomentosos u hojas coriáceas.
	Crestas y depresiones dunares	Lastonar de dunas <i>Medicagini marinae-Ammophiletum australis</i> Especies características: <i>Ammophila australis</i> , <i>Elymus farctus</i> , <i>Aetheorrhiza bulbosa</i> , <i>Medicago marina</i> , <i>Otanthus maritimus</i> , <i>Pancratium maritimum</i> , <i>Lotus creticus</i> . Especies acompañantes: <i>Ononis natrix</i> , <i>Sporobolus pungens</i> , <i>Reichardia picrioides</i> , <i>Reichardia tingitana</i> , <i>Helichrysum maritimum</i> , etc.	Comunidad colonizadora de crestas de dunas móviles. Asociación menos halófila y más xérica que la anterior, lo que se reconoce por la disminución de los tejidos crasos y una mayor presencia de xerófilos.
Dunas semi-fijas	Matorral de dunas <i>Loto cretici - Crucianelletum maritima</i> Especies características: <i>Teucrium dunense</i> , <i>Lotus creticus</i> , <i>Ononis natrix</i> , <i>Helichrysum maritimum</i> . Especies acompañantes: <i>Phagnalon saxatile</i> , <i>Erodium bipinnatum</i> , <i>Silene ramosissima</i> , <i>Limonium lobatum</i> , <i>Lobularia maritima</i> , etc.	Asociación termomediterránea que coloniza las dunas semifijas, preparan el suelo para que aparezca vegetación arbustiva. Comunidad de cobertura alta (70-80%) dominada por pequeños arbustos adaptados a las condiciones estresantes de hábitat que ocupan.	
Dunas fijas	Lentiscar-Sabinar <i>Rubio angustifoliae-Juniperetum turbinatae</i> Especies características: <i>Juniperus turbinata</i> , <i>Daphne gnidium</i> , <i>Rhamnus angustifolia</i> , <i>Pistacia lentiscus</i> , <i>Rubia longifolia</i> . Especies acompañantes: <i>Lygeum spartium</i> , <i>Teucrium dunense</i> , <i>Ballota hirsuta</i> , <i>Artemisia barrelieri</i> , <i>Lycium intricatum</i> , <i>Launea arborescens</i> .	Máximo biológico que se alcanza en estos sistemas dunares estabilizados. Formación asentada sobre suelos arenosos ricos en materia orgánica de las dunas estabilizadas. En ella dominan la sabina y el lentisco, de forma regularia, dejando claros que son ocupados por matorral sufruticoso.	
	Tomillar <i>Teucrio belionis-Helianthemetum scopulori</i> Especies características: <i>Teucrium dunense</i> . Especies acompañantes: <i>Phagnalon saxatile</i> , <i>P. rupestre</i> , <i>Lobularia maritima</i> , <i>Frankenia corymbosa</i> , <i>Sporobolus pungens</i> .	Matorral rico en labiadas de escaso porte y cobertura. Se desarrollan sobre sustrato con costra caliza.	
	Tomillar subnitrofilo <i>Artemisio barrelieri-Salsoletum genistoidis</i> Especies características: <i>Artemisia barrelieri</i> , <i>Salsola genistoides</i> , <i>Launea arborescens</i> . Especies acompañantes: <i>Asparagus horridus</i> , <i>Phagnalon saxatile</i> , <i>Teucrium almeriense</i> , <i>Thymus hyemalis</i> , <i>Thymelaea hirsuta</i> .	Tomillar abierto donde dominan las bojas, junto a otros elementos de bajo porte. La comunidad tiene en conjunto baja cobertura y diversidad. En las zonas con mayor degradación y salinidad, el lentiscar-sabinar ha desaparecido y es sustituido por esta comunidad.	
	Pastizal terofítico efímero y psammófilo <i>Triplachno nitentis-Silenetum ramosissimae</i> Especies características: <i>Silene ramosissima</i> , <i>Triplanche nitens</i> , <i>Cutandia menphitica</i> , etc. Especies acompañantes: <i>Lobularia maritima</i> , <i>Lotus creticus</i> , <i>Reichardia tingitana</i> , <i>Ononis hispanica</i> .	Comunidad de hierbas sobre arenas costeras, sometidas a una intensa influencia marina. Se encuentra en claros de la vegetación perenne, especialmente en la última franja.	

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**Vegetative and reproductive
phenological patterns in coastal dunes
in S Spain**

Capítulo 1

Vegetative and reproductive phenological patterns in coastal dunes in S Spain

Abstract

The phenology of Mediterranean species has been extensively studied in different types of ecosystems. However, very little research has been conducted in dune ecosystems. The objective of this research is the phenological characterization and comparison among phenological patterns in coastal dunes in S Spain. For this purpose, we apply the methodology proposed by Orshan (1989) and the quantification of key phenological indexes described by Castro-Díez and Montserrat-Martí (1998) and Pérez-Latorre and Cabezudo (2002). Seasonality of species from coastal dunes in S Spain is comparable to 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 predominates 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 relation to the comparison within dunes. Using the NLPCA analysis based on phenological indexes, four phenological groups of species have been determined. These groups point out the importance of developing different strategies of management which may be in relation to the high diversity of ecomorphology and phenomorphology that characterize the coastal dunes.

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

Resumen

La fenología de las especies 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 dunas costeras del sur de España. Para ello, se ha aplicado la metodología propuesta por Orshan (1989) así como la cuantificación de índices fenológicos descritos por Castro-Díez y Montserrat-Martí (1998) y Pérez-Latorre y Cabezudo (2002). 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 periodos menos favorables. 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 la importancia del índice de secuenciación fenofásica se ha puesto de relevancia en la distinción entre los sectores de la duna. Finalmente, se han determinado cuatro grupos fenológicos mediante el empleo del análisis NLPCA basado en los índices fenológicos. Estos grupos ponen de manifiesto la necesidad de desarrollar diferentes estrategias de gestión que estén en consonancia con la elevada diversidad ecomorfológica y fenomorfológica que albergan las dunas costeras.

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

1. Introduction

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

Phenological patterns of Mediterranean species show a clear reciprocation between phenological phases and some important climate factors (Mooney et al., 1974; Reader, 1984), such as rainfall variability (Cowling et al., 2005), photoperiod (Arroyo, 1990) and summer drought (Mitrakos, 1980; Roche et al., 1997). Low winter temperatures and summer drought involve unfavourable periods (Mitrakos, 1980; Castro-Díez et 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 et al., 1989; Cabezudo et 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 and Montserrat-Martí, 1998). This diversity may respond to a huge variety of structural and floristic backgrounds (Mooney et al., 1977; Kummerow, 1983).

The use of phenology (phenological pattern) and ecomorphology (plant traits related to the adaptation to the environmental conditions) to study Mediterranean vegetation was first proposed by Orshan (1989) and subsequently improved by the development of specific methodologies such as the quantification of key phenological indexes (Castro-Díez and Montserrat-Martí, 1998; Pérez-Latorre and Cabezudo, 2002). By using this approach, different Mediterranean communities have been characterized in phenological terms (e.g. Pérez-Latorre and Cabezudo, 2006; Pérez-Latorre et al., 2010), but this is the first time that this eco-phenological 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 et al., 2001; Ley Vega de Seoane et al., 2007). These features affect the composition and abundance of vegetation and functional characters (García-Mora et 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 and McLachlan, 1994).

Coastal dunes are extremely fragile and very vulnerable to human activity, which is particularly striking in the Mediterranean (Curr et 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 and 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 et al., 1999, 2000, 2001; Acosta et al., 2003, 2005; Martínez et al., 2006), very little is known regarding phenological patterns (Herrera 1986; Laguna et al., 1986; Moreno Duran et 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 and Johnson, 1994; Montserrat-Martí et 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, M-subtropical and M-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 phenology of dune plant species on fixed and mobile semi-fixed

dunes; and (3) to define the main patterns of specialisation based on eco-phenology and discuss their ecological meaning in the context of coastal dunes.

2. Material and methods

2.1. Study area

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

Figure 2 summarised the medium values of temperatures and rainfall along the year. In P.N. del Estrecho, the average annual rainfall (R) is 794 mm, with maximum values in November (133 mm) and minimum in August (0 mm). Temperatures (T) are milder than those in the other two dunes (mean–minimum of 13.4°C in January and mean-maximum of 23.5°C in August). 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 month (mean–minimum of 12.5°C) and August the hottest (mean–maximum 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–minimum of 10.8°C in January and mean-maximum of 25.9°C in August (Fig. 2).

Three dunes sectors were differentiated from the sea area to the internal area, in relation to the organization of the particular environmental traits that characterize these ecosystems (e.g. Van der Maarel, 1997; Carter, 1988; Brown and McLachlan, 1994). In this study, the nomenclature of dune sectors was the one based up sands mobility (Van der Maarel, 1993). This differentiated between fixed dunes, semi-fixed and mobile dunes. However, the two last dunes were unified in this work in one common sector. Fixed dunes are formed by shrubs and trees and 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 and Valle-Tendero, 2004; Ley Vega de Seoane, 2007).

2.2. Data collection, phenological information and phenological indexes

The inventories were made following Braun-Blanquet (1979), by a selection of 78 major representative perennial species with the highest cover values (Van der Maarel, 1997; Costa-Pérez and Valle-Tendero, 2004; Navarro et al., 2006).

The ecomorphological traits (growth forms, deciduousness, leaf consistence and colour) were determined for each species in the field (Table 1).

For the phenological study we followed a proposal put forward by Orshan (1989). Data was sampled during the period of 2009-2012 on a minimum of 10 individuals of each species, concerning information about vegetative and reproductive phenological phases. Voucher

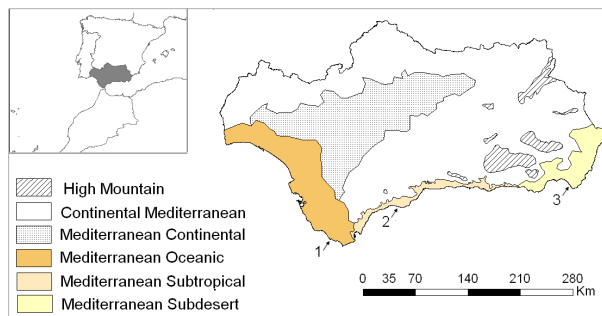


Fig. 1. Different climates in S Spain and study areas. Black dots show the study areas: (1.) P.N. del Estrecho, (2.) M.N. Artola-Cabopino, (3.) P.N. Cabo de Gata-Níjar. Data source: DERA, 2013.

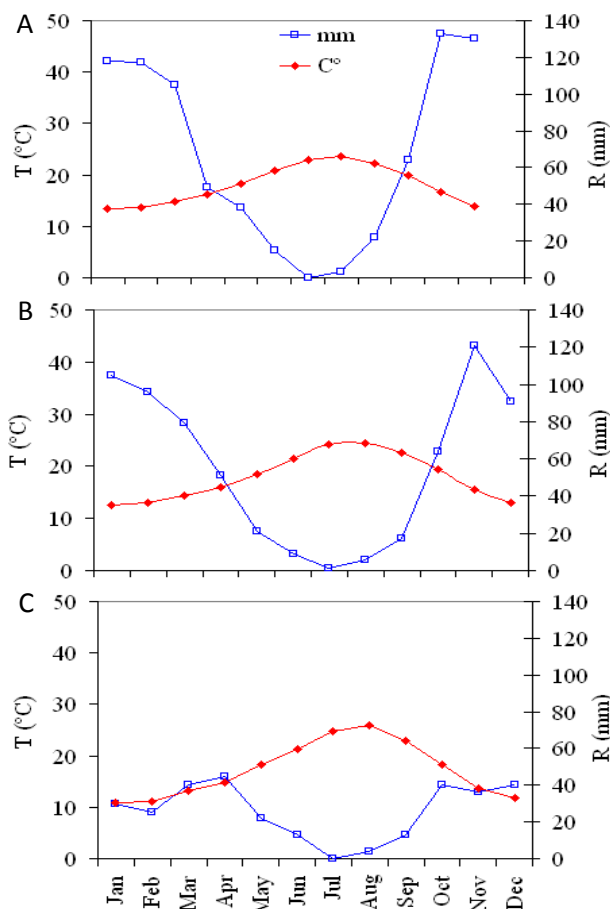


Fig. 2. Climatic diagrams (a) P.N. del Estrecho, (b) M.N. Artola-Cabopino and (c) P.N. Cabo de Gata-Níjar. Data source: Rivas-Martínez and Rivas-Saenz, 2009.

specimens of the studied species were kept in the MGC Herbarium. Botanical nomenclature follows Castroviejo (1986-2007).

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 vegetative phases, we analysed 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 and 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 and Cabezudo, 2002), it has been converted 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 and 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 ($PSI \geq 0.6$), 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 and 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.

$$FD = d (F)$$

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) medium ($151 \leq OF < 212$), (4) late ($212 \leq OF < 304$) and (5) clearly late ($304 \leq OF < 365$).

2.3. 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 and its dune sectors. In the case of not verifying the Levene's test, and for the ecomorphological traits, the Mann-Whitney and Kruskal-Wallis analyses were done.

To identify phenological patterns of specialization, 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 and Altman, 1997).

3. Results

3.1. Phenology of coastal dunes in S Spain

In table 1, the distribution of some important ecomorphological traits in the study area are summarized. Most of the analysed 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. 2-3). In summer (Jun-Sep), when drought is highest (Fig. 2-3), 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 medium flowering duration, which began in late winter and was extended to early summer (Fig. 3-4, Appendix B). The exceptions were the species with continuous flowering all year long (*Malcolmia littorea*, *Launea arborescens* and *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 ($PSI \geq 0.6$) with medium activity period (APS) and predominance of the vegetative phase ($RVA < 1$) over the reproductive ($RVA > 1$) (Fig. 4).

Table 1. Some important ecomorphological characters 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		Fixed		Mobile semi-fixed		Fixed		Mobile semi-fixed	
	N	%	N	%	N	%	N	%	N	%	N	%
<i>Growth forms</i>												
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 shrubs	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
<i>Deciduousness</i>												
Evergreen	17	43.59	1	7.69	10	41.67	1	9.09	5	45.45	3	21.43
Semi-deciduous	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
<i>Leaf colour</i>												
Green	35	89.74	7	53.85	23	95.83	4	40	9	90	7	53.85
Green-grey	2	5.13	0	0	1	4.17	0	0	0		0	0
Grey	2	5.13	6	46.15	0	0	6	60	1	10	6	46.15
<i>Leaf consistence</i>												
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

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).

3.2. Variation of phenology among dunes

Among the studied ecomorphological traits, only growth forms showed significant differences among the three coastal dunes ($KW=5.14$, $P<0.1$). This distinction was the result of a lower presence of large shrub and the absence of trees in P.N. Cabo de Gata-Níjar.

However, significant differences of all the studied ecomorphological traits, except deciduousness ($U=1317$, $P>0.1$), 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 ($U=397$, $P<0.001$) and the higher percentage of species with white ($U=786.5$, $P<0.001$) malacophyllous ($U=851$, $P<0.001$) leaves.

Specific patterns within the general phenological tendency have been found in the studied coastal dunes. ANOVA test did not show any significant difference of phenology among the three localities. 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-Níjar was differentiated from the other two dunes by its absence of DVG in summer (especially in Jul- Aug), a pattern which was very close to the observed in mobile semi-fixed dunes from the three localities. In addition, fixed dunes in P.N. Cabo de Gata-Níjar showed higher DVG values in autumn (between Sep and Nov) than the observed in the non M-subdesert 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) (Fig. 3). 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).

3.3. Phenological patterns

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 (Cronbach alpha 0.88). The first principal component explained 46.20% of the total trait variation (Cronbach 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 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). The second component explained a further 21.69% of variation (Cronbach alpha 0.10). This was strongly correlated with APS (0.84).

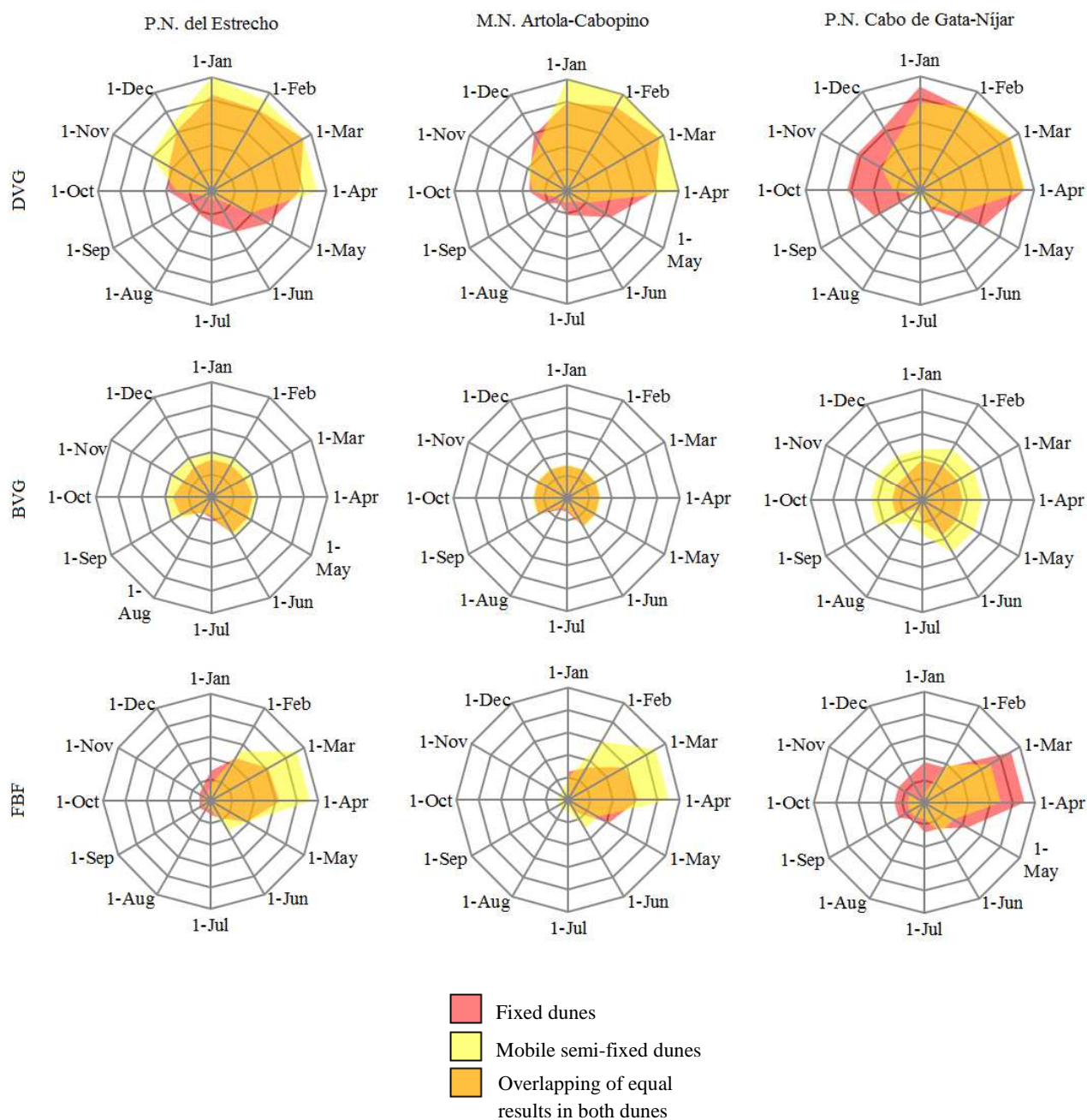
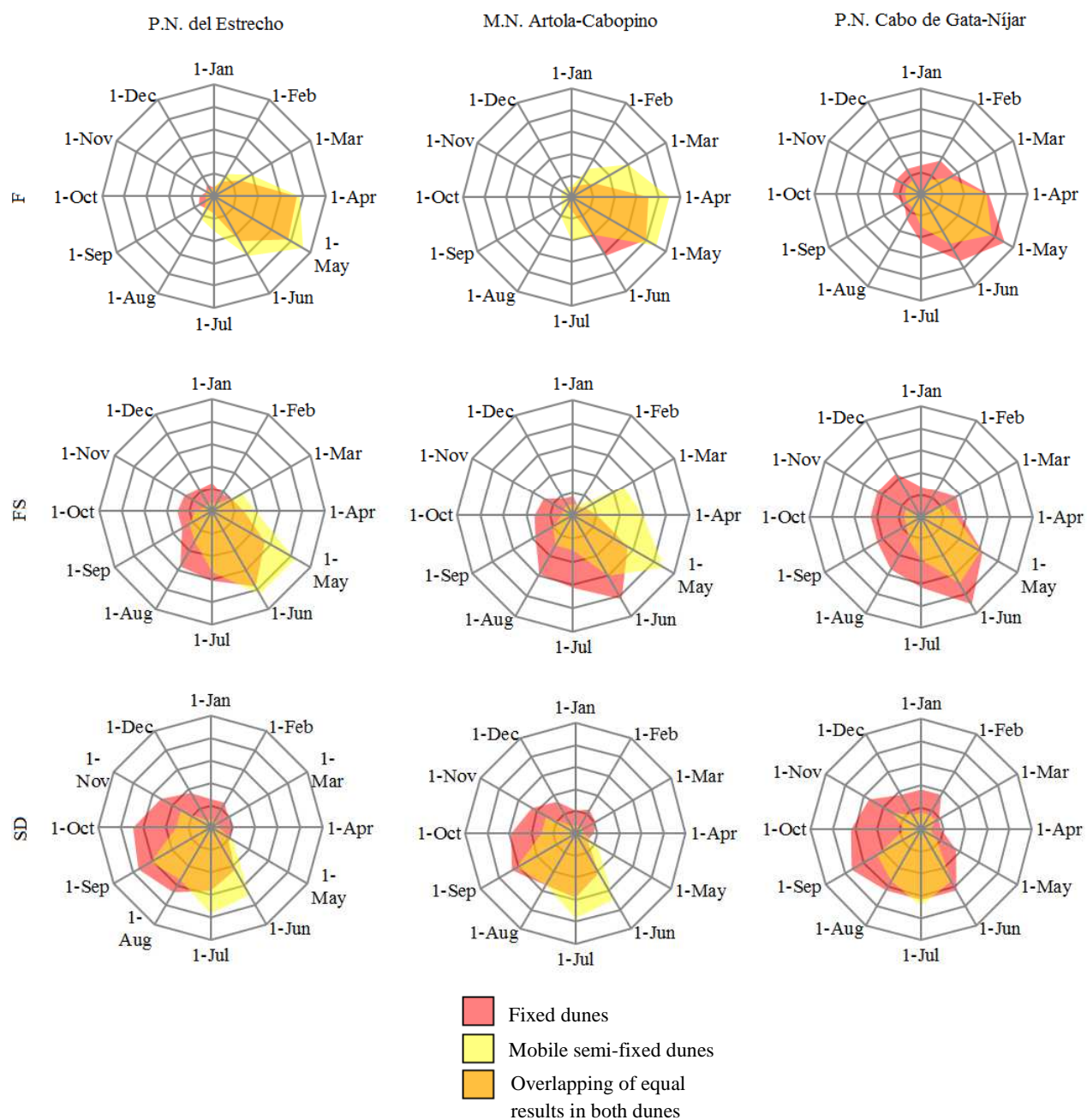


Fig. 3. Distribution of the vegetative phenological phases throughout the year in the studied The radius of the polar angle varies from 0, in the centre of the circle (no species developing



coastal dunes, expressed as the monthly percentage of species that show each phenophase. the phenophase) to 100 (all species showing the phenophase).

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 . In the majority of species of this group, vegetative phenophases predominated over the reproductive phenophases (86.25%). It was mainly formed by shrubs (82.5%) with malacophyll 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 malacophyll leaves (66.67%) and without a dominant leaf deciduousness (50% are evergreen and 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 malacophyll (81.82%) leaves, which were over represented on mobile semi-fixed dunes (63.64%) (e.g. *Viola arborescens* and *Othantus maritimus*);

(G4) Group 4: high APS (10-12) and PSI (>0.7), $FD < 92$. These were trees (69.23%) and shrubs (30.77%) of sclerophyll 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*).

4. Discussion

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

4.1. Phenological characterization of coastal dunes in S Spain

The sequencing organization of phenophases (PSI) plays an important role in the survival on coastal dunes, because it permits species to accumulate resources through the period of phenophase development (Ratcke and Lacey, 1985) as well as making it possible to minimize intraplant competition (Castro-Díez and Montserrat-Martí, 1998).

Similar APS values have been observed in other Mediterranean ecosystems, a result that points out the great similarity in the phenological activities of Mediterranean communities, despite the differences that exist in ecological, ecomorphological, and phytosociological aspects (Pérez-Latorre et 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 et al., 1977). These results coincide with Mediterranean shrubland (Pérez-Latorre and Cabezudo, 2002; Pérez-Latorre et al., 2010) and contrast with those

observed in other woody Mediterranean communities, such as *Quercus suber* forest, where some species reach values of 7 (Pérez-Latorre et al., 2010).

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

In coastal dunes, DVG starts in winter and it is maximum when precipitation has gone 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) which the plant growth involves (Kummerow, 1983) and the limited storage capacity of dampness that characterized the coastal dunes (Ley vega de Seoane et al., 2007).

According to previous studies on other coastal dune ecosystems (Cordazzo and Seeliger, 1998), medium 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 et 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 et 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 and 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 et al., 1997) and arid ecosystems in the South East of Spain (Navarro et al., 1993), and it can be interpreted with reference to avoid summer water stress (Castro-Díez and Montserrat-Martí, 1998; Perez-Latorre and Cabezudo, 2002) and competition for pollinators (Dafni, 1996; da Cruz et al., 2006).

Fruit setting and seed dispersal occur between late spring and early autumn, which shows the different functional strategies of the species (Navarro and 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 intricatum*) 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 et 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 and 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

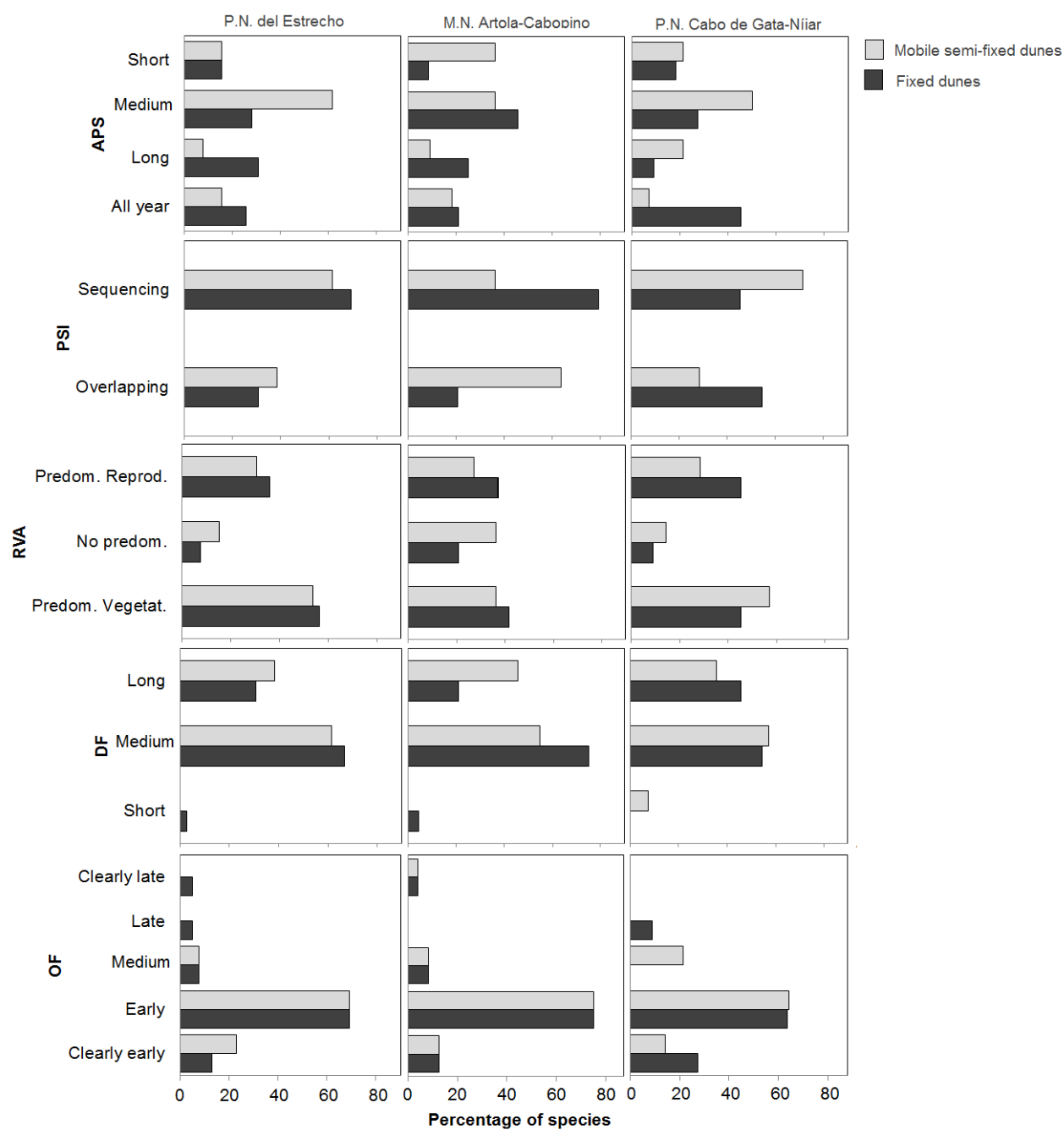


Fig. 4. Percentage of species in each of the qualitative classes defined for the different phenological indexes.

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).

4.2. Variations of phenology among dunes

Some interesting differences of phenology have been found among the studied coastal dunes. These are mainly related to the fixed dunes, results which agree with 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 et al., 1999), and as a consequence, they show very close functional characters and diversity of species (Ley Vega de Seane et 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 climate (Godoy et 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 and Lacey, 1985; Sánchez et 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). Fixed dunes follow the general trend of predominating sequencing species, whereas in mobile semi-fixed

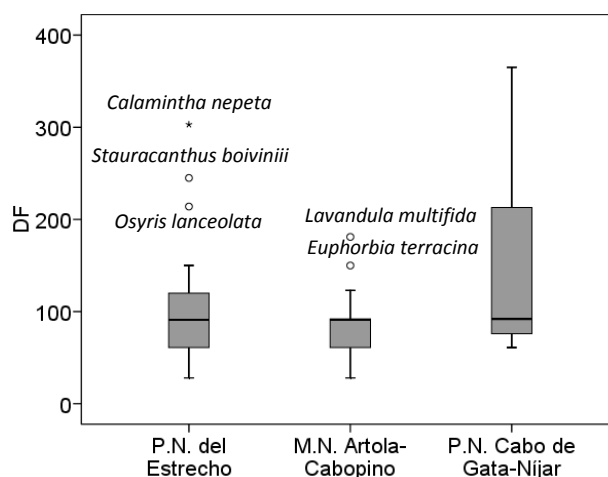


Fig. 5. Variation of FD (Flowering duration) among fixed coastal dunes in S Spain. Box plots show median, quartiles, outliers (O) and extreme (*) values of FD

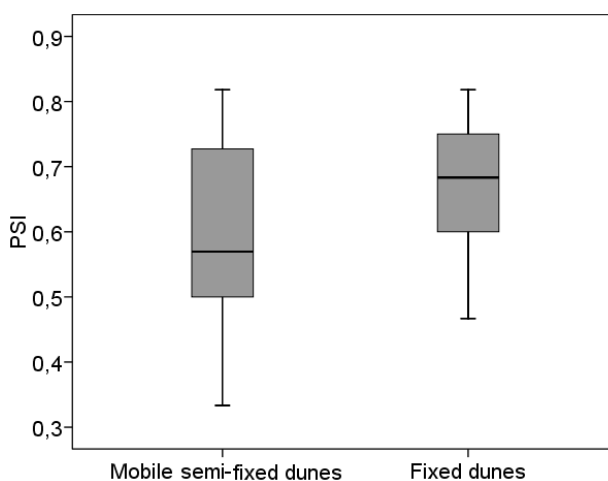


Fig. 6. Variation of PSI (Phenophase sequence index) between fixed and mobile-semifixed dunes in M.N. Artola-Cabopino. Box plots show median and quartiles values of PSI.

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.

4.3. Phenological patterns

The species tend to employ different strategies in order to complete their life cycle (Floret et al., 1989) and to reduce the interspecific competition for the resources (Navarro and Cabezudo, 1998). In the studied coastal dunes, the nonlinear principal components analysis indicates 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 medium 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 malacophyll leaves). Within this general group, different phenophasic patterns previously identified in other studies in Mediterranean environments (Montenegro et al., 1989; Pérez-Latorre and Cabezudo, 2006; Pérez-Latorre et 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 and Lacey, 1985), like *Launaea arborescens* (Carrión et al., 2003), that appeared in the study area during the early to mid-Miocene, before the Mediterranean climate (Sánchez et 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 and Montserrat-Martí (1998).

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 show the traits closer to those obtained in Mediterranean forest (e.g. Pérez-Latorre and Cabezudo, 2002.), such as the predominance of trees with evergreen sclerophyll leaves and heavy fruits. These species show a long phenological activity during the year and a high sequencing of their phenophases, 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 et al., 2003). Their differentiation is evidence of the high phenological diversity that is represented in coastal dunes, and coastal dunes, and it could be an important tool for the improvement of the management and conservation of these fragile ecosystems.

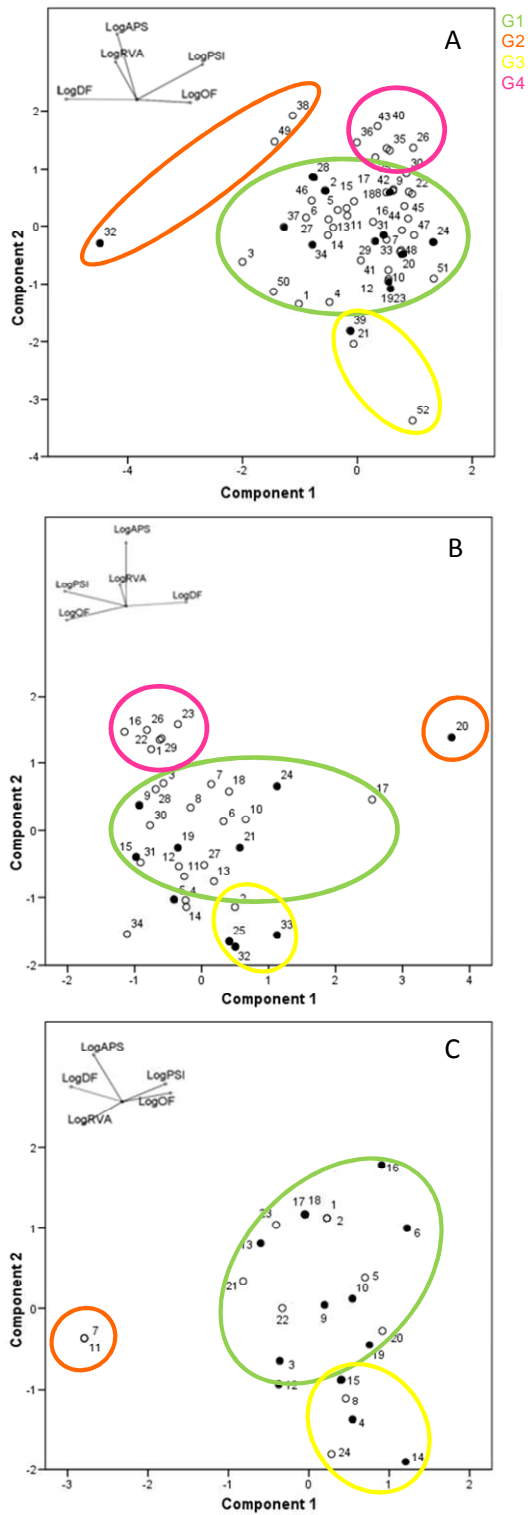


Fig. 7. Phenological patterns in coastal dunes of S Spain. (A) P.N. del Estrecho, (B) M.N. Artola-Cabopino, (C) P.N. Cabo de Gata-Níjar. Legend: The numbered points represent plant species (Appendix 2); (white point) Fixed dunes, (black point) Mobile-semimobile dunes; (G1) Group 1; (G2) Group 2; (G3) Group 3; (G4) Group 4.

5. Acknowledgements

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Appendix A. Phenophasic calendar of species in Mediterranean coastal dunes in S Spain. (A.1) P.N. del Estrecho, (A.2) M.N. Artola-Cabopino, (A.3) P.N. Cabo de Gata-Níjar.

A.1	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D												
P.N. del Estrecho. Fixed dunes																																																
<i>Adenocarpus telonensis</i>													<i>Dianthus broteri</i>												<i>Phyllirea angustifolia</i>													DVG FBF F FS SD BVG APS DVG FBF										
<i>Calamintha nepeta</i> subsp. <i>nepeta</i>													<i>Erica scoparia</i>												<i>Phlomis purpurea</i>													F FS SD BVG APS DVG FBF										
<i>Calicotome villosa</i>													<i>Fumana thymifolia</i>												<i>Pistacia lentiscus</i>													F FS SD BVG APS DVG FBF										
<i>Calluna vulgaris</i>													<i>Galium tricornutum</i>												<i>Quercus coccifera</i>													F FS SD BVG APS DVG FBF										
<i>Chamaerops humilis</i>													<i>Halimium halimifolium</i>												<i>Rhamnus alaternus</i>													F FS SD BVG APS DVG FBF										
<i>Cistus albidus</i>													<i>Juniperus oxycedrus</i> subsp. <i>macrocarpa</i>												<i>Rhamnus lycioides</i> subsp. <i>oleoides</i>													F FS SD BVG APS DVG FBF										
<i>Cistus crispus</i>													<i>Juniperus phoenicea</i> subsp. <i>turbinata</i>												<i>Ruscus aculeatus</i>													F FS SD BVG APS DVG FBF										
<i>Cistus ladanifer</i>													<i>Lavandula stoechas</i>												<i>Ruta chalepensis</i>													F FS SD BVG APS DVG FBF										
<i>Cistus monspeliensis</i>													<i>Lonicera implexa</i>												<i>Sideritis arborescens</i> subsp. <i>perezlarae</i>													F FS SD BVG APS DVG FBF										
<i>Cistus salviifolius</i>													<i>Marrubium vulgare</i>												<i>Stauracanthus boivinii</i>													F FS SD BVG APS DVG FBF										
<i>Corema album</i>													<i>Myrtus communis</i>												<i>Teucrium fruticans</i>													F FS SD BVG APS DVG FBF										
<i>Cytisus striatus</i>													<i>Olea europaea</i> var. <i>sylvestris</i>												<i>Ulex australis</i>													F FS SD BVG APS DVG FBF										
<i>Daphne gnidium</i>													<i>Osyris lanceolata</i>												<i>Viola arborescens</i>													F FS SD BVG APS										

A.2	J	F	M	A	My	Jn	Jl	Ag	S	O	N	D	J	F	M	A	My	Jn	Jl	Ag	S	O	N	D	J	F	M	A	My	Jn	Jl	Ag	S	O	N	D			
M.N. Artola-Cabopino. Fixed dunes																																							
<i>Asparagus aphyllus</i>													<i>Genista umbellata</i>													<i>Phyllirea angustifolia</i>													DVG FBF F FS SD BVG APS DVG FBF F FS SD BVG APS DVG FBF F FS SD BVG APS DVG FBF F FS SD BVG APS DVG FBF F FS SD BVG APS
<i>Calicotome villosa</i>													<i>Halimium calycinum</i>													<i>Phlomis purpurea</i>													DVG FBF F FS SD BVG APS DVG FBF F FS SD BVG APS DVG FBF F FS SD BVG APS DVG FBF F FS SD BVG APS
<i>Chamaerops humilis</i>													<i>Halimium halimifolium</i>													<i>Pistacia lentiscus</i>													DVG FBF F FS SD BVG APS DVG FBF F FS SD BVG APS DVG FBF F FS SD BVG APS DVG FBF F FS SD BVG APS
<i>Cistus monspeliensis</i>													<i>Juniperus phoenicea subsp. turbinata</i>													<i>Quercus coccifera</i>													DVG FBF F FS SD BVG APS DVG FBF F FS SD BVG APS DVG FBF F FS SD BVG APS DVG FBF F FS SD BVG APS
<i>Cistus salviifolius</i>													<i>Lavandula multifida</i>													<i>Rhamnus lycioides subsp. oleoides</i>													DVG FBF F FS SD BVG APS DVG FBF F FS SD BVG APS DVG FBF F FS SD BVG APS DVG FBF F FS SD BVG APS
<i>Daphne gnidium</i>													<i>Lavandula stoechas</i>													<i>Rubia peregrina</i>													DVG FBF F FS SD BVG APS DVG FBF F FS SD BVG APS DVG FBF F FS SD BVG APS DVG FBF F FS SD BVG APS
<i>Dianthus broteri</i>													<i>Myrtus communis</i>													<i>Ruta chalepensis</i>													DVG FBF F FS SD BVG APS DVG FBF F FS SD BVG APS DVG FBF F FS SD BVG APS DVG FBF F FS SD BVG APS
<i>Euphorbia terracina</i>													<i>Olea europaea var. sylvestris</i>													<i>Ulex australis</i>													DVG FBF F FS SD BVG APS DVG FBF F FS SD BVG APS DVG FBF F FS SD BVG APS DVG FBF F FS SD BVG APS
M.N. Artola-Cabopino. Mobile-semifixed dunes																																							
<i>Crucianella maritima</i>													<i>Malcolmia littorea</i>													<i>Phagnalon saxatile</i>													DVG FBF F FS SD BVG APS DVG FBF F FS SD BVG APS DVG FBF F FS SD BVG APS DVG FBF F FS SD BVG APS
<i>Eryngium maritimum</i>													<i>Medicago marina</i>													<i>Scrophularia frutescens</i>													DVG FBF F FS SD BVG APS DVG FBF F FS SD BVG APS DVG FBF F FS SD BVG APS DVG FBF F FS SD BVG APS
<i>Helichrysum stoechas</i>													<i>Ononis natrix sub sp. ramosissima</i>													<i>Silene niceensis</i>													DVG FBF F FS SD BVG APS DVG FBF F FS SD BVG APS DVG FBF F FS SD BVG APS DVG FBF F FS SD BVG APS
<i>Lotus creticus</i>																																					DVG FBF F FS SD BVG APS DVG FBF F FS SD BVG APS DVG FBF F FS SD BVG APS DVG FBF F FS SD BVG APS		

A.3	J	F	M	A	My	Jn	Jl	Ag	S	O	N	D		J	F	M	A	My	Jn	Jl	Ag	S	O	N	D		J	F	M	A	My	Jn	Jl	Ag	S	O	N	D	
P.N. Cabo de Gata-Níjar. Fixed dunes																																							
<i>Asparagus albus</i>	[Grid]												<i>Launaea nudicaulis</i>	[Grid]												<i>Thymus hyemalis</i>	[Grid]												DVG FBF F FS SD BVG APS DVG FBF
<i>Asparagus horridus</i>	[Grid]												<i>Lycium intricatum</i>	[Grid]												<i>Withania frutescens</i>	[Grid]												F FS SD BVG APS DVG FBF
<i>Frankenia boissieri</i>	[Grid]												<i>Teucrium hieronymi</i>	[Grid]												<i>Ziziphus lotus</i>	[Grid]												F FS SD BVG APS
<i>Launaea arborescens</i>	[Grid]												<i>Thymelaea hirsuta</i>	[Grid]																									DVG FBF F FS SD BVG APS
P.N. Cabo de Gata-Níjar. Mobile-semifixed dunes																																							
<i>Asteriscus maritimus</i>	[Grid]												<i>Medicago marina</i>	[Grid]												<i>Plantago albicans</i>	[Grid]												DVG FBF F FS SD BVG APS DVG FBF
<i>Crucianella maritima</i>	[Grid]												<i>Ononis natrix</i>	[Grid]												<i>Salsola oppositifolia</i>	[Grid]												F FS SD BVG APS DVG FBF
<i>Helichrysum stoechas</i>	[Grid]												<i>Otanthus maritimus</i>	[Grid]												<i>Salsola vermiculata</i>	[Grid]												F FS SD BVG APS DVG FBF
<i>Limonium lobatum</i>	[Grid]												<i>Phagnalon saxatile</i>	[Grid]												<i>Teucrium dunense</i>	[Grid]												F FS SD BVG APS
<i>Lotus creticus</i>	[Grid]																																						DVG FBF F FS SD BVG APS

Appendix B. Phenological indexes of the species, some important ecomorphological characters and phenological groups in coastal dunes of S Spain. Legend: (APS) Active phenophasic period of species, (PSI) Phenophase sequence index), (RVA) Index of reproductive/vegetative activity of the species, (FD) Flowering duration and (OF) Onset flowering; (GF) Growth forms: (H) Herbs, (SS) Small shrubs, (LS) Large shrubs, (T) Trees; (LC) Leaf consistency:

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

	APS	PSI	RVA	FD	OF	GF	LH	LC	PCA number	Phenological group
P.N. del Estecho. Mobile semi-fixed dunes										
<i>Asteriscus maritimus</i>	8	0.7	2	120	31	SS	SD	M	2	G1
<i>Crucianella maritima</i>	6	0.63	1	61	90	SS	SD	S	12	G1
<i>Eryngium maritimum</i>	9	0.73	1.4	62	181	H	D	M	18	G1
<i>Euphorbia paralias</i>	7	0.6	0.83	61	120	H	D	M	19	G1
<i>Frankenia laevis</i>	9	0.67	0.4	61	90	SS	D	M	20	G1
<i>Helichrysum picardii</i>	9	0.82	0.3	61	120	SS	SD	M	24	G1
<i>Limonium emarginatum</i>	12	0.59	1.29	153	90	SS	SD	M	28	G1
<i>Limonium sinuatum</i>	9	0.67	0.5	91	90	SS	SD	M	29	G1
<i>Lotus creticus</i>	8	0.73	0.67	91	90	H	D	M	31	G1
<i>Malcolmia littorea</i>	12	0.33	1	365	1	H	D	M	32	G2
<i>Medicago marina</i>	7	0.58	1.5	153	59	H	D	M	34	G1
<i>Ononis natrix</i> subsp. <i>ramosissima</i>	11	0.56	0.58	181	31	SS	E	M	37	G1
<i>Phagnalon saxatile</i>	6	0.55	0.4	92	59	SS	SD	M	39	G3
Mean value	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										
<i>Asparagus aphyllus</i>	12	0.79	1.11	92	120	SS	SD	S	1	G4
<i>Calicotome villosa</i>	6	0.5	1	92	59	LS	D	M	2	G3
<i>Chamaerops humilis</i>	9	0.5	1.33	91	90	LS	E	S	6	G1
<i>Cistus monspeliensis</i>	11	0.82	0.5	91	90	SS	SD	M	3	G1
<i>Cistus salviifolius</i>	7	0.7	0.4	91	90	LS	SD	M	4	G1
<i>Daphne gnidium</i>	12	0.57	0.67	123	181	LS	E	M	7	G1
<i>Dianthus broteri</i>	11	0.67	0.4	91	90	SS	D	S	8	G1
<i>Euphorbia terracina</i>	8	0.62	1.2	150	31	H	D	M	10	G1
<i>Genista umbellata</i>	7	0.64	1	61	59	SS	E	M	12	G1
<i>Halimium calycinum</i>	7	0.67	0.56	122	59	LS	SD	M	13	G1
<i>Halimium halimifolium</i>	7	0.7	0.33	91	90	LS	SD	M	14	G1
<i>Juniperus phoenicea</i> subsp. <i>turbinata</i>	12	0.77	1.2	28	31	T	E	S	16	G4
<i>Lavandula multifida</i>	9	0.47	0.67	181	1	SS	SD	M	17	G1
<i>Lavandula stoechas</i> subsp. <i>stoechas</i>	11	0.6	0.58	122	59	SS	SD	M	18	G1
<i>Myrtus communis</i>	11	0.8	1.4	92	151	LS	E	S	22	G4
<i>Olea europaea</i> var. <i>sylvestris</i>	12	0.7	1.8	91	90	T	E	S	23	G4
<i>Phillyrea angustifolia</i>	10	0.78	3.33	61	59	T	E	S	26	G4
<i>Phlomis purpurea</i>	8	0.6	0.6	91	90	LS	SD	M	27	G1
<i>Pistacia lentiscus</i>	10	0.71	1	61	90	T	E	S	28	G1
<i>Quercus coccifera</i>	12	0.67	1.43	61	90	T	E	S	29	G4
<i>Rhamnus lycioides</i> subsp. <i>oleoides</i>	9	0.75	0.67	61	90	LS	SD	S	30	G1
<i>Rubia peregrina</i>	7	0.57	1	61	90	SS	D	S	11	G1
<i>Ruta chalepensis</i>	7	0.75	1	61	120	SS	D	M	31	G1
<i>Ulex australis</i>	5	0.71	1.33	62	334	LS	E	S	34	G1
Mean value	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 semi-fixed dunes										
<i>Crucianella maritima</i>	6	0.63	1	61	90	SS	SD	S	5	G1
<i>Eryngium maritimum</i>	9	0.73	1.4	62	181	H	D	M	9	G1
<i>Helichrysum stoechas</i>	9	0.82	0.3	61	120	SS	SD	M	15	G1
<i>Lotus creticus</i>	8	0.73	0.67	91	90	H	D	M	19	G1
<i>Malcolmia littorea</i>	12	0.33	1	365	1	H	D	M	20	G2
<i>Medicago marina</i>	7	0.58	1.5	153	59	H	D	M	21	G1
<i>Ononis natrix</i> subsp. <i>ramosissima</i>	11	0.56	0.58	181	31	SS	E	M	24	G1

	APS	PSI	RVA	FD	OF	GF	LH	LC	PCA number	Phenological group
<i>Phagnalon saxatile</i>	6	0.55	0.4	92	59	SS	SD	M	25	G3
<i>Scrophularia canina</i>	5	0.5	1	92	59	SS	SD	M	32	G3
<i>Silene niceensis</i>	5	0.45	1.25	120	31	H	D	M	33	G3
Mean	8.18	0.56	0.92	65.45	149.36					
SD	2.64	0.16	0.39	53.48	113.19					
P.N. Cabo de Gata-Níjar. Fixed dunes										
<i>Asparagus albus</i>	12	0.79	1.11	92	120	SS	SD	S	1	G1
<i>Asparagus horridus</i>	12	0.79	1.11	92	120	SS	E	S	2	G1
<i>Frankenia boissieri</i>	9	0.67	0.44	61	90	SS	D	S	5	G1
<i>Launaea arborescens</i>	12	0.41	2.4	365	1	LS	E	M	7	G2
<i>Launaea nudicaulis</i>	6	0.67	1	91	90	SS	E	M	8	G3
<i>Lycium intricatum</i>	12	0.41	2.4	365	1	LS	D	M	11	G2
<i>Teucrium hieronymi</i>	7	0.67	0.45	61	120	SS	SD	M	20	G1
<i>Thymelaea hirsuta</i>	10	0.42	0.75	273	212	SS	E	M	21	G1
<i>Thymus hyemalis</i>	9	0.53	0.6	120	31	SS	D	M	22	G1
<i>Withania frutescens</i>	12	0.55	0.7	153	90	LS	D	S	23	G1
<i>Ziziphus lotus</i>	6	0.57	1.67	61	120	LS	E	S	24	G3
Mean value	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 semi-fixed dunes										
<i>Asteriscus maritimus</i>	8	0.7	2	120	31	SS	SD	M	3	G1
<i>Crucianella maritima</i>	6	0.63	1	61	90	SS	SD	S	4	G1
<i>Helichrysum stoechas</i>	9	0.82	0.3	61	120	SS	SD	M	6	G1
<i>Limonium lobatum</i>	9	0.67	1	91	90	SS	SD	M	9	G1
<i>Lotus creticus</i>	8	0.73	0.67	91	90	H	D	M	10	G1
<i>Medicago marina</i>	7	0.58	1.5	153	59	H	D	M	12	G1
<i>Ononis natrix</i>	11	0.56	0.58	181	31	SS	E	M	13	G1
<i>Othantus maritima</i>	5	0.57	0.6	30	151	SS	SD	M	14	G3
<i>Phagnalon saxatile</i>	6	0.55	0.4	92	59	SS	SD	M	15	G3
<i>Plantago albicans</i>	12	0.75	0.25	61	90	H	D	M	16	G1
<i>Salsola oppositifolia</i>	11	0.63	0.58	184	181	SS	E	M	17	G1
<i>Salsola vermiculata</i>	11	0.63	0.58	184	181	SS	E	M	18	G1
<i>Teucrium dunense</i>	7	0.6	0.45	61	120	SS	SD	M	19	G1
Mean value	8.36	0.64	0.80	102.21	98.79					
SD	2.21	0.08	0.50	53.02	47.95					



**Dispersal traits and patterns in
coastal dunes in S Spain**

Capítulo 2

Dispersal traits and patterns in coastal dunes in S Spain

Abstract

This study describes and compares the dispersal traits and patterns of 78 perennial plant species in three coastal dunes in S Spain, which differs in Mediterranean macroclimate (Mediterranean-oceanic, M-subtropical, M-subdesert). Different sectors from the sea area to the internal area were analysed (mobile-semifixed dunes and fixed dunes). Diaspores were collected when ripe, just before they started to fall off the plant. In the laboratory, they were air-dried, weighed, measured and averaged into ranges. Diaspores were essentially small seeds (2-4 mm, from 10^{-5} to 1g) without dispersal structures. This research revealed that diaspore size and mass are key traits in the differentiation among dunes (smallest diaspores were found in subdesert and mobile semi-fixed dunes) and growth forms (biggest ones were characteristic of trees and large shrubs). Small shrubs included the highest variability of dispersal traits, and also the 100% of anemochoric species. The analyses showed the predominance of species developing restricted dispersal, semachory and antitelechoric mechanisms. The present work has found that the combination of these dispersal and regenerative traits by a NLPCA test involves five dispersal patterns that clearly separate between dispersal and survival strategies. This new insight is of high interest for conservation of the vulnerable coastal dune ecosystems.

Keywords: Antitelechoric mechanisms, coastal dunes, diaspore mass, dispersal modes, Mediterranean vegetation, spatial dispersal.

Resumen

Este trabajo describe y compara los caracteres y patrones de dispersión en 78 especies perennes procedentes de tres dunas costeras del S de España con diferencias dentro de macroclima Mediterráneo (clima Mediterráneo-oceánico, M-subtropical y M-subdesértico). Diferentes sectores de duna fueron analizados, desde la orilla del mar hasta la zona más interior (dunas móviles y semi-fijas vs. dunas fijas). Las diásporas fueron recolectadas cuando estuvieron maduras, justo antes de caer de la planta. En el laboratorio, estas fueron secadas al aire, pesadas, medidas y promediadas en rangos. De este modo se determinó que las diásporas de dunas costeras son esencialmente pequeñas (2-4 mm, desde 10^{-5} hasta 1g) y carentes de estructuras de dispersión. Este estudio reveló el papel fundamental del tamaño de la diáspora como carácter diferenciador entre dunas (las diásporas más pequeñas se encontraron en las dunas subdesérticas y en las móviles y semi-fijas) así como entre formas de crecimiento (las diásporas de mayor tamaño fueron características de árboles y arbustos). Los arbustos de pequeña talla albergaron la mayor variabilidad de caracteres de dispersión, incluyendo además al 100% de las especies anemocóricas. Los análisis demostraron la predominancia de especies semacoras, de dispersión restringida y con presencia de mecanismos antitelecóricos. El presente trabajo determinó que la combinación de los caracteres de dispersión y regeneración mediante el empleo del test NLPCA da lugar a la distinción de cinco patrones de dispersión en dunas costeras, los cuales claramente separan las estrategias de dispersión de las de supervivencia. El nuevo conocimiento generado es de elevado interés para la conservación de los vulnerables sistemas de dunas costeras.

Keywords: Mecanismos antitelecóricos, dunas costeras, masa de la diáspora, modos de dispersión, vegetación mediterránea, dispersión espacial.

1. Introduction

Seed dispersal, the departure of a diaspore (seed or fruit) (Weiher et al., 1999) from the parent plant (Howe and Smallwood, 1982), is a central life-history trait with a wide variety of significant ecological and evolutionary consequences (Clobert et al., 2001; Levin et al., 2003; Kokko and López-Sepulcre, 2006). It is a critical event regulating the spatial and temporal distribution of plants (Navarro et al., 2008) and determining many key aspects in plant biology (Grime, 2001; Ozinga et al., 2005) and in plant communities (Cain et al., 2000). In addition, at species level, dispersal failure can lead to species extinction (Cowie and Holland, 2006; Ozinga et al., 2009; Mello et al., 2011; Purschle et al., 2012). Consequently, seed dispersal is a key factor in conservation biology (Cooper and Walters, 2002; Haddad et al., 2003; Trakhtenbrot et al., 2005) and in restoration ecology (Uhl et al., 1988; Guimares-Vieira et al., 1994; Palmer et al., 1997).

Among dispersal traits, seed mass is a key functional trait of plant regeneration strategies (Westoby, 1998; Weiher et al., 1999; Kleyer, 1999; Leishman et al., 2000). It is related to many biological factors (Weiher et al., 1999), especially dispersal ability (Grime, 2001; Leishman et al., 1995; Thompson et al., 1998), habitat (Mazer, 1998; Salisbury, 1942, 1974; Baker, 1972) and growth forms (Rockwood, 1985; Jurado, 1991, 2001; Westoby et al., 2002; Moles et al., 2005).

Dispersal mode and spatial dispersal facilitate the colonization of new landscapes, which are more suitable for the survival and the establishment of the seedling (Navarro et al., 2008). However, there are situations where spatial dispersal could involve serious dangers for the survival of the diaspore, especially in areas of

unsuitable habitat surrounding the mother plant (Ellner and Schmid, 1981) or in those exposed to unpredictable environmental conditions (Navarro et al., 2008). In these cases, plants develop mechanisms of restricted dispersal (antitelechoric) (Ellner and Schmid, 1981; Van Rheede van Oudtshoorn and Van Rooyen, 1990; Ehrman and Cocks, 1996) which will protect diaspores from predation and other dangers, and which will regulate the intra- and inter-year timing of dispersal and germination (Guterman, 1993, 1994, 2001).

The combination of dispersal traits involves the determination of dispersal patterns, whose analyses provide information about groups of species characterized by the same strategies for colonization and recolonization, establishment, occupation and maintenance of habitats, and facilitation to assess the degree to which a plant community is endangered. Information about these patterns is critical for optimising and determining the success of *in situ* and *ex situ* conservation efforts (Mattana et al., 2011).

Consequently, dispersal studies are conformed as a tool of high interest in coastal dunes ecosystems. However, there are few studies on dispersal traits of species in these ecosystems, and those which exist mainly focus on sea-water dispersal (e.g. García-Mora et al., 1999; Guja et al., 2010; Yang et al., 2012).

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 et al., 2001; Ley Vega de Seoane et al., 2007; Fenu et al., 2012), which involve specific functional

strategies that characterize its particular vegetation (García-Mora et al., 1999; Ley Vega de Seoane, 2007).

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

The information obtained by this research would be very interesting for the complete characterization of biotic and abiotic components that have been suggested as a field of research needed in coastal dunes (Gracia, 2009). This new approach would also involve important applications in terms of management, conservation and restoration ecology (Bakker et al., 1996). 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, M-subtropical and M-subdesert) and different oceanic influences (from transitional dunes between the Atlantic Ocean and the Mediterranean Sea to typically Mediterranean dunes). As a consequence, the results obtained in this research would be useful at a larger scale.

In the present work, dispersal patterns of perennial species in three coastal dunes are

examined in order to answer the following questions: (1) What are the main dispersal traits in coastal dunes? (2) Do the frequency and richness of dispersal traits differ among dunes with different climate conditions? And between different dune sectors? (3) Do the dispersal traits vary among growth forms, as it has been shown in other ecosystems? (e.g. Jurado, 1991, 2001; Navarro et al., 2008, 2009) (4) What are the main dispersal patterns in these ecosystems?

2. Material and methods

2.1. Study area

The study was carried out in three coastal dunes in S Spain with different Mediterranean climate (DERA, 2013): P.N. del Estrecho in Cádiz (Mediterranean-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).

Figure 2 summarised the medium values of temperatures and rainfall along the year. 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-maxima of 23.5°C in August). 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 month (mean-minima of 12.5°C) and August the hottest (mean-maxima 24.5°C). P.N. Cabo de Gata-Níjar shows the driest dunes (average annual rainfall of

308 mm) and a different rainy season (maximum 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.

Three dunes sectors were recognized, depending on the distance from the sea and which have contrasting vegetation structure (e.g. Van der Maarel, 1997; Carter, 1988; Brown and McLachlan, 1994). In this study, the nomenclature of dune sectors was the one based up on sands mobility (Van der Maarel, 1993): fixed dunes, semi-fixed and mobile dunes. However, the two last dunes were unified in this work in one common sector. Fixed dunes are formed by shrubs and trees and represent the mature stage of the ecosystem. Mobile semi-fixed dune vegetation is constituted by pioneer communities of herbs and small shrubs, which are adapted to tolerate the intense disturbance that is associated to the proximity of the sea (Costa-Pérez and Valle-Tendero, 2004; Ley Vega de Seoane, 2007).

2.2. Samples and measurements

Field sampling were carried out during the period of 2009-2012 in the 78 major representative perennial species with the highest cover values (Van der Maarel, 1997; Costa-Pérez and Valle-Tendero, 2004; Navarro et al., 2006). The inventories were made following Braun Blanquet (1979) and voucher specimens of the studied species were kept in the MGC Herbarium. Botanical nomenclature follows Castroviejo (1986-2007).

Six easily measured dispersal traits and three antitelechoric mechanisms were analyzed (Table

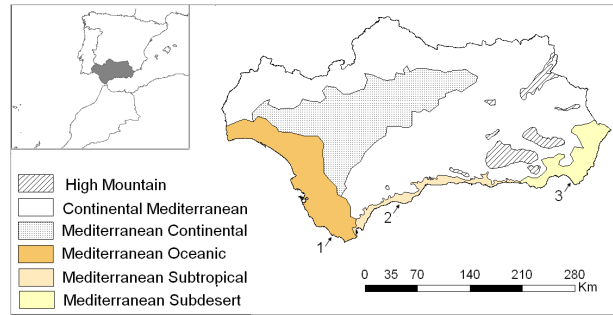


Fig. 1. Different climates in S Spain and study areas. Black dots show the study areas: (1.) P.N. del Estrecho, (2.) M.N. Artola-Cabopino, (3.) P.N. Cabo de Gata-Níjar. Data source: DERA, 2013.

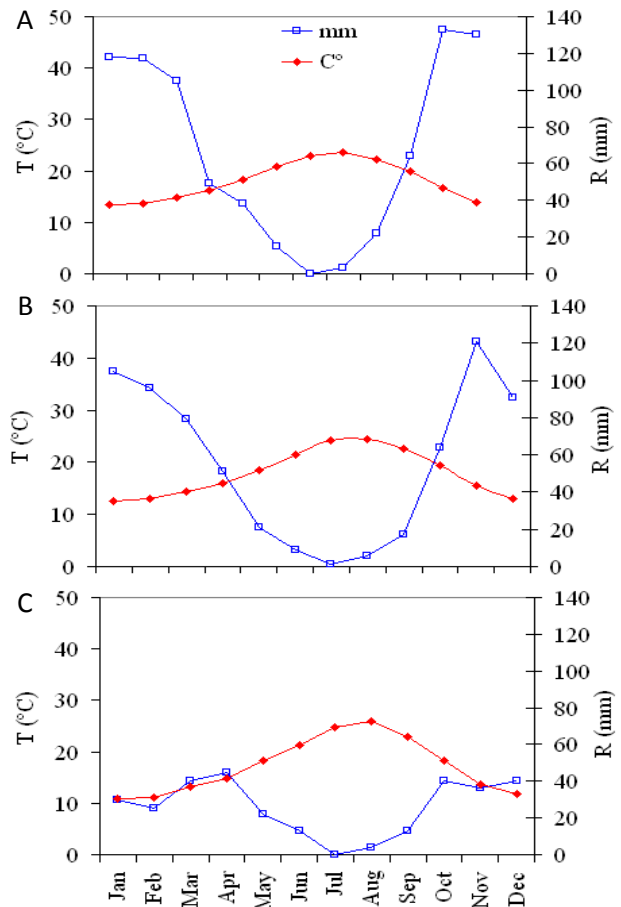


Fig. 2. Climatic diagrams (a) P.N. del Estrecho, (b) M.N. Artola-Cabopino and (c) P.N. Cabo de Gata-Níjar. Data source: Rivas-Martínez and Rivas-Saenz, 2009.

1, Appendix). Resprouting ability and clonality were also studied because they would be critical processes for the regeneration of the ecosystem (Bond and Midgley, 2001; Clarke et al., 2013).

The term diaspora was used to name the dispersal unit (Weiher et al., 1999). The following options are used: species dispersed by seed or entire fruit. If a fruit is dehiscent, the dispersal unit is usually the seed. Indehiscent fruits do not open to release their seeds. In these cases, the seeds are distributed together with the entire fruit or part of the fruit.

For each individual, 20 seeds and fruits (100 for small seeded species) were collected when ripe, just before they started to fall off the plant. Once in the laboratory, these were air-dried, weighed, measured and averaged into ranges (Cornelissen et al., 2003). In the case of diaspores with structures that characterized their morphology (pappus, spines, hairs, etc.), the whole was measured. Whenever a diaspore lent itself to more than one type of dispersal mode, the mechanism judged to be predominant was assigned. We considered that species with developed spatial dispersal are those whose diaspores are equipped with structures that facilitate spatial dispersal, such as flying structures (dispersed by abiotic vectors) or nutrient structures (dispersed by biotic vectors) (Ellner and Schmid, 1981; Venable and Levin, 1985; Cain et al., 2000; Higgins et al., 2003). Species with restricted dispersal were those whose diaspores lack such dispersal-enhancing characters (Willson, 1993). Sea-water dispersal species were determined by consulting previous bibliography (García-Mora et al., 1999).

Table 1. Traits recorded on 78 species in coastal dunes in S Spain, and used for analysis.

Trait	Description	References
Diaspore mass (weight)	Log-scaled diaspore mass	
Diaspore size (length)	Tiny : <2mm; Small: 2-4mm; Medium: 4-10mm; Large: >10mm	Díaz and Cabido (1997)
Diaspore type	Achene; berry; calyx; drupe; galbulus; glande; nutlet; pod; samara; seed; twin-fruit.	
Diaspore morphology	Hooked appendages; nutrient structures; nothing; open balloon; pappus; wings.	van Rheede van Oudtshoorn and van Rooyen (1990), Knevel et al. (2005)
Dispersal mode	Anemochory; ballistic dispersal; barochory; ombrohydrochory; semachory; zoochory.	van der Pijl (1982), van Rheede van Oudtshoorn and van Rooyen (1999)
Spatial dispersal	RD, restricted dispersal; DDA, developed spatial dispersal by abiotic vectors; DDB, developed spatial dispersal by biotic vectors.	Navarro et al. (2009)
Bradyspory	Absent; present.	
Myxospermy	Absent; present.	
Synaptospermy	Absent; present.	
Resprouting ability and/or clonality	Absent; present.	

Among the antitelechoric mechanisms (Van Rheede van Oudtshoorn and Van Rooyen, 1999), bradyspory, synaptospermy and myxospermy were studied. Bradyspory is shown in those species with delayed diaspore release, which are partially retained and protected by the lignified floral structures and by dry and fleshy fruits. Synaptospermy is the formation of diaspores containing more than one seed which are dispersed as an unit (Cheplick, 1992). Some diaspores produce mucilage which upon being wetted serves to anchor the diaspore. This mechanism is known as myxospermy (van Rheede van Oudtshoorn and van Rooyen, 1999).

Species were distinguished among growth forms in trees (woody plants with main canopy elevated on a substantial trunk), larger shrubs (woody plants taller than 0.8 m with main canopy deployed relatively close to the soil surface on one or more relatively short trunks), small shrub (woody plants up to 0.8 m tall) and perennial herbs (non woody plants) (Cornelissen et al., 2003).

2.3. Statistical analysis

Continuous characters were \log_{10} -transformed prior to statistical analysis in order to normalise their distributions. All statistical analyses were performed with SPSS 15.0 (SPSS Inc).

To test for significant differences of dispersal traits among coastal dunes, one-way analysis of variance ANOVA and Bonferroni were applied for numerical dispersal trait (dispersal mass), after verifying the homogeneity of variance by Levene's test ($P > 0.05$). Whereas Kruskal-Wallis analysis were done for categorical traits (diaspore seed, type and morphology, dispersal mode, spatial

dispersal, anithelechoric mechanisms, resprouting and/or clonality ability). Differences between sectors of dune (fixed and mobile semi-fixed dunes) were tested using t -test for numerical dispersal trait and U de Mann-Whitney for categorical traits.

ANOVA and Kruskal-Wallis analysis were used to determine the differences among growth forms, but in this case, no difference between fixed and mobile semi-fixed dunes was made.

A nonlinear principal components analysis (NLPCA, De Leeuw, 1982) was undertaken for the identification of the decisive attributes that distinguish dispersal strategies. It was performed by the program CATPCA, included in the software SPSS 15.0 (SPSS Inc). NLPCA can handle variables of different type simultaneously and deal with nonlinear relationships between variables. Alpha of Cronbach was calculated (Cronbach, 1951) for each extracted component. If this value was high to a specific component, it would be interpreted as an indicator of the weight of the component. Also, it serves to explain the total variance. In general, an alpha value of 0.7 or greater is considered reliable (Bland and Altman, 1997).

3. Results

3.1. Dispersal traits in coastal dunes in S Spain

Diaspore mass in the study area ranged from 7492.22 mg in *Quercus coccifera* (on fixed dunes in P.N. del Estrecho) to 0.02 mg in *Erica scoparia* (in the same locality) (Appendix). The frequency of diaspore mass classes on a logarithmic scale produced an approximately normal distribution

between 10^{-5} to 1g. The class of 10^{-3} was predominant (36.7%) (Fig. 3).

The most common diaspore in coastal dunes showed small size (2-4 mm) (44.5%) and absence of dispersal structures (51.8%). These were mainly seeds (39.1%), achenes (14.5%) and berries (12.7%), whose predominant dispersal mode was semachory (40%) by restricted dispersal (51.8%). Four species showed sea-water dispersal (*Eryngium maritimum*, *Euphorbia paralias*, *Medicago marina* and *Othantus maritimus*).

Antitelechoric mechanisms were over represented in coastal dunes (76%). Bradyspory was the most common among the studied species (48.18%), whereas myxosperry was only found in eight species (Appendix). Resprouting ability and/or clonality were also poorly represented, only 10 species showed this ability (Appendix).

3.2. Comparison of dispersal traits among coastal dunes

Perennial species on fixed dunes spanned 10^5 ranges of diaspore mass, from 10^{-5} to 1g, whereas

in mobile semi-fixed dunes it was reduced to 10^3 ranges, from 10^{-5} to 10^{-2} g (Fig.3). However, only M.N Artola-Cabopino showed this difference between fixed and mobile semi-fixed dunes as significant ($t = -2.21, P < 0.05$). The ANOVA test revealed that there were not significant differences of diaspore mass among the three studied coastal dunes.

Table 2 shows the dispersal spectrum of qualitative dispersal traits in the different study areas.

No significant differences of diaspore size were shown by Kruskal-Wallis analysis among coastal dunes ($KW = 0.37, P > 0.10$), and only P.N. Cabo de Gata-Níjar confirmed differences between fixed and mobile semi-fixed dunes ($U = 45, P < 0.10$).

Seed was the predominant diaspore type in P.N. del Estrecho and M.N. Artola, whereas in P.N. Cabo de Gata-Níjar, diaspores were over represented by fruits (69.2%) ($K-W = 7.13, P < 0.05$); berries in fixed dunes and achenes in mobile semi-fixed dunes.

Among the different diaspore morphologies found in fixed dunes, nutrient structures were over

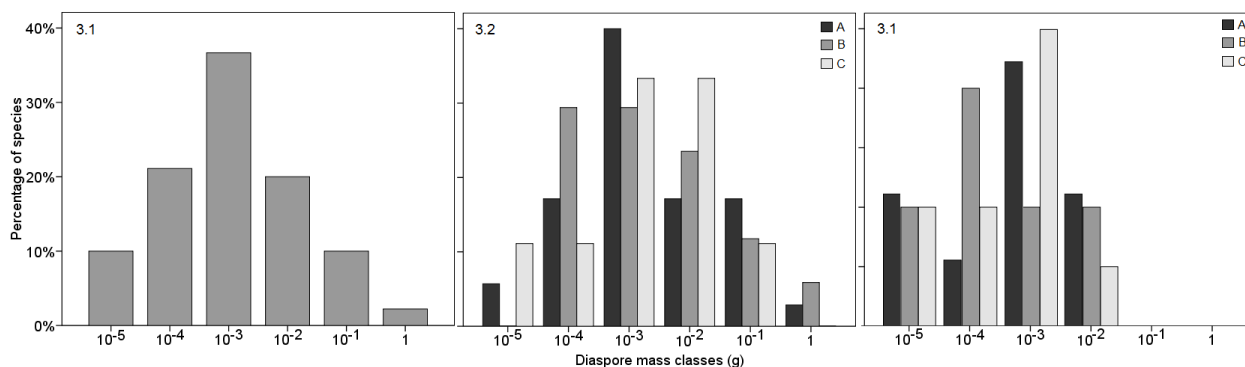


Fig. 3. Diaspore mass distribution of perennial species in coastal dunes in S Spain. (3.1) Complete dunes, (3.2) Fixed dunes, (3.3.) Mobile semi-fixed dunes. Legend. A (P.N. del Estrecho); B (M.N. Artola-Cabopino); C (P.N. Cabo de Gata-Níjar).

Table 2. Dispersal spectrum of qualitative dispersal and regenerative traits in coastal dunes in S Spain

	P.N. del Estrecho				M.N. Artola-Cabopino				P.N. Cabo de Gata-Níjar			
	Fixed dunes		Mobile semi-fixed dunes		Fixed dunes		Mobile semi-fixed dunes		Fixed dunes		Mobile semi-fixed dunes	
	N	%	N	%	N	%	N	%	N	%	N	%
<i>Diaspore size</i>												
Tiny	8	20.51	5	38.46	2	8.33	3	30	1	9.09	3	23.08
small	16	40.02	5	38.46	12	50	5	50	4	36.36	7	53.85
Medium	11	28.20	2	15.38	8	33.33	1	10	5	45.45	3	23.08
Large	4	10.26	1	7.69	2	8.33	1	10	1	9.09	0	0
<i>Diaspore type</i>												
Achene	1	2.56	5	38.46	1	4.17	2	20	2	18.18	5	38.46
Berry	6	16.67	0	0	4	16.67	0	0	4	36.36	0	0
Calyx	0	0	0	0	0	0	0	0	2	18.18	1	7.69
Drupe	6	16.67	0	0	4	16.67	0	0	1	9.09	0	0
Galbulus	2	5.13	0	0	1	4.17	0	0	0	0	0	0
Glande	1	2.56	0	0	1	4.17	0	0	0	0	0	0
Nutlet	6	16.67	0	0	3	12.5	0	0	2	18.18	0	0
Pod	0	0	1	7.69	0	0	1	10	0	0	1	7.69
Samara	0	0	0	0	0	0	0	0	0	0	2	15.38
Seed	17	43.59	6	46.15	10	41.67	6	60	0	0	4	30.77
Twin-fruit	0	0	1	7.69	0	0	1	10	0	0	0	0
<i>Diaspore morphology</i>												
Hooked appendages	1	2.56	2	15.38	0	0	2	20	0	0	1	7.69
Nothing	23	58.97	7	53.84	14	58.33	5	50	3	27.27	5	38.46
Nutrient structures	15	38.46	0	0	10	41.67	0	0	5	45.45	0	0
Open balloon	0	0	0	0	0	0	0	0	1	9.09	1	7.69
Pappus	0	0	3	23.08	0	0	2	20	2	18.18	3	23.08
Wings	0	0	1	7.69	0	0	1	10	0	0	3	23.08
<i>Antitelechory</i>												
Bradyspory (presence)	22	56.41	2	15.38	16	66.67	3	30	5	45.45	5	38.46
Synaptospermy (presence)	9	23.08	5	38.46	6	25	4	40	8	72.72	5	38.46
Myxospermy (presence)	3	7.69	1	7.69	3	12.5	1	10	1	9.09	1	7.69
<i>Dispersal mode</i>												
Anemochory	1	2.56	3	23.08	0	0	3	30	3	27.27	7	53.85
Ballistic dispersal	2	5.13	2	15.38	2	8.33	1	10	0	0	1	7.69
Barochory	7	17.95	0	0	6	25	0	0	3	27.27	0	0
Ombro-hydrochory	0	0	1	7.69	0	0	0	0	0	0	3	23.08
Semachory	20	51.58	5	38.46	11	45.83	4	40	3	27.27	1	7.69
Zoichory	9	23.08	2	15.38	5	20.83	2	20	2	18.18	1	7.69
<i>Spatial dispersal</i>												
RD	23	58.97	8	61.54	13	54.17	5	50	3	27.27	5	38.46
DDA	0	0	3	23.08	0	0	3	30	3	27.27	7	53.85
DDB	16	41.02	2	15.38	11	45.83	2	20	5	45.45	1	7.69
<i>Resprouting ability and/or clonality (presence)</i>												
	5	12.82	0	0	5	20.83	0	0	4	36.36	0	0

represented in P.N. Cabo de Gata-Níjar, while in P.N. del Estrecho and M.N. Artola-Cabopino, the absence of dispersal structures was predominant ($K-W=7.13$; $P<0.05$).

In mobile semi-fixed dunes, the majority of diaspores showed absence of dispersal structures, but these dunes included all the species with seeds provided of wings (*Crucianella maritima*, *Salsola oppositifolia*, *S. vermiculata*).

In P.N. del Estrecho and M.N. Artola-Cabopino dunes, semachory was the predominant dispersal mode. Anemochory was over represented in mobile semi-fixed dunes from P.N. Cabo de Gata-Níjar, but the U Mann-Whitney test did not support this difference between dune sectors ($U= 59$, $P>0.10$).

Significant differences of spatial dispersal were also found among coastal dunes ($K-W= 6.32$, $P<0.05$). Restricted dispersal was predominant in M.N. Artola-Cabopino and P.N. del Estrecho, whereas in P.N. Cabo de Gata-Níjar spatial dispersal by biotic factors was predominant in fixed dunes and spatial dispersal by abiotic factors was over represented in mobile semi-fixed dunes ($U=63.5$, $P>0.10$). The high number of species with spatial dispersal by abiotic vectors in fixed dunes in P.N. Cabo de Gata-Níjar contrasted with that observed in P.N. del Estrecho and in M.N. Artola-Cabopino, where it was absent. Seawater dispersal species were found in all the studied mobile semi-fixed dunes (Appendix).

The presence of species with antitelechoric mechanisms increased from P.N. del Estrecho (69.27% in fixed dunes and 46.15% in mobile

semi-mobile dunes) to P.N. Cabo de Gata-Níjar (100% in fixed dunes and 61.53% in mobile semi-mobile dunes) and from the mobile semi-fixed dune to the fixed dunes ($K-W= 9.17$, $P>0.10$). Bradispority showed significant differences among dune sectors in P.N. del Estrecho ($U= 149.5$, $P<0.01$) and M.N. Artola-Cabopino ($U= 76$, $P<0.05$). It was less represented in mobile semi-fixed dunes than in fixed dunes. Sinaptospermy was significantly more abundant in fixed dunes in P.N. Cabo de Gata-Níjar than in the other two studied fixed dunes ($K-W= 10.35$, $P<0.01$).

All the species that showed resprouting ability and/or clonality were found in fixed dunes (Appendix). The highest number of species showing this trait was found in P.N. Cabo de Gata-Níjar ($U= 52$, $P<0.05$).

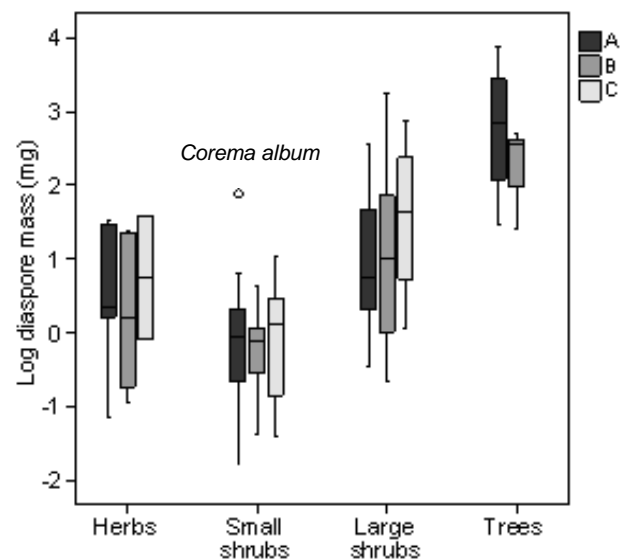


Fig. 4. Diaspore mass grouped by growth forms in box plots showing median, quartiles and outliers (O) of diaspore mass (log) of perennial species in coastal dunes in S Spain. Legend: A (P.N. del Estrecho); B (M.N. Artola-Cabopino); C (P.N. Cabo de Gata-Níjar).

3.3. Comparison of dispersal traits among growth forms

Among the studied dispersal traits, diaspore mass was the only one that maintained significant differences among growth forms in the three coastal dunes. Diaspore mass was significantly higher in trees and large shrubs than in small shrubs (P.N. del Estrecho: $F= 11.06$, $P<0.001$; M.N. Artola-Cabopino: $F=6.02$, $P<0.01$; P.N. Cabo de Gata-Níjar: $F=5.07$, $P<0.05$) (Fig. 4).

P.N. del Estrecho showed the highest number of dispersal traits which differ among growth forms: diaspore size ($K-W= 8.08$, $P<0.05$), diaspore morphology ($K-W= 14.98$, $P<0.01$), dispersal mode ($K-W= 9.99$, $P<0.05$), spatial dispersal ($K-W= 8.28$, $P<0.05$) and resprouting ability and/or clonality ($K-W= 7.44$, $P<0.10$).

In M.N. Artola-Cabopino, significant differences of diaspore morphology ($K-W= 11.57$, $P<0.01$) and dispersal mode ($K-W= 6.29$, $P<0.10$) were found.

In P.N. Gata-Níjar only diaspore type significantly varied among growth forms ($K-W= 6.63$, $P<0.05$). The percentages and number of species that showed each of these dispersal traits are included in Table 3.

Herbs of coastal dunes showed the smallest diaspores (tiny-small), which were mainly seeds without dispersal structures.

Small shrubs were semachorics and their diaspores were mainly small, without dispersal structures. This growth form included the 100% of species with anemochory (diaspores with wings or pappus). They also showed the highest diversity of types of diaspore.

Large shrub diaspores were similar to the found in small shrubs, but with a higher presence of berries and drupes. Large shrubs and trees had resprouting ability and/or clonality.

Trees showed the biggest diaspores (medium-large) with nutrient structures that strengthened the dispersal by biotic factors (barochory and zoochory).

3.4. Dispersal patterns

The principal component analysis (Fig.5, Table 4) showed the general pattern of dispersal (first axis) and survival (second axis) traits in coastal dunes.

In all the studied dunes, component 1 had a high positive loading with dispersal mode and negative with diaspore morphology. In this axis, semachoric species such as *Malcolmia littorea*, *Halimium* sp. and *Thymus hyemalis* were associated to the most positive values, whereas barochoric species with nutrient structures such as *Chamaerops humilis*, *Juniperus* sp. and *Ziziphus lotus* were related to the most negative values. In P.N. Cabo de Gata-Níjar, component 1 separated the species in different dune sectors. The majority of species from mobile semi-fixed dunes showed positive values, whereas species from fixed dunes showed a wider distribution.

Component 2 in P.N. del Estrecho had a high negative loading with synaptospermy and positive with resprouting ability and/or clonality. The most negative values were shown in a clear group of species (*Chamaerops humilis*, *Olea europaea* and *Ruscus aculeatus*) whose diaspores were drupes. This group also included all the species with resprouting ability and/or clonality, except

Table 3. Dispersal and persistence traits among growth forms. Only the traits with significant differences in Kruskal-Wallis test ($P < 0.1$) are represented. Legend. T (trees), LS (large shrubs), SS (small shrubs), H (herbs); RD (restricted dispersal, DDA (developed dispersal by abiotic factors), DDB (developed dispersal by biotic factors).

	P.N. del Estrecho								M.N. Artola-Cabopino								P.N. Cabo de Gata-Níjar					
	H		SS		LS		T		H		SS		LS		T		H		SS		LS	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
<i>Diaspore size</i>																						
<2	2	33.33	7	33.33	4	21.05																
2-4	1	16.67	9	42.86	10	52.53	1	16.67														
4-10	2	33.3	5	23.81	3	15.79	3	50														
>10	1	16.67			2	10.53	2	33.33														
<i>Diaspore morphology</i>																						
Hooked appendage	2	33.3	1	4.76					2	33.3												
Nothing	4	66.67	15	71.43	11	57.89			4	66.67	9	69.23	6	60								
Nutrient structure			1	4.76	8	41.10	6	100			1	7.69	4	40	5	100						
Open ballons																						
Pappus			3	14.29							2	15.38										
Wings			1	4.76							1	7.69										
<i>Dispersal mode</i>																						
Anemochory			4	19.05							3	23.08										
Ballistic dispersal	2	33.33			2	10.53			2	33.33			1	10								
Barochory					2	10.53	5	83.33			1	7.69	1	10	4	80						
Ombro-hydrochory			1	4.76																		
Semachory	2	33.33	14	66.67	9	47.37			2	33.33	8	61.54	5	50								
Zoochory	2	33.33	2	9.52	6	31.58	1	16.67	2	33.33	1	7.69	3	30	1	20						
<i>Spatial dispersal</i>																						
RD	4	66.67	16	76.19	11	57.89																
DDA			3	14.29																		
DDB	2	33.3	2	9.52	8	42.11	6	100														
Present					3	15.79	2	33.33	3	15.79	2	33.33										
Present																						
<i>Diaspore type</i>																						
Achene																	6	35.29	1	25		
Berry																	2	11.76	2	50		
Calyx																	3	17.64				
Drupe																			1	25		
Nutlet																			2	4.76		
Samara																			2	11.76		
Seed																	2	66.67	2	11.76		
Pod																	1	33.33				

Daphne gnidium, species which also shows resprouting ability and/or clonality but whose diaspores were berries. The highest values in the component 2 were found in species such as *Phagnalon saxatile*, *Asteriscus maritimus* and *Rhamnus* sp. These species had synaptospermy (in relation to the presence of pappus and berries) and lack of resprouting ability and/or clonality (Fig. 5A).

In M.N. Artola-Cabopino and P.N. Cabo de Gata, component 2 showed the highest positive loading for bradyspory, whereas myxospermy had the highest negative. Bradisporic and myxospermic species, such as *Halimium* sp. and *Plantago albicans*, were located at the top of the figure 5B-C, while species like *Phagnalon saxatile* and *Frankenia boissieri* could be found at the bottom of this figure.

4. Discussion

The results of this study show the high dispersal diversity in coastal dunes, and how dispersal traits vary among growth forms. Dispersal diversity is a good indicator of the ecological and functional richness of the study area (Cain et al., 2000; Navarro et al., 2009), and this research provides new information that will be useful for comparative ecological studies and for developing scientific conservation initiatives in coastal dunes.

4.1. Dispersal characterization in coastal dunes

Coastal dunes include a high variety of seed sizes, which agrees with the results of Díaz et al. (1998) in similar ecosystems, such as woodlands and xerophytic shrublands. Diaspore mass range for studied species on fixed dunes coincided with the range found in Indiana dunes (Mazer, 1989) and in sandy soils in China (Zhao et al., 2011), but with one order less of magnitude (the class of 10^{-3} mg). The approximately normal distribution of diaspore mass on a log scale means that selection favours relatively small seeds more often than relatively large ones (Jurado et al., 1991). The harsher environmental conditions that characterize the coastal dunes involve the selection of species with small seeds which would have a larger number of them, and hence a greater chance that some of its seeds would land on a site suitable for establishment (Jurado et al., 1991).

According to Ellner and Schmid (1981), the predominance of diaspores without structures for dispersal and with restricted dispersal by semachory in coastal dunes can be also explained by the unfavourable environmental conditions of these ecosystems. These

characteristics can be interpreted as the result of selection for diaspores to remain near the mother plant, a location proven to be suitable for establishment in an environment where the surroundings include areas of unsuitable habitat.

The high percentage of species showing antitelechoric mechanisms in all the studied dunes support the importance of remaining in the safe site (Howe and Smallwood, 1982; Navarro et al., 2008). In spite of the high number of previous studies that have confirmed this strategy in arid ecosystems (e.g. Ellner and Schmid, 1981; Van Rooyen et al., 1990; Kamenetsky and Gutterman, 1994; Navarro et al., 2008, 2009), this is the first research that supports it in coastal dune ecosystems. Among these antitelechoric mechanisms, bradyspory was the best represented in coastal fixed dunes. This mechanism is important for dispersal in time (Navarro et al., 2009). However, the low number of species developing myxospory (only eight in the three studied dunes) demonstrates that this antitelechoric mechanism is not efficient in coastal dunes.

Sea-water dispersal species are characteristic of coastal ecosystems. According to García-Mora et al. (1999) this dispersal mode is usually combined with leaf adaptations to coastal environmental stress and capability to withstand deep sand burial. These species are located in mobile dunes, which are occasionally flooded by sea water (Van der Maarel, 1993). As individuals, coastal plants may be uprooted and killed in such cases, but their seeds may become dispersed by the action of waves (Yang et al., 2012).

4.2. Comparison of dispersal traits among dunes and growth forms

The results of this study point out the particular dispersal characteristics of Mediterranean-subdesert coastal dunes in P.N. Cabo de Gata-Níjar compared with the most Mediterranean-oceanic (P.N. del Estrecho) and Mediterranean-subtropical dunes (M.N. Artola-Cabopino), as well as the poor dispersal differences between fixed and mobile semi fixed dunes in the three studied cases.

Significant dispersal difference between dune sectors has been found in relation to diaspore weight and size. Diaspore mass range in mobile semi-fixed dunes is shorter than the found in fixed dunes and it is closer to those found in arid environments (Jurado et al., 1991; Navarro et al., 2009), but between one and two orders less of magnitude. The higher presence of tiny and small fruits in mobile semi-fixed dunes than in fixed dunes could be explained by differences in the type of habitat. Several studies have found correlations

between seed mass and habitat (e.g. Salisbury, 1942; Baker, 1972; Mazer, 1989; Westoby et al., 1992). These researches have shown the presence of small-seeded species in open, early-successional habitats, such as mobile semi-fixed dunes, and large-seeded species in relatively late-successional habitats, like fixed dunes. According to most reports, this is due to differences in shade-tolerance. In fixed dunes, where the canopy cover is higher than in mobile semi-fixed dunes, there is severe competition that involves a lower probability of seedling establishment of species with small seeds than those with large seeds (Thompson et al., 1993; De Villiers et al., 2002). However, in mobile semi-fixed dunes small-seeded species could be abundant as a result of their good colonization ability, even if they are competitively inferior (Harper et al., 1970; Andersen, 1993; Rees, 1995). This difference of seed mass among sectors of dune is also supported by the distribution of growth forms. Bigger plants (trees and large shrubs), which are mainly located on fixed dunes, tend to have larger seeds than smaller shrubs and

Table 4. Loading of the dispersal traits on the first two components from Nonlinear Principal Components Analysis (NLPCA). Percentage of variance explained and Cronbach's Alpha are given for each component.

	Component					
	P.N. del Estrecho		M.N. Artola-Cabopino		P.N. Cabo de Gata-Níjar	
	1	2	1	2	1	2
Diaspore mass	-0.82	-0.22	-0.76	0.11	-0.69	0.24
Diaspore size	-0.67	-0.33	-0.85	0.16	-0.86	-0.17
Diaspore morphology	-0.94	0.24	-0.93	-0.07	-0.98	0.11
Dispersal mode	0.95	-0.15	0.98	0.02	0.96	-0.17
Bradyspory	-0.47	-0.20	-0.31	0.78	-0.16	0.77
Myxospermy	-0.34	0.09	-0.42	-0.64	-0.37	-0.55
Synaptospermy	0.61	-0.73	0.49	0.38	0.51	0.57
Resprouting ability and/or clonality	0.53	0.64	0.70	-0.22	0.76	-0.10
Cronbach alpha	0.85	0.21	0.87	0.23	0.86	0.30
Explained variance (%)	76.15	23.85	76.72	23.28	75.29	24.71

perennial herbs, which are over represented in mobile semi-fixed dunes. This result agrees with previous studies in different types of ecosystems (e.g. Thompson and Rabinowitz, 1989; Jurado et al., 1991; Navarro et al., 2009), where it has been confirmed that larger seeds may require larger plants for support and dispersal and may require more time to mature, which in turn sets lower limits on longevity (Rees and Venable, 2007).

In P.N. Cabo de Gata-Níjar fruits were the predominant diaspore, whereas in the other two studied dunes, seeds were over represented as dispersal unit. This result is related to the different dispersal modes among coastal dunes, which involves the presence of diverse diaspore types and morphologies. Dispersal by wind (anemochory), which is a typical characteristic of arid ecosystems (Howe and Smallwood, 1982; Gutterman, 1993; Navarro et al., 2008), is an important dispersal mode in mobile semi-fixed dunes in the three localities, but also in fixed dunes in P.N. Cabo de Gata-Níjar. In these dunes the vegetation tends to be not too dense and wind can be a major dispersal agent (Gentry, 1982) for species that are relatively tall, such as small shrubs, within their respective habitats (Fenner, 2000). The presence of species which are dispersed by closed balloon, such as *Teucrium dunense* and *T. hieronymi*, is also an indicator of the Mediterranean subdesert climate of P.N. Cabo de Gata-Níjar. This diaspore type has been described as typical of open dry vegetation (Dansereau and Lems, 1957; Navarro et al., 1993; 2006). Dunes in P.N. Cabo de Gata-Níjar also differed to the non subdesert dunes in antitelechoric mechanisms. Whereas in P.N. del Estrecho and M.N. Artola, bradyspory is predominant, synaptospermy is over represented in P.N. Cabo de Gata-Níjar. Bradyspory is, according to Navarro et

al. (2009), an important mechanism for dispersal in time and for colonization of establishment sites, while synaptospermy is advantageous in subdesert environments because it protects the diaspores against mechanical damage and spreads germination over time until there are favourable conditions (Ellner and Schmidha, 1981; Van Rheede van Oudtshoorn and Van Rooyen, 1990; Gutterman, 1994).

4.3. Dispersal patterns

The non-linear principal component analysis clearly separates between colonization and survival strategies, which characterize the most important dispersal patterns in coastal dune ecosystems.

Species whose dispersal strategies are led to the potential colonization of new habitats were differed regarding the type of environment where they would be dispersed:

(1) Developing of wind-flying diaspores (small diaspores with pappus or wings) is predominant in disturbed open areas (Willson, 1986, 1992; Navarro et al., 2008), such as mobile semi-fixed dunes (e.g. *Phagnalon saxatile*, *Helycrisum* sp., *Otanthus maritimus*) and P.N. Cabo de Gata (e.g. *Launea* sp.).

(2) Animal-dispersed diaspores (middle diaspores with nutrient structures or hooked appendages) are over represented in denser vegetation sites (Herrera, 1984), like fixed dunes (e.g. *Corema album*, *Rhamnus* sp., *Asparagus* sp.). Species dispersed by biotic factors play a prominent role in the maintenance of Mediterranean plant-disperser systems owing to

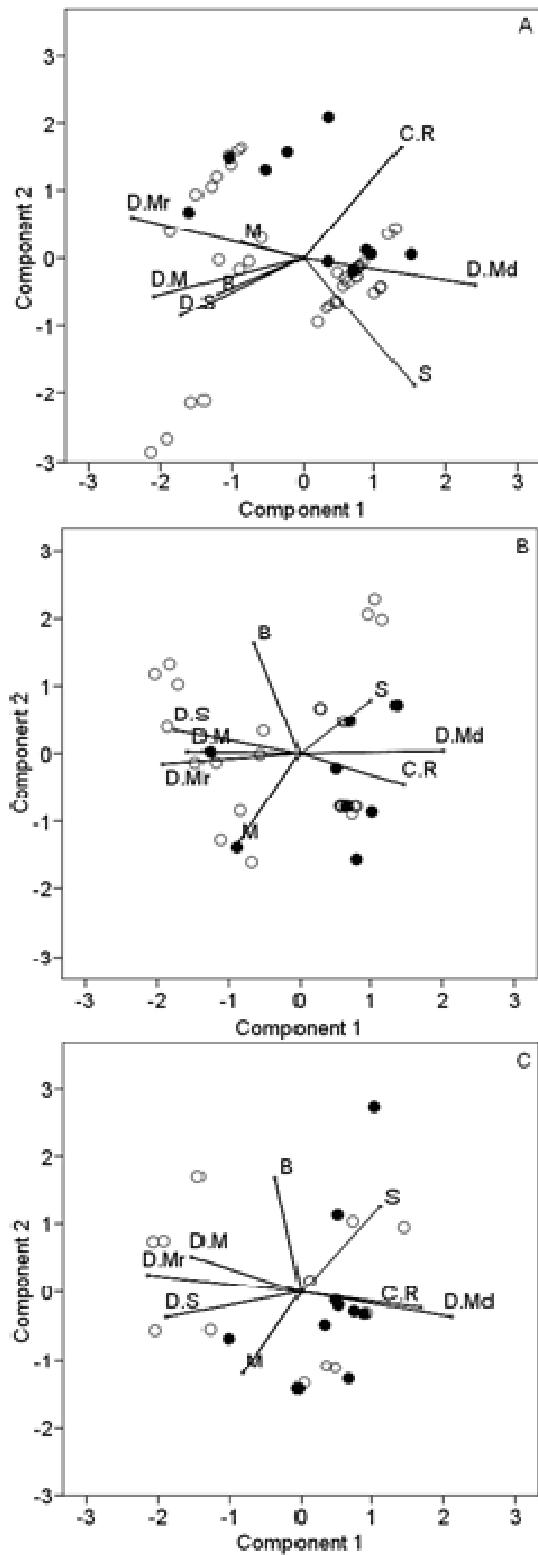


Fig. 5. Ordination plot of perennial species in coastal dunes in S Spain using Nonlinear Principal Component Analysis (NLPCA). Legend. A (P.N. del Estrecho), B (M.N. Artola-Cabopino), C (P.N. Cabo de Gata-Níjar); dark points represent species from fore-back dunes; white points represent species from shrub dunes; Dispersal traits: D.M (diaspore mass), D.S (diaspore size), D.Mr (diaspore morphology), D.Md (dispersal mode), B (bradyspory), M (myxospermy), S (synaptospermy), C.R (clonality and/or resprouting ability).

their abundance and, in many cases, to the nutritional characteristics of their fruits (Herrera, 1995). Synaptospermy combined with wind-flyer and animal-dispersal has shown to be an important strategy of protection of seeds during their transport, either by their union by pappus, or into nutrient fruits such as berries.

(3) In mobile semi-fixed dunes, sea water surging beyond average high tide lines can wash away all the things on coasts in the form of dense waves (Yang et al., 2012), condition that give advance to species showing the ability to be dispersed by sea-water (*Eryngium maritimum*, *Euphorbia paralias*, *Medicago marina* and *Othanthus maritimus*). These species combine sea-water dispersal with other dispersal modes, such as anemochory, zoochory or ballistic dispersal. In case of swell, storms or floods, the seeds can be dispersed as long as they remain floating, until someday they can be carried back to coasts where they may establish, keeping stable by this way the existence of the species they represent (Yang et al., 2012).

The survival of the original community is achieved in coastal dunes by the combination of three dispersal patterns:

(4) Species showing resprouting ability and/or clonality (e.g. *Chamaerops humilis*, *Olea europaea*, *Quercus coccifera* and *Ziziphus lotus*) have a low presence in coastal dunes (Nzunda et al., 2007), a result that has been interpreted as a predominance of regeneration based on seed traits in this type of ecosystem. However, resprouting ability and/or clonality has a key role in the persistence and vegetative regeneration in shrubland communities under unfavourable conditions (Díaz and Cabido, 1997; Puigdefabregas and Pugnaire, 1999; Navarro

et al. 2008). According to previous studies in semi-arid shrublands in SE Spain (Navarro et al., 2008), these species are generally shrubs and trees which are mainly dispersed by barochory (Jurado et al., 1991, 2001; Leishman and Westoby, 1994) and with a less persistent seed bank (Thompson et al., 1993).

(5) Species that combine various antitelechoric mechanisms are mainly located on fixed dunes (e.g. *Halimium* sp., *Lavandula multifida*). According to Navarro et al. (2009), this strategy allows the maximum survival *in situ* after disturbances such as severe drought or events related to the proximity to the sea. These are species with small semachoric seeds. According to previous studies in Spain (Buide et al., 1998: NW Spain; Giménez et al., 2004: S Spain) semachoric species are predominant in coastal dunes. Semachory combined with bradyspory (*Cistus* sp., *Ononix natrix*, or *Silene nicensis*) involves the establishment of canopy seed banks and also the enriching of the soil seeds bank, which makes possible the auto-regeneration of the ecosystem, and also the storing of diaspores during unsuitable periods or after disasters (Navarro et al., 2008) such as storms, floods or sandy burial, which are characteristic of coastal dunes (e.g. Barbour et al., 1985; Hesp, 1991; Kumler, 1997).

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Anexo Capítulo 2

100

Appendix. Dispersal traits in species in coastal dunes in S Spain. Maximum, minimum and mean values \pm sd of diaspore mass in each dune are pointed out in bold. Species with sea-water dispersal are marked with an asterisk (*). Legend. Growth forms: T (trees), LS (large shrubs), SS (small shrubs), H (herbs); Antitelechoric mechanism: B (bradyspory), M (myxosperry), S (synaptosperry); Spatial dispersal: RD (restricted dispersal, DDA (developed dispersal by abiotic factors), DDB (developed dispersal by biotic factors).

	GF	Diaspore mass (mg)	Diaspore size	Diaspore type	Diaspore morphology	Antitelechoric Mechanism	Dispersal mode	Spatial dispersal	Resprouting/clonality
P.N. del Estrecho. Fixed dunes									
<i>Adenocarpus telonensis</i>	LS	5.66	Large	Seed	Nothing	Absent	Semachory	RD	Absent
<i>Calamintha nepeta</i> subsp. <i>nepeta</i>	H	1.64	Medium	Nutlet	Nothing	Absent	Semachory	RD	Absent
<i>Calicotome villosa</i>	LS	10.59	Small	Seed	Nothing	Absent	Semachory	RD	Absent
<i>Calluna vulgaris</i>	SS	0.06	Tiny	Seed	Nothing	Absent	Semachory	RD	Absent
<i>Cistus albidus</i>	LS	1.21	Tiny	Seed	Nothing	B	Semachory	RD	Absent
<i>Cistus crispus</i>	SS	0.47	Tiny	Seed	Nothing	B	Semachory	RD	Absent
<i>Cistus ladanifer</i>	LS	0.36	Tiny	Seed	Nothing	B	Semachory	RD	Absent
<i>Cistus monspeliensis</i>	SS		Small	Seed	Nothing	B	Semachory	RD	Absent
<i>Cistus salvifolius</i>	LS	1.27	Tiny	Seed	Nothing	B	Semachory	RD	Absent
<i>Cytisus striatus</i>	LS	3.89	Small	Seed	Nothing	M	Semachory	RD	Absent
<i>Corema album</i>	SS	77.75	Medium	Berry	Nutrient str.	S, B	Zoochory	DDB	Absent
<i>Chamaerops humilis</i>	LS	311.83	Medium	Drupe	Nutrient str.	B	Barochory	DDB	Present
<i>Daphne gnidium</i>	LS	6.40	Small	Berry	Nutrient str.	S	Zoochory	DDB	Present
<i>Dianthus broteri</i>	SS		Small	Seed	Nothing	Absent	Semachory	RD	Absent
<i>Erica scoparia</i>	SS	0.02	Tiny	Seed	Nothing	Absent	Semachory	RD	Absent
<i>Fumana thymifolia</i>	SS	1.32	Small	Seed	Nothing	M	Semachory	RD	Absent
<i>Galium tricornutum</i>	SS	6.28	Small	Achene	Hooked app.	S, B	Zoochory	DDB	Absent
<i>Halimium halimifolium</i>	LS	0.47	Tiny	Seed	Nothing	M, B	Semachory	RD	Absent
<i>Juniperus oxycedrus</i> subsp. <i>macrocarpa</i>	T	986.92	Large	Galbulus	Nutrient str.	S, B	Barochory	DDB	Absent
<i>Juniperus phoenicea</i> subsp. <i>turbinata</i>	T	475.3	Medium	Galbulus	Nutrient str.	S, B	Barochory	DDB	Absent
<i>Lavandula stoechas</i>	SS	0.61	Medium	Nutlet	Nothing	B	Semachory	RD	Absent
<i>Lonicera implexa</i>	LS	11.56	Small	Berry	Nutrient str.	S, B	Zoochory	DDB	Absent
<i>Marrubium vulgare</i>	SS	0.9	Medium	Nutlet	Nothing	Absent	Anemochory	RD	Absent
<i>Myrtus communis</i>	LS	121.37	Small	Berry	Nutrient str.	S, B	Zoochory	DDB	Absent
<i>Olea europaea</i> var. <i>sylvestris</i>	T		Medium	Drupe	Nutrient str.	B	Barochory	DDB	Present
<i>Osyris lanceolata</i>	LS	167.56	Small	Drupe	Nutrient str.	B	Zoochory	DDB	Absent
<i>Phlomis purpurea</i>	LS	4.09	Medium	Nutlet	Nothing	B	Semachory	RD	Absent
<i>Phyllirea angustifolia</i>	T		Medium	Drupe	Nutrient str.	Absent	Barochory	DDB	Absent
<i>Pistacia lentiscus</i>	T	30.09	Small	Drupe	Nutrient str.	B	Zoochory	DDB	Absent
<i>Quercus coccifera</i>	T	7492.22	Large	Nutlet	Nutrient str.	B	Barochory	DDB	Present
<i>Rhamnus alaternus</i>	LS	63.23	Small	Berry	Nutrient str.	S	Zoochory	DDB	Absent
<i>Rhamnus lycioides</i>	LS	33.73	Small	Berry	Nutrient str.	S	Zoochory	DDB	Absent
<i>Ruscus aculeatus</i>	LS	366.02	Large	Drupe	Nutrient str.	B	Zoochory	DDB	Present
<i>Ruta chalepensis</i>	SS	0.22	Tiny	Seed	Nothing	B	Semachory	RD	Absent
<i>Sideritis arborescens</i> subsp. <i>perezlarae</i>	SS	1.95	Medium	Nutlet	Nothing	B	Semachory	RD	Absent
<i>Stauracanthus boivinii</i>	LS	1.84	Small	Seed	Nothing	Absent	Ballistic disp.	RD	Absent
<i>Teucrium fruticans</i>	LS	3.69	Medium	Nutlet	Nothing	Absent	Semachory	RD	Absent
<i>Ulex australis</i>	LS	2.33	Small	Seed	Nothing	Absent	Ballistic disp.	RD	Absent
<i>Viola arborescens</i>	SS	2.22	Small	Seed	Nothing	Absent	Semachory	RD	Absent
		291.28\pm1267.81							

	GF	Diaspore mass (mg)	Diaspore size	Diaspore type	Diaspore morphology	Antitelechoric Mechanism	Dispersal mode	Spatial dispersal	Resprouting/ clonality
P.N. del Estrecho. Mobile semi-fixed dunes									
<i>Asteriscus maritimus</i>	SS	0.22	Medium	Achene	Pappus	S	Ombro-hydroc.	RD	Absent
<i>Crucianella maritima</i>	SS	4.81	Small	Seed	Wings	Absent	Anemochory	DDA	Absent
<i>Eryngium maritimum</i>	H	28.94	Large	Twin-fruit	Hooked app.	S, B	Zoochory	DDB*	Absent
<i>Euphorbia paralias</i>	H	2.03	Small	Seed	Nothing	Absent	Ballistic disp.	RD*	Absent
<i>Frankenia laevis</i>	SS		Small	Seed	Nothing	Absent	Semachory	RD	Absent
<i>Helicrysum picardii</i>	SS		Small	Achene	Pappus	S, B	Anemochory	DDA	Absent
<i>Limonium emarginatum</i>	SS		Tiny	Achene	Nothing	Absent	Semachory	RD	Absent
<i>Limonium sinuatum</i>	SS		Tiny	Achene	Nothing	Absent	Semachory	RD	Absent
<i>Lotus creticus</i>	H	2.33	Tiny	Seed	Nothing	Absent	Ballistic disp.	RD	Absent
<i>Malcolmia littorea</i>	H	0.07	Tiny	Seed	Nothing	M	Semachory	RD	Absent
<i>Medicago marina</i>	H	33.31	Medium	Pod	Hooked app.	S	Zoochory	DDB*	Absent
<i>Ononis natrix</i> subsp. <i>ramosissima</i>	SS	1.04	Small	Seed	Nothing	Absent	Semachory	RD	Absent
<i>Phagnalon saxatile</i>	SS	0.05	Tiny	Achene	Pappus	S	Anemochory	DDA	Absent
		8.09±13.19							
M.N. Artola-Cabopino. Fixed dunes									
<i>Asparagus aphyllus</i>	SS		Medium	Berry	Nutrient str.	S, B	Barochory	DDB	Present
<i>Calicotome villosa</i>	LS	10.55	Small	Seed	Nothing	Absent	Semachory	RD	Absent
<i>Cistus monspeliensis</i>	SS	0.98	Small	Seed	Nothing	B	Semachory	RD	Absent
<i>Cistus salviifolius</i>	LS	0.7	Small	Seed	Nothing	B	Semachory	RD	Absent
<i>Chamaerops humilis</i>	LS	1754.62	Large	Drupe	Nutrient str.	B	Barochory	DDB	Present
<i>Daphne gnidium</i>	LS		Small	Berry	Nutrient str.	S	Zoochory	DDB	Present
<i>Dianthus broteri</i>	SS		Small	Seed	Nothing	Absent	Semachory	RD	Absent
<i>Euphorbia terracina</i>	H	3.76	Small	Seed	Nothing	Absent	Ballistic disp.	RD	Absent
<i>Rubia peregrina</i>	SS		Medium	Achene	Nothing	S, B	Zoochory	DDB	Absent
<i>Genista umbellata</i>	SS	0.63	Small	Seed	Nothing	Absent	Semachory	RD	Absent
<i>Halimium commutatum</i>	LS		Tiny	Seed	Nothing	M, B	Semachory	RD	Absent
<i>Halimium halimifolium</i>	LS	0.21	Tiny	Seed	Nothing	M, B	Semachory	RD	Absent
<i>Juniperus phoenicea</i> subsp. <i>turbinata</i>	T	354.01	Medium	Galbulus	Nutrient str.	S, B	Barochory	DDB	Absent
<i>Lavandula multifida</i>	SS	0.59	Small	Nutlet	Nothing	M, B	Semachory	RD	Absent
<i>Lavandula stoechas</i>	SS	1.16	Medium	Nutlet	Nothing	B	Semachory	RD	Absent
<i>Myrtus communis</i>	LS	90.57	Medium	Berry	Nutrient str.	S, B	Zoochory	DDB	Absent
<i>Olea europaea</i> var. <i>sylvestris</i>	T	494.41	Medium	Drupe	Nutrient str.	B	Barochory	DDB	Present
<i>Phlomis purpurea</i>	LS	1.49	Medium	Nutlet	Nothing	B	Semachory	RD	Absent
<i>Phyllirea angustifolia</i>	T		Medium	Drupe	Nutrient str.	Absent	Barochory	DDB	Absent
<i>Pistacia lentiscus</i>	T	25.34	Small	Drupe	Nutrient str.	B	Zoochory	DDB	Absent
<i>Quercus coccifera</i>	T		Large	Nutlet	Nutrient str.	Absent	Barochory	DDB	Present
<i>Rhamnus lycioides</i>	LS	57.4	Small	Berry	Nutrient str.	S	Zoochory	DDB	Absent
<i>Ruta chalepensis</i>	SS	1.1	Small	Seed	Nothing	B	Semachory	RD	Absent
<i>Ulex australis</i>	LS	9.4	Small	Seed	Nothing	Absent	Ballistic disp.	RD	Absent
		165.11±432.82							

Anexo Capítulo 2

102

	GF	Diaspore mass (mg)	Diaspore size	Diaspore type	Diaspore morphology	Antitelechoric Mechanism	Dispersal mode	Spatial dispersal	Resprouting/ clonality
M.N. Artola-Cabopino. Mobile semi-fixed dunes									
<i>Crucianella maritima</i>	SS	4.38	Small	Seed	Wings	Absent	Anemochory	DDA	Absent
<i>Eryngium maritimum</i>	H	23.6	Large	Twin-fruit	Hooked app.	S, B	Zoochory	DDB*	Absent
<i>Helicrysum picardii</i>	SS	0.06	Small	Achene	Pappus	S, B	Anemochory	DDA	Absent
<i>Lotus creticus</i>	H	0.71	Small	Seed	Nothing	Absent	Ballistic disp.	RD	Absent
<i>Malcolmia littorea</i>	H	0.11	Tiny	Seed	Nothing	M	Semachory	RD	Absent
<i>Medicago marina</i>	H	23.06	Medium	Pod	Hooked app.	S	Zoochory	DDB*	Absent
<i>Ononis natrix</i>	SS	3.48	Small	Seed	Nothing	Absent	Semachory	RD	Absent
<i>Phagnalon saxatile</i>	SS	0.04	Tiny	Achene	Pappus	S, B	Anemochory	DDA	Absent
<i>Scrophularia canina</i>	SS	0.29	Medium	Seed	Nothing	B	Semachory	RD	Absent
<i>Silene niceensis</i>	H	0.18	Tiny	Seed	Nothing	Absent	Semachory	RD	Absent
		5.59±9.47							
P.N. Cabo de Gata-Níjar. Fixed dunes									
<i>Asparagus albus</i>	SS	10.6	Medium	Berry	Nutrient str.	S, B	Barochory	DDB	Present
<i>Asparagus horridus</i>	SS		Medium	Berry	Nutrient str.	S, B	Barochory	DDB	Present
<i>Frankenia boissieri</i>	SS	1.98	Small	Calyx	Nothing	S	Semachory	RD	Absent
<i>Launaea arborescens</i>	LS	1.13	Small	Achene	Pappus	S	Anemochory	DDA	Absent
<i>Launaea nudicaulis</i>	SS	0.59	Medium	Achene	Pappus	S	Anemochory	DDA	Absent
<i>Lycium intricatum</i>	LS	25.84	Large	Berry	Nutrient str.	S	Zoochory	DDB	Present
<i>Teucrium hieronymi</i>	SS	2.9	Small	Calyx	Open ballon	S, B	Anemochory	DDA	Absent
<i>Thymelaea hirsuta</i>	SS		Small	Nutlet	Nothing	B	Semachory	RD	Absent
<i>Thymus hyemalis</i>	SS	0.05	Tiny	Nutlet	Nothing	M	Semachory	RD	Absent
<i>Withania frutescens</i>	LS	75.72	Medium	Berry	Nutrient str.	S	Zoochory	DDB	Absent
<i>Ziziphus lotus</i>	LS	750	Medium	Drupe	Nutrient str.	B	Barochory	DDB	Present
		96.53±246.26							
P.N. Cabo de Gata-Níjar. Mobile semi-fixed dunes									
<i>Asteriscus maritimus</i>	SS		Medium	Achene	Pappus	S	Ombro-hydroc.	RD	Absent
<i>Crucianella maritima</i>	SS	5.33	Small	Seed	Wings	Absent	Anemochory	DDA	Absent
<i>Helichrysum stoechas</i>	SS	0.04	Small	Achene	Pappus	S, B	Anemochory	DDA	Absent
<i>Limonium lobatum</i>	SS	0.36	Tiny	Achene	Nothing	Absent	Ombro-hydroc.	RD	Absent
<i>Lotus creticus</i>	H	0.81	Tiny	Seed	Nothing	Absent	Ballistic disp.	RD	Absent
<i>Medicago marina</i>	H	39.03	Medium	Pod	Hooked app.	S	Zoochory	DDB*	Absent
<i>Ononis natrix</i>	SS	1.55	Small	Seed	Nothing	Absent	Semachory	RD	Absent
<i>Othantus maritimus</i>	SS	1.04	Medium	Achene	Nothing	Absent	Anemochory	DDA*	Absent
<i>Phagnalon saxatile</i>	SS	0.06	Tiny	Achene	Pappus	S	Anemochory	DDA	Absent
<i>Plantago albicans</i>	H		Small	Seed	Nothing	M, B	Ombro-hydroc.	RD	Absent
<i>Salsola oppositifolia</i>	SS		Small	Samara	Wings	B	Anemochory	DDA	Absent
<i>Salsola vermiculata</i>	SS		Small	Samara	Wings	B	Anemochory	DDA	Absent
<i>Teucrium dunense</i>	SS	2.98	Small	Calyx	Open ballon	S, B	Anemochory	DDA	Absent
		5.69±12.62							



**A comparative study of leaf traits
relationships in coastal dunes
in S Spain**

Capítulo 3

A comparative study of leaf traits relationships in coastal dunes in S Spain

Abstract

The characterization of leaf functional traits is very important in the prediction of ecosystem functioning, area of research with a high interest in fragile dune ecosystems. However, this is the first study where a complete sample of leaf traits have been collected and analysed separately among coastal dunes under different variations of Mediterranean climate (Mediterranean-oceanic, M-subtropical and M-subdesert) and different dune sectors (fixed dunes and mobile semi-fixed dunes). The objective of this work is to explore patterns of (co)variation of leaf functional traits in 78 perennial species of coastal dunes in S Spain. The methodology proposed by Cornelissen et al. (2003) has been followed for the samples and measurement of leaves. In the study area, species of nanophyll leaves with low values of specific leaf area (from 4.8 to 272.3 cm²g⁻¹) and low leaf nutrient content (N>Ca>K>Mg>P>Fe>Mn) are predominant. For many species, especially among the located on mobile semi-fixed dunes, this is the first time that their leaf traits have been analysed. The co-variations of the leaf economic spectrum (Wright et al., 2004a) have been confirmed in the studied coastal dunes. Specific leaf area, leaf [N] and [P] are positively correlated. However, leaf [K] could also be used as part of the leaf economic spectrum in these dunes. Variations of leaf traits have been found among taxonomic families (Amaranthaceae, Caryophyllaceae and Fabaceae show the maximum leaf nutrient content) and among functional groups. Perennial herbs and small shrubs with deciduous/semi-deciduous and malacophyll leaves show the highest values of specific leaf area and leaf nutrient content. They are competitive species which are mainly located on mobile semi-mobile dunes and fixed dunes under M-subdesert climate. Stress tolerant species (evergreen and sclerophyllous species showing lower values of leaf traits) are over represented in fixed dunes under M-oceanic and M-subtropical climate.

Keywords: Leaf size, specific leaf area, leaf nitrogen concentration, leaf nutrient concentrations, leaf consistence, deciduousness.

Resumen

La caracterización de caracteres funcionales de la hoja es muy importante en la predicción del funcionamiento de los ecosistemas, área de gran interés en los frágiles ecosistemas de dunas. Sin embargo, este es el primer estudio que lleva a cabo un completo análisis de caracteres funcionales foliares en dunas expuestas a distintas variantes del macroclima Mediterráneo (Mediterráneo-oceánico, M-subtropical y M-subdesértico) así como entre distintos sectores de duna (duna fija y duna móvil y semi-fija). El objetivo de este trabajo es el estudio de los patrones de co-variación de los caracteres funcionales foliares in 78 especies perennes de dunas costeras del sur de España. La metodología seguida para los muestreos y medidas es la propuesta por Cornelissen et al. 2003. En el área de estudio predominan las especies de hoja nanófila, con bajos valores de SLA y de concentración de nutrientes (N>Ca>K>Mg>P>Fe>Mn). Para muchas de las especies estudiadas, especialmente entre las que se encuentran sobre duna móvil y semi-fija, los datos aportados son nuevos. Las co-variaciones del espectro económico foliar (Wright et al., 2004a) han sido confirmadas en estas dunas. Área específica de la hoja, contenido en N y P se correlacionan positivamente. Sin embargo, los resultados indican que el K podría incluirse también como parte del espectro económico en el área de estudio. Además, se han encontrado variaciones de los caracteres foliares entre familias (Amaranthaceae, Caryophyllaceae y Fabaceae muestran las máximas concentraciones de nutrientes foliares) y entre grupos funcionales. Las hierbas perennes y pequeños arbustos de hoja decidua/semi-decidua y malacófila presentan mayores valores de área específica y mayor concentración de nutrientes. Estas son especies competitivas, las cuales se encuentran principalmente sobre dunas móviles y semifijas, y en dunas fijas de clima M-subdesértico. Las especies tolerantes al estrés (esclerófilas siempre-verdes con menores valores de los caracteres foliares analizados) predominan en dunas fijas bajo clima M-oceánico y M-subtropical.

Keywords: Tamaño foliar, área específica de la hoja, concentración foliar de nitrógeno, concentración foliar de nutrientes, consistencia de la hoja, deciduidad.

1. Introduction

Leaf functional traits such as leaf structure and nutrient content are key determinants of biogeochemical cycles that link soil, climate and atmosphere at the same scales (Reich et al., 2007). Thus, characterization of leaf functional traits is an important tool in the prediction of ecosystem functioning (Ehleringer and Field, 1993; Peterson et al., 1999; Norby and Luo, 2004; He et al., 2006).

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

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

of many plant cell components, including amino and nucleic acids (Wright et al 2004b; Hu and Schmidhalter, 2005). Other nutrients such as K, Ca, Fe, Mg and Mn are less often studied in relation to leaf functional traits (Niinemets and Kull 2003). Mineral nutrient concentrations in leaves vary depending on genetic factors and phylogenetic constraints, but they are also influenced by local soil conditions (Hobbie and Gough, 2002; Bombonato et al., 2010).

Considerable attention has been focused on the ecological significance of leaf size (LS) variation (Parkhurst and Loucks, 1972; Givnish and Vermeij, 1976; Chiariello, 1984). Leaf size directly affects light interception and leaf balance, and leaves are often smaller in species occupying habitats with high light, low nutrients or low moisture availability (e.g. Körner et al. 1989; Niinemets and Kalevi, 1994), conditions that are also associated with thick leaves, low nitrogen content and low photosynthetic rates (Reich et al., 1992).

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 et al., 2001; Ley Vega de Seoane et al., 2007; Fenu et al., 2012), which involve specific functional strategies that characterize its particular vegetation (García-Mora et al., 1999; Ley Vega de Seoane, 2007).

Coastal dunes are extremely fragile and very vulnerable to the human activity, which is particularly striking in the Mediterranean (Curr et al., 2000). The current situation of coastal dunes ecosystems constitutes a serious danger for all the ecosystem services that they provide, such as protection against sea waves, wind, floods or

erosion (Kiehl and Isermann, 2007) and for the survival of the important habitats and endangered species 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 priority interest according to Red Natura 2000 (VV.AA., 2009).

The objective of this study was to explore patterns of (co)variation of leaf functional traits in 78 perennial species on coastal dunes in S Spain with differences within the Mediterranean macroclimate (Mediterranean-oceanic, M-subtropical, M-subdesert) and between dune sectors (mobile semi-fixed and fixed dunes).

We aimed to answer the following questions: (1) Do that coastal dunes have particularly high/low values of leaf functional traits?; (2) Are correlation patterns among leaf traits in coastal dunes consistent with previously published analyses of leaf economics spectrum?; (3) Are trait correlation patterns scale similar in different types of dunes? (4) Do different taxonomic families and major functional groups have contrasting leaf traits?; (5) Do the three dunes with contrasting climates and the two types of dune sectors have different leaf traits?; (6) Do these dunes show similar patterns of specialization based on leaf traits?

2. Material and methods

2.1. Study area

The study was carried out in three coastal dunes in S Spain with different Mediterranean climate (DERA, 2013): P.N. del Estrecho in Cádiz (Mediterranean-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).

Figure 2 summarised the medium values of temperatures and rainfall along the year. In P.N. del Estrecho, the average annual rainfall is 794 mm, with maximum values in November (133 mm) and minimum in August (0 mm). Annual temperatures are milder than in the other two dunes (mean –minima of 13.4°C in January and mean-maxima of 23.5°C in August). M.N. Artola-Cabopino shows an average annual rainfall of 659 mm, with similar rainy season to P.N. del Estrecho. January was also the coldest month (mean-minima of 12.5°C) and August the hottest (mean-maxima 24.5°C). P.N Cabo de Gata-Níjar shows the driest dunes (average annual rainfall of 308 mm) and a different rainy season (maximum rainfall values are observed in March and December, 40 mm). The seasonal amplitude of temperature is different from the other studied dunes, with mean-minima of 10.8°C in January and mean-maxima of 25.9°C in August.

Three dunes sectors were recognized, depending on the distance from the sea and which have contrasting vegetation structure (e.g. Van der Maarel, 1997; Carter, 1988; Brown and McLachlan, 1994). In this study, the nomenclature of dune sectors was the one based up on sands mobility (Van der Maarel, 1993): fixed dunes, semi-fixed and mobile dunes. However, the two last dunes were unified in this work in one common sector. Fixed dunes are formed by shrubs and trees and represent the mature stage of the ecosystem. Mobile semi-fixed dune vegetation is constituted by pioneer communities of herbs and small shrubs, which are adapted to tolerate the

intense disturbance that is associated to the proximity of the sea (Costa-Pérez and Valle-Tendero, 2004; Ley Vega de Seoane, 2007).

2.2. Samples and measurements

Data were gathered for 78 major representative perennial species with the highest cover values (Van der Maarel, 1993; Costa-Pérez and Valle-Tendero, 2004; Navarro et al., 2006) in the period of 2009-2012. Voucher specimens of the studied species were kept in the MGC Herbarium. Botanical nomenclature follows Castroviejo (1986-2007). The family of each species follows APG III (Angiosperm Phylogenetic Group) (2009).

We classified each species based on growth form, deciduousness and leaf consistence, which yielded different major functional groups of species. These functional groups provided the possibility of describing natural correlations between leaf functional traits.

Samples were collected from fully expanded and hardened leaves from adult plants in full-light situations and without obvious symptoms of pathogen, herbivore attack or substantial cover of epiphylls. Between ten and twenty leaves were collected from at least five individuals of each species. The leaves sample were transported to the laboratory in plastic bags and conserved in low temperatures (2-6°C) for their measurements. At these same dates, dried and ground soils were sampled between 0 and 20 cm in each study areas.

Leaf size (LS) was measured by scanning and digitalizing fresh leaves to computers using

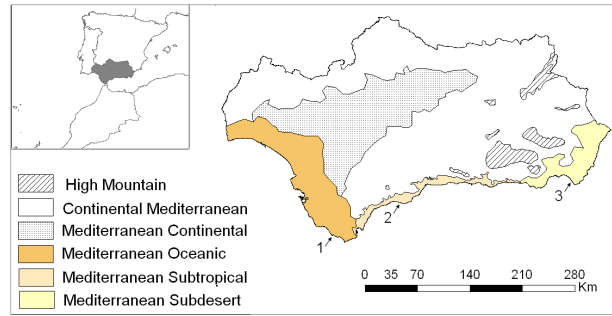


Fig. 1. Different climates in S Spain and study areas. Black dots show the study areas: (1.) P.N. del Estrecho, (2.) M.N. Artola-Cabopino, (3.) P.N. Cabo de Gata-Níjar. Data source: DERA, 2013.

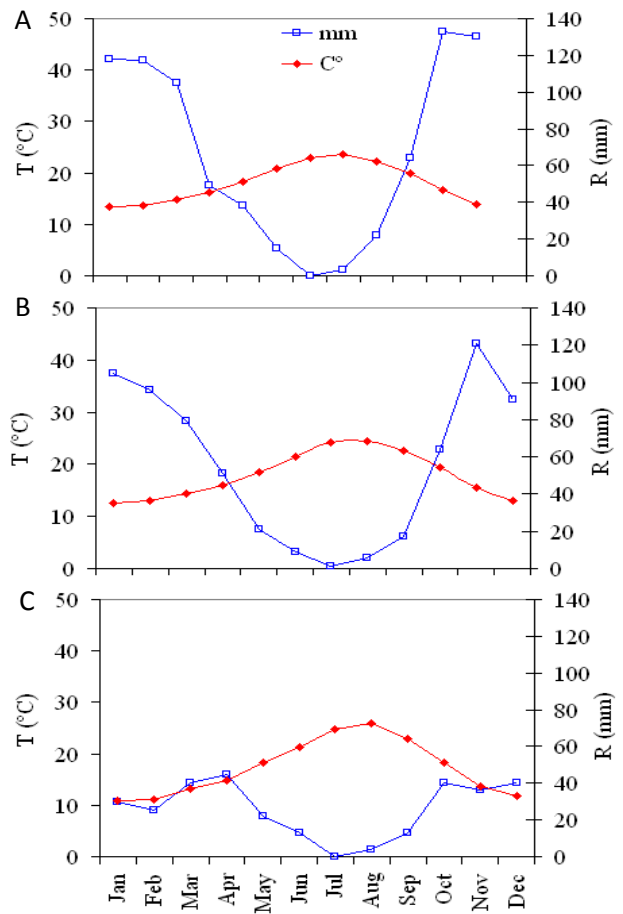


Fig. 2. Climatic diagrams (a) P.N. del Estrecho, (b) M.N. Artola-Cabopino and (c) P.N. Cabo de Gata-Níjar. Data source: Rivas-Martínez and Rivas-Saenz, 2009.

Visilog 6.3 image analysis software. For the measurements of leaf size, leaf laminae (or leaflets in compound leaves) without petiole or rachis were analysed, whereas for calculating specific leaf area (SLA), entire leaves were used (Cornelissen et al., 2003).

Leaf dry mass was determined after oven drying at 60 °C for at least 72 h. Specific leaf area is the one-side area of a fresh leaf divided by its oven-dry mass (Cornelissen et al., 2003).

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

Soil samples were extracted in AcNH₄ pH 7 (for major nutrients: Ca, Mg, K), or with AcNH₄-EDTA pH 8.5 for [Fe], [Mn] and [P]. Nutrients were determined by ICP-OES.

2.4. Data analyses

Continuous characters were log₁₀-transformed prior to statistical analysis in order to normalise their distributions. All statistical analyses were performed with SPSS 15.0 (SPSS Inc).

t-Tests, One-way analysis of variance ANOVA and Bonferroni were applied, after verifying the homogeneity of variance by Levene's test ($P > 0.05$), to test for differences of leaf traits among families, major functional groups and dunes. When assumptions of ANOVA were not

met, Mann-Whitney and Kruskal-Wallis analysis were done.

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

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

3. Results

The distribution of major functional groups in the study area is summarized in the table 1. Shrubs with green malacophyllous leaves were predominant (Table 1).

Soil characteristics of the study areas are included in Table 2. Site differences in base of soil nutrient content resulted from significantly higher [Ca] in mobile semi-fixed dunes in P.N. Cabo de Gata-Níjar ($F = 8.75$, $P < 0.001$) and higher [Mn] in fixed dunes from M.N. Artola-Cabopino ($F = 3.35$, $P < 0.01$) than in the other dunes.

3.1. Leaf functional traits in coastal dunes in S Spain

Average leaf traits are given in Appendix.

Leaf size (LS) spanned 10^4 ranges, from 10^{-2} to 10^2 cm². Maximum values were found in *Eryngium maritimum*, on M.N. Artola-Cabopino (36.4 cm²), whereas species on P.N. Cabo de Gata-Níjar showed the minimum LS (0.03cm²) (e.g. *Thymelea hirsuta* and *Thymus hyemalis* on fixed dunes, *Salsola vermiculata* on mobile semi-fixed dunes). Nanophyll was the dominant leaf size class (between 70% of species on mobile semifixed dunes in M.N. Artola-Cabopino to 33.3% oin fixed dunes in P.N. Cabo de Gata-Níjar) (Fig. 3). Microphyll and micro-mesophyll species were shown in less than 10% of species in all the studied dunes (Fig. 3).

Specific leaf area (SLA) spanned 10^2 ranges,

from 10^2 (maximum in *Corema album*, 390.5 cm²g⁻¹) to 1 cm²g⁻¹ (minimum in *Calluna vulgaris*, 4.8 cm²g⁻¹).

Leaf C concentration ranged from 55.6% in *Corema album* to 29.4% in *Lycium intricatum*. It was followed by leaf [N]-[Ca] > [K] > [Mg]. Leaf N was maximum in *Cytisus striatus* (4%) and minimum in *Thymus hyemalis* (0.7%). However, the other nutrients were even more variable among species, with the highest concentration being between 16-18 times the lowest.

Leaf [P], [Fe] and [Mn] were shown in smaller concentrations than 10⁻¹%. Leaf [P] ranged from 0.04% (*Calluna vulgaris*, *Erica scoparia* and *Stauracanthus boivinii*) to 0.4% (*Frankenia laevis*), whereas [Mn] and above all, [Fe] were more variable among species. Mn showed differences of 20 times between the lowest and the highest values (from 0.001% in *Teucrium* sp. to

Table 1. Major functional groups for the studied species in coastal dunes in S Spain. N = number of species.

	P.N. del Estrecho		M.N. Artola-Cabopino				P.N. Cabo de Gata-Níjar					
			Mobile semi-fixed		Fixed		Mobile semi-fixed		Fixed		Mobile semi-fixed	
	N	%	N	%	N	%	N	%	N	%	N	%
<i>Growth forms</i>												
Herbs	1	2.6	5	38.5	1	4.2	6	54.5	0	0	3	21.4
small shrubs	13	33.3	8	61.5	8	33.3	5	45.4	7	63.6	11	78.6
Large shrubs	19	48.7	0	0	10	41.7	0	0	4	36.4	0	0
Trees	6	15.4	0	0	5	20.8	0	0	0	0	0	0
<i>Deciduousness</i>												
Evergreen	17	43.6	1	7.7	10	41.7	1	9.1	5	45.4	3	21.4
Semi-deciduous	15	38.5	6	46.1	9	37.5	4	36.4	2	18.2	7	50
Deciduous	7	18	6	46.1	5	20.8	6	54.5	4	36.4	4	28.6
<i>Leaf colour</i>												
Green	35	89.7	7	53.8	23	95.8	4	40	9	90	7	53.8
Green-grey	2	5.1	0	0	1	4.2	0	0	0		0	0
Grey	2	5.1	6	46.1	0	0	6	60	1	10	6	46.1
<i>Leaf consistence</i>												
Sclerophyllous	17	43.6	1	7.7	12	50	1	9.09	5	45.4	1	7.1
Malacophyllous	22	56.4	12	92.3	12	50	10	90.9	6	54.5	13	92.9

Table 2. Soil conditions (mean±sd) of coastal dunes in S Spain. F (Fixed dunes), M (Mobile semi-fixed dunes). ns (not significant) $P>0.10$, $\cdot P<0.10$, $* P<0.05$, $** P<0.01$, $*** P<0.001$.

	pH	N %	Ca %	K %	Mg %	P %	Fe %	Mn%	N
P.N. del Estrecho									
F	7.5	0.15±0.01	1.57±1.88	0.05±0.06	0.15±0.20	0.004±0.004	0.011±0.012	0.004±0.004	2
M	8.5	0.01±0.01	1.98±0.15	0.02±0.01	0.04±0.01	0.008±0.003	0.011±0.004	0.008±0.003	6
M.N. Artola-Cabopino									
F	7.0	0.20±0.01	1.10±0.62	0.04±0.03	0.07±0.04	0.015±0.012	0.021±0.010	0.033±0.021	3
M	7.8	0.07±0.07	1.73±0.05	0.03±0.01	0.04±0.003	0.005±0.002	0.014±0.003	0.018±0.003	6
P.N. Cabo de Gata-Níjar									
F	8.0	0.09±0.04	1.50±1.10	0.05±0.04	0.04±0.02	0.008±0.002	0.013±0.002	0.011±0.003	3
M	7.6	0.09±0.02	4.00±0.94	0.04±0.01	0.05±0.003	0.014±0.001	0.009±0.002	0.010±0.001	3
P values	n.s.	1.37 n.s.	8.75 ***	1.29 n.s.	1.73 n.s.	2.86 *	2.13 n.s.	5.35 **	

0.030% in *Phagnalon saxatile*) and Fe, even reach differences of 75 times (from 0.004% in *Rhamnus alaternus* and *Lonicera implexa* to 0.3% in *Silene niceensis* and *Phlomis purpurea*).

3.2. Correlations among leaf traits

Table 3 summarised the results of correlation analysis among leaf traits in coastal dunes. The most significant correlations were found in fixed dunes in M.N. Artola-Cabopino. Leaf nutrients were mainly positively correlated among them and with SLA, but negatively with LS. The exception was leaf [C], which showed the contrary tendency in all the cases.

Particularly, in relation to leaf economic spectrum, SLA and leaf [N] were positively correlated in P.N. del Estrecho and in M.N. Artola-Cabopino (Fig. 4a). Leaf [N] and [P] were significantly correlated only in fixed dunes in P.N. del Estrecho (Fig. 4b). SLA and leaf [P] were positively associated in fixed dunes in P.N. del Estrecho and M.N. Artola-Cabopino (Fig. 4c).

P.N. Cabo de Gata did not confirm any of these relationships.

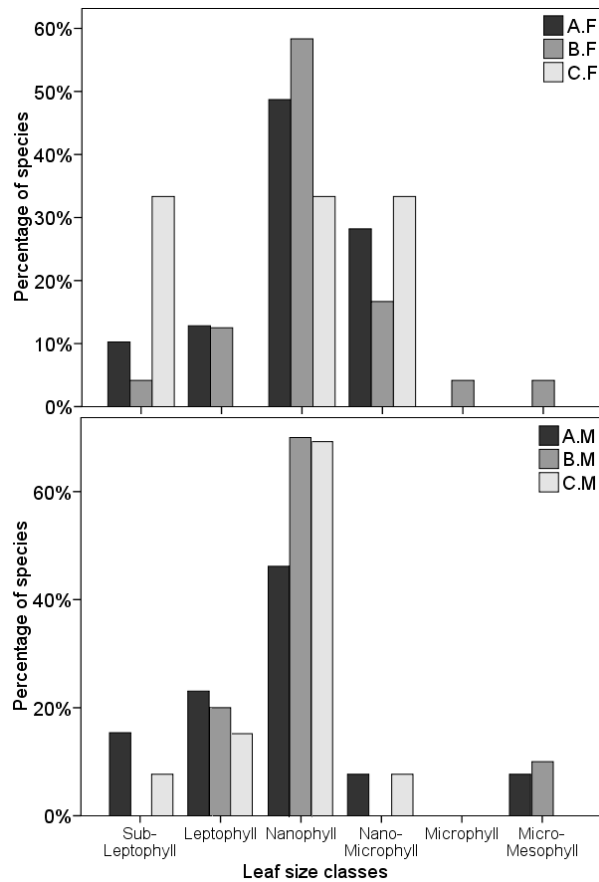


Figure 3. Leaf size classes by Raunkier-Orshan (Orshan, 1989). Legend. A (P.N. del Estrecho); B (M.N. Artola-Cabopino); C (P.N. Cabo de Gata-Níjar); F (Fixed dunes); M (Mobile semi-fixed dunes).

3.3. Variation of leaf traits among taxonomic families and major functional groups

Significant differences of leaf trait among taxonomic families, growth forms, deciduousness and consistence are summarized in table 4. All of these showed significant differences. Leaf size and leaf [Mn] were the less variable traits, whereas leaf [Ca] showed significant differences among the five evaluated groups.

In table 5, the average values of each leaf trait are shown separately for the studied categories.

Maximum [Ca], [K] and [Mn] were found in Amaranthaceae. Frankeniaceae showed the highest values of [Mg] and [P]. Cistaceae and Cupressaceae were the richest in [C], Violaceae and Fabaceae in [N], and Caryophyllaceae in [Fe]. The maximum LS were shown by Fagaceae, and the highest SLA, in Empetraceae.

Small growth forms (perennial herbs and small shrubs) with malacophyll deciduous/semideciduous leaves showed the highest values of leaf traits (Table 5). The exception was [C], whose maximums were found in trees and large shrubs with sclerophyll evergreen leaves.

3.4. Variation of leaf traits among studied coastal dunes

Table 6 include the results of the ANOVA test performed among the three studied coastal dunes and the ones obtained by *t*-test between dune sectors.

The analyses among dunes were done by comparing the three fixed dunes and mobile semi-fixed dunes separately. Fixed dunes included the main differences, showing that leaves in P.N. del

Estrecho are the poorest in nutrients such as [Fe], [Mg] and [Mn]. This dune also showed lower SLA values and higher leaf [C] than P.N. Cabo de Gata-Níjar (Appendix).

The analysis intra-dunes revealed that the differences between fixed and mobile semi-fixed dunes decrease from P.N. del Estrecho (where mobile semi-fixed dunes showed higher [P], [Ca], [Mg] and [Mn], and lower [C] than fixed dunes) to P.N. Cabo de Gata-Níjar, where any significant difference was found (Appendix).

3.5. Leaf patterns of specialization in coastal dunes

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

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

This analysis clearly separated among studied dunes (Fig. 4). Inter-dunes analysis showed that P.N. Cabo de Gata-Níjar dunes were over represented in the bottom left corner of the figure (predominance of malacophyll and deciduous herbs and small shrubs, with small leaves size and high nutrient concentrations), whereas the other two dunes showed a wider pattern.

Intra-dunes analysis demonstrated that fixed dunes species were mainly located on the right area of the figure, showing positive values of axis 1 and

Table 3. Correlations among leaf traits in coastal dunes in S Spain. *ns* (not significant) $P > 0.10$, $\cdot P \leq 0.10$, $* P \leq 0.05$, $** P \leq 0.001$, $*** P \leq 0.0001$,

		P.N. del Estrecho								
		N	P	Ca	Fe	K	Mg	Mn	SLA	LS
C		-0.35 *	-0.52**	-0.52**	ns	-0.51**	ns	ns	-0.31	-0.30
	ns	ns	-0.61*	ns	ns	ns	ns	ns	ns	ns
N			0.48**	ns	ns	0.45**	ns	ns	0.30	ns
	ns		ns	ns	ns	ns	ns	0.64*	ns	ns
P				0.28	ns	0.70***	ns	ns	0.30	ns
	ns			ns	ns	ns	ns	ns	ns	ns
Ca					0.38 *	0.45**	ns	ns	0.30	ns
	ns				ns	ns	ns	ns	ns	ns
Fe						ns	ns	ns	ns	-0.47**
	ns					-0.54	ns	ns	ns	ns
K							ns	ns	0.41**	ns
	ns						ns	ns	ns	ns
Mg								0.43**	ns	ns
	ns							ns	ns	ns
Mn									ns	-0.42**
	ns								ns	ns
SLA										ns
	ns									ns

		M.N. Artola-Cabopino								
		N	P	Ca	Fe	K	Mg	Mn	SLA	LS
C		ns	ns	ns	-0.57*	-0.82***	ns	ns	-0.67***	ns
	ns				-0.68*	ns	-0.76*	-0.79*	ns	ns
N			ns	ns	ns	0.47*	ns	ns	0.55**	ns
	ns				ns	ns	ns	ns	ns	ns
P				0.61**	0.61**	0.66**	0.62**	0.48**	0.46*	ns
	ns				-0.29	ns	ns	ns	ns	ns
Ca					0.52*	ns	0.60***	0.40	0.54*	ns
	ns				ns	ns	ns	-0.50	ns	ns
Fe						0.56**	0.69***	0.40	0.54*	ns
	ns					ns	0.68*	ns	0.39	-0.62
K							ns	ns	0.60**	ns
	ns						0.71*	ns	ns	ns
Mg								0.66***	0.47*	ns
	ns							ns	ns	ns
Mn									ns	ns
	ns								ns	ns
SLA										ns
	ns									ns

		P.N. Cabo de Gata-Níjar								
		N	P	Ca	Fe	K	Mg	Mn	SLA	LS
C		ns	ns	ns	ns	ns	ns	ns	ns	ns
	ns								-0.698*	ns
N			ns	ns	ns	ns	ns	ns	ns	-0.86**
	ns				0.57	ns	ns	ns	ns	ns
P				ns	-0.73	ns	ns	0.79	ns	ns
	ns				-0.69*	ns	ns	ns	ns	ns
Ca					0.87*	ns	ns	ns	ns	ns
	ns				0.57	ns	0.59	0.60	ns	ns
Fe						ns	ns	ns	ns	ns
	ns					ns	ns	ns	ns	ns
K							ns	ns	ns	ns
	ns						ns	ns	ns	ns
Mg								ns	ns	ns
	ns							ns	ns	ns
Mn									ns	ns
	ns								ns	ns
SLA										ns
	ns									ns

Table 4. Variations of leaf functional traits among families and major functional groups. Legend. Growth forms: H (herbs), SS (small shrubs), LS (large shrubs), T (trees); Deciduousness: D (deciduous), E (evergreen); leaf consistence M (malacophyllous), S (sclerophyllous).

	Families		Growth forms		Deciduousness		Leaf consistence	
	F	Sign.	F	Sign.	F	Sign.	t	Sign.
LS (cm ²)	3.63	***	5.24	H,SS>LS>T **	0.33	ns	0.51	ns
SLA (cm ² g ⁻¹)	3.70	***	8.79	SS, H>LS,T ***	6.30	E<S,D ***	-2.40	S>M *
C%	3.15	***	3.15	H,SS<LS,T ***	9.25	E>S,D ***	2.82	S>M **
N (%)	2.21	**	2.69	H>T *	8.93	E<D ***	-2.33	M>S *
Ca (%)	2.23	**	6.55	H,SS>LS>T ***	7.38	E<D ***	-2.53	M>S *
Fe (%)	1.57	.	4.59	SS>T **	3.25	E<S,D **	-2.38	M>S *
K (%)	6.68	***	5.17	H,SS>LS,T **	7.09	E<S,D ***	-2.28	M>S *
Mg (%)	2.49	**	5.79	SS, H>LS,T ***	4.24	E<S,D **	-3.56	M>S ***
Mn (%)	1.30	ns	2.77	H,SS>T *	1.17	ns	-2.31	M>S *
P (%)	2.38	**	4.21	H>SS>LS>T **	14.36	E<S,D ***	-3.31	M>S ***

ns (not significant) $P>0.10$, . $P\leq 0.10$, * $P\leq 0.05$, ** $P\leq 0.01$, *** $P\leq 0.001$

variable values of axis 2, whereas mobile semi-fixed dunes were found in the left area of the figure.

4. Discussion

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

4.1. Leaf functional traits in coastal dunes

In coastal dunes, leaf area spanned four orders of magnitude, ranging from sub-lepto- to micro-

mesophyll leaf classes. It agrees with leaf class distribution observed in other Mediterranean ecosystems (Ackerly et al. 2002; Navarro et al. 2010). However, the mean values are closer to harsher Mediterranean ecosystems, such as halophytic vegetation in drained soils and open xerophytic shrublands (Díaz and Cabido, 1997).

Values of SLA in coastal dunes from S Spain are in the same range as in previous studies in Mediterranean ecosystems (49-360 cm²g⁻¹, e.g. Garnier et al 1997; Lavergne et al., 2003, 2004) and in other sand dunes (86-282 cm²g⁻¹, e.g. Yulin et al., 2005).

Species leaf [N] fitted in the range obtained before (1-4%N, e.g. Garten, 1976; Duarte, 1992; Thompson et al., 1997; Niinemets and Kull, 2003), but the mean values obtained in the dunes are mainly located in the lowest level of the range (1.61-2%).

The concentration of P and K were closer to the obtained by Foulds (1993) in Mediterranean south-western Australian plants (1900 µg g⁻¹ P and

Table 5. Leaf functional traits of perennial species in coastal dunes in S Spain grouped by families and major functional groups. Growth forms: H (herbs), SS (small shrubs), LS (large shrubs), T (trees); Deciduousness: D (deciduous), E (evergreen); leaf consistence M (malacophyllous), S (sclerophyllous).

		N	LS cm ²	SLA cm ² g ⁻¹	C%	N%	Ca%	Fe%	K%	Mg%	Mn%	P%
<i>Family</i>	Amaranthaceae	2	48.40	71.60	48.39	1.94	2.93	0.08	3.30	0.66	0.014	0.09
	Anacardiaceae	2	5.98	31.58	40.76	1.20	0.93	0.01	0.59	0.21	0.005	0.07
	Apiaceae	2	40.76	49.13	36.83	2.17	1.62	0.01	1.30	0.24	0.007	0.28
	Araceae	2	0.89	34.46	44.46	1.16	0.19	0.00	0.92	0.13	0.002	0.11
	Asteraceae	11	36.83	133.09	40.36	1.64	2.32	0.08	1.22	0.44	0.011	0.12
	Brassicaceae	2	0.52	65.25	30.83	1.89	5.18	0.07	0.85	0.29	0.005	0.20
	Caprifoliaceae	1	44.46	54.41	45.13	0.99	1.80	0.00	1.35	0.24	0.005	0.10
	Caryophyllaceae	3	2.70	93.02	48.90	1.95	2.52	0.16	2.05	0.65	0.013	0.16
	Cistaceae	11	40.36	62.60	55.6	1.61	1.24	0.04	0.53	0.27	0.005	0.13
	Cupressaceae	3	1.10	24.81	52.88	0.95	1.43	0.03	0.59	0.20	0.005	0.12
	Empetraceae	1	30.83	390.50	40.8	0.87	0.42	0.01	0.54	0.13	0.002	0.06
	Ericaceae	2	0.20	40.09	44.12	1.28	0.72	0.04	0.39	0.21	0.008	0.04
	Euphorbiaceae	2	45.13	153.95	48.21	1.81	1.54	0.03	1.69	0.19	0.003	0.21
	Fabaceae	17	2.07	95.58	41.55	2.52	1.62	0.05	0.81	0.31	0.008	0.14
	Fagaceae	2	48.90	78.06	44.50	1.34	0.71	0.01	0.51	0.15	0.004	0.09
	Frankeniaceae	1	0.87	34.50	45.62	1.36	2.81	0.05	0.78	0.78	0.008	0.41
	Lamiaceae	12	55.60	103.40	46.11	1.81	1.51	0.11	1.87	0.26	0.005	0.17
	Liliaceae	4	0.53	65.52	48.45	1.67	0.50	0.03	1.46	0.10	0.004	0.08
	Myrtaceae	2	52.89	61.41	45.09	1.09	1.05	0.03	0.63	0.21	0.004	0.08
	Oleaceae	4	0.02	45.99	39.58	1.53	1.09	0.02	0.69	0.21	0.003	0.10
	Plantaginaceae	1	40.80	55.10	40.15	1.25						
	Plumbaginaceae	3	0.78	53.67	45.835	1.50	0.78	0.03	1.10	0.73	0.004	0.16
	Rhamnaceae	4	44.12	86.84	37.94	2.06	1.84	0.04	1.06	0.20	0.007	0.11
	Rubiaceae	5	0.31	199.45	43.165	2.22	2.86	0.05	1.58	0.37	0.005	0.19
	Santalaceae	1	48.21	47.23	47.74	1.01	1.32	0.02	1.33	0.16	0.002	0.20
	Scrophulariaceae	1	7.76	102.94	47.87	2.37	1.51	0.06	0.43	0.26	0.006	0.23
	Solanaceae	2	41.55	105.33	36.295	2.24	1.96	0.06	3.02	0.67	0.003	0.10
	Thymelaeaceae	3	0.16	106.27	46.02	1.39	1.39	0.06	0.83	0.20	0.006	0.11
	Violaceae	1	44.50	119.13	48.39	3.77	1.24	0.02	2.13	0.64	0.004	0.15
<i>Growth forms</i>	Herbs	15	5.10	95.19	40.45	2.10	2.54	0.07	1.30	0.36	0.007	0.19
	Small shrubs	50	1.02	117.50	42.84	1.81	1.90	0.07	1.38	0.38	0.008	0.15
	Large shrubs	33	3.18	69.00	45.30	1.85	1.20	0.05	0.96	0.24	0.006	0.12
	Trees	11	3.45	43.42	48.56	1.24	1.09	0.02	0.61	0.20	0.004	0.10
<i>Leaf habit</i>	Deciduous	29	3.11	95.79	41.51	2.21	2.15	0.060	1.48	0.36	0.007	0.18
	Semi-deciduous	46	1.67	99.14	43.04	1.80	1.74	0.068	1.17	0.34	0.006	0.14
	Evergreen	34	3.10	77.63	47.05	1.47	1.21	0.034	0.89	0.24	0.006	0.10
<i>Leaf consistence</i>	Sclerophyllous	36	2.94	86.99	45.85	1.59	1.36	0.03	0.94	0.24	0.005	0.11
	Malacophyllous	73	2.28	94.14	42.76	1.92	1.82	0.07	1.26	0.35	0.007	0.15

10800 µg g⁻¹ K) and by Niinemets and Kull (2003) in wooded meadow on calcareous alkaline soils in Laelatu (0.2-0.09%P and 2.5-0.2%K). In all the mentioned cases, the soils were dry and/or calcareous, such as the found in coastal dunes,

characters that are associated to reduced uptake of P by plants (Hu and Schmidhalter, 2005).

Leaf [Mg] and [Mn] in coastal dunes were also within the range reported by previous studies (0.3-0.2% [Mg] Thompson et al., 1997; Bombato et al.,

Table 6. Variations of leaf traits among the three coastal dunes in S Spain with different Mediterranean climate and between sectors of dunes. Legend: A (P.N. del Estrecho), B (M.N. Artola-Cabopino), C (P.N. Cabo de Gata-Níjar); F (Fixed dunes), M (Mobile semi-fixed dunes).

	Differences inter-dunes				Differences intra-dunes (dune sectors)					
	Fixed dunes		Mobile semi-fixed dunes		P.N. del Estrecho		M.N. Artola-Cabopino		P.N. Cabo de Gata-Níjar	
	<i>F</i>	Signif.	<i>F</i>	Signif.	<i>t</i>	Signif.	<i>t</i>	Signif.	<i>t</i>	Signif.
LS cm ²	1.34	ns	0.78	ns	-1.05	ns	-0.53	ns	-0.02	ns
SLA (cm ² g ⁻¹)	0.49	A<C **	1.64	A<C ·	0.85	ns	1.33	ns	-0.51	ns
C%	3.78	A>C *	0.41	ns	-4.49	F>M ***	-2.38	F>M *	-1.09	ns
N%	0.29	ns	2.22	ns	1.06	ns	0.92	ns	-0.34	ns
P%	0.64	ns	0.16	ns	2.50	F<M *	1.69	ns	0.32	ns
Ca%	2.31	ns	0.16	ns	2.67	F<M *	3.16	F<M **	0.32	ns
Fe%	17.93	A<B,C ***	12.88	A<B,C ***	0.09	ns	0.35	ns	1.06	ns
K%	1.60	ns	0.46	ns	0.94	ns	0.60	ns	-0.45	ns
Mg%	4.36	C>A*	1.21	ns	3.46	F<M ***	2.33	F<M *	1.18	ns
Mn%	2.77	A<B ·	1.89	ns	1.87	F<M ·	1.49	ns	0.85	ns

ns (not significant) $P>0.10$, · $P\leq 0.10$, * $P\leq 0.05$, ** $P\leq 0.01$, *** $P\leq 0.001$

2010; 10-100 $\mu\text{g g}^{-1}$ [Mn] Foulds, 1993; Thompson et al., 1997; Hänsch and Mendel, 2009).

Leaf [Ca] (from 6.1 to 0.3%) was higher in the studied coastal dunes than the obtained in different ecosystems (0.02-3.9%Ca, Foulds, 1993; Glew et al., 1997; Thompson et al., 1997; Niinemets and Kull, 2003).

Leaf [Fe] (from 0.004 to 0.3) was also higher in these coastal dunes (0.001-0.06 %Fe, Glew et al., 1997; Hänsch and Mendel 2009).

According to Bakker et al. (2005), the higher leaf [Ca] and [Fe] in the study area may be related to the seepage. Depending on the origin of the water and the mineral composition of the layers that it passed through, seepage water may contain high concentrations of Ca^{2+} , HCO_3^- and Fe^{2+} (Stuyfzand, 1993; Bakker et al., 2005), which is reflected by leaf nutrients concentration.

Additionally, previous studies (e.g. Hobbie and Gough, 2002) have shown that alkaline soils, such as the analysed in this study, shows higher amount

of exchangeable Ca, situation that involved a high leaf [Ca].

However, the high variability of leaf nutrient concentration obtained among species may suggest that foliar nutrient concentration is as much a species-level trait as it is reflective of soil nutrient availability.

4.2. Correlation patterns among leaf traits

The strong positive correlation between leaf concentrations of all elements, and in particular between N and P is consistent with the findings of other surveys (Garten, 1976; Duarte, 1992; Bedford et al., 1999; Güsewell and Koerselman, 2002; Güsewell, 2004). However, these relationships are highly variable among the studied coastal dunes and specially reduced in all mobile semi-fixed dunes, and in fixed dunes from P.N. Cabo de Gata-Níjar. This evidence suggests that the correlation between leaf traits may vary

depending on environmental conditions (Wilson et al., 1999).

The co-variations of the leaf economic spectrum (Wright et al., 2004a) have been confirmed in the studied coastal dunes. SLA, leaf [N] and [P] are broadly correlated. Interestingly, K apparently also follows the same pattern in our result.

Species with high SLA tend to have high nutrient concentrations (Fields and Mooney, 1986; Reich et al., 1992, 1997; Niinemets, 1999; Wright et al. 2005). Particularly, strong correlation has been found between SLA and leaf [N]. This relationship may be used to predict accurately the maximum photosynthetic rate of a wide range of species (Reich et al. 1997), and both traits are related to leaf life-span, rapid production of biomass and an efficient conservation of nutrients (Poorter and Garnier, 1999).

According to the leaf economics spectrum (Wright et al., 2004), leaf correlation patterns obtained in coastal dunes involve that this vegetation is mainly formed by species with slow potential rate of return, low rates of photosynthesis and respiration, which need a higher investment per unit leaf area. These characteristics point out the stress-tolerant strategy that predominates in the studied dunes.

4.3. Taxonomic families and leaf traits

Leaf nutrient concentrations are strongly influenced by habitat, but also the taxonomic families play an important role in their distribution among species (e.g. Thompson et al., 1997).

Milewski (1982) suggested that K is the critical nutrient in the determination of succulence

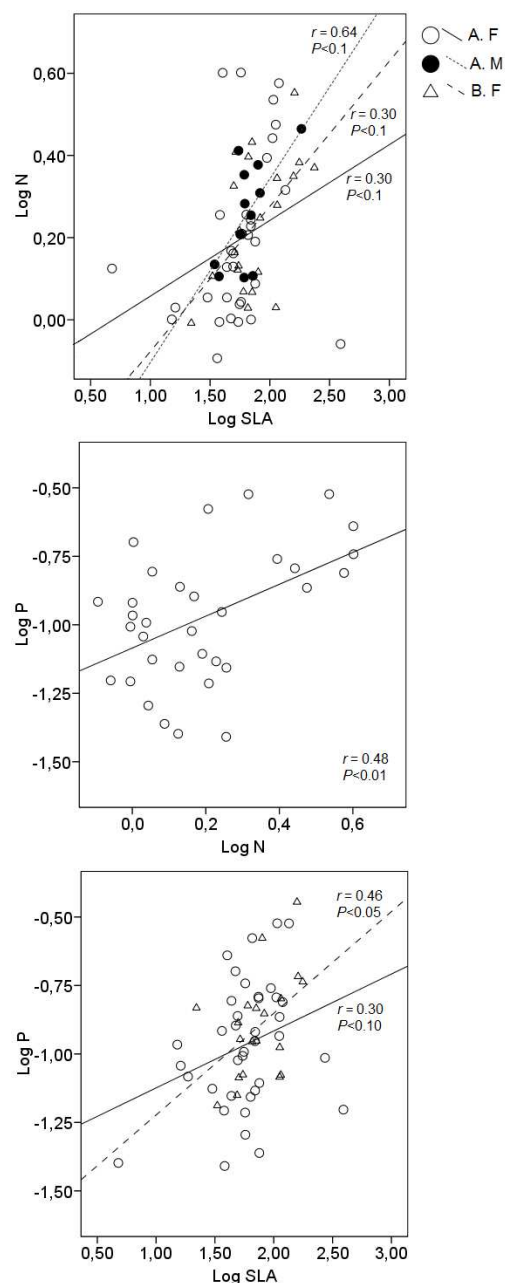


Fig. 4. Relationships between leaf N, P and SLA in coastal dunes. r^2 are calculated for a linear dependence. Lines provide a regression equation fitted to the data from each analysed dunes. Only significant correlations are included. Legend. A (P.N. del Estrecho); B (M.N. Artola-Cabopino); F (Fixed dunes); M (Mobile semi-fixed dunes). $P \leq 0.10$, * $P \leq 0.05$, ** $P \leq 0.001$, *** $P \leq 0.0001$,

(maintaining turgidity). The present study confirms that succulent-leaved families, like Amaranthaceae, have significantly greater concentrations of this element. However, according to the results obtained by Foulds (1993), our results show that this family also contains higher concentration of [Ca] and [Mn].

Maximum of leaf [N] values were obtained in N-fixing species (Fabaceae) (Foulds, 1993; Killingbeck, 1996; Wright and Westoby, 2003; Wright et al. 2004a). This family also show low ratio of K to Ca, which has been interpreted as a consequence of their Ca requirement for nitrogen fixation (Foulds, 1993).

Caryophyllaceae species showed maximum leaf [Fe], but also high values of other nutrients. This result agrees with Broadley et al. (2003), and it has been hypothesized to be related to ancestral Caryophyllales that evolved in dry, mineral-rich environments (Ehrendorfer, 1976; Cuénoud et al., 2002).

4.4. Major functional groups and leaf traits

Consistent with previous studies, species with short leaf turnover times (herbs and deciduous shrubs) generally had higher leaf nutrient concentrations and SLA than species with long leaf turnover times (evergreen shrubs and trees) (Reich et al., 1997; Reich et al., 1999; Aerts and Chapin, 2000; Ackerly et al., 2002; Hobbie and Gough, 2002). Low values of leaf nutrients and SLA are also related to sclerophyll and small leaves, conditions which are likely to be favoured because these leaves show the greatest carbon gain profits over transpirational losses (Turner, 1994).

This last strategy has been identified as a higher nutrient use-efficiency in habitats experiencing high light, low nutrient, or low moisture availability (Niinemets and Kalevi, 1994; Aerts, 1995; Ackerly and Reich, 1999; Bombonato et al. 2010), such as coastal dunes, and it has been known as nutrient-stress tolerant strategy (Chapin, 1980).

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

Climate-related variations of leaf traits have been observed in previous researches (e.g. Reich et al., 1999; Wright et al. 2001, 2004a, 2005). In the present work, it has been shown how coastal dunes under variations into the Mediterranean climate could show differences of leaf functional traits.

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

The leaves found in M-subdesert dunes are the smallest of all the studied dunes (medium LS value in M-subdesert dunes is between 2 and 4 times lower than in M-oceanic and M-subtropical dunes, respectively), and they showed the highest SLA (two times the medium SLA obtained in M-oceanic dunes).

Small leaf size avoids convective heat loss, facilitating maintenance of leaf energy balance, and improving water use efficiency under summer conditions (Blanca, 1990; Ackerly et al. 2002).

Traditionally, dry-site species have been associated to low SLA (Reich et al., 1999; Wright et al., 2001; Wright and Westoby, 2003). A new perspective has been shown in this study. The relationship between dry-conditions and low SLA has been based on the drought tolerance strategy selected in these places. Dry-placed species are expected to be evergreen showing leaf thickness and sclerophylly (Mooney and Dunn, 1970; Parson, 1976), characteristics which are linked to low SLA (Wilson et al., 1999; Fonseca et al., 2000; Ackerly et al., 2002). Low SLA contributes to long leaf-life span, high nutrient retention and protection from desiccation (Mooney and Dunn, 1970; Ackerly et al., 2002), strategy which is extended in resource-poor environments, such as coastal dunes (Van der Valk, 1974). However,

most of the species in these dunes use a contrasting strategy, they are xerophytic malacophyllous, strategy which has been determined as of high interest in plants on semi-deserts in warm temperate regions (Blanca, 1990; Grubb, 1998) and in disturbed environments where the human activity has involved an increase of the aridity (Catro-Díez et al., 2001). These species have relatively soft leaves that live only a short time, often a few months. The loss of leaves during the drought time has been seen as of value in cutting down transpiration and respiration during periods when plants are rarely able to achieve positive net assimilation (Mooney et al., 1975).

Leaf nutrient content also showed significant differences among dunes, showing the most

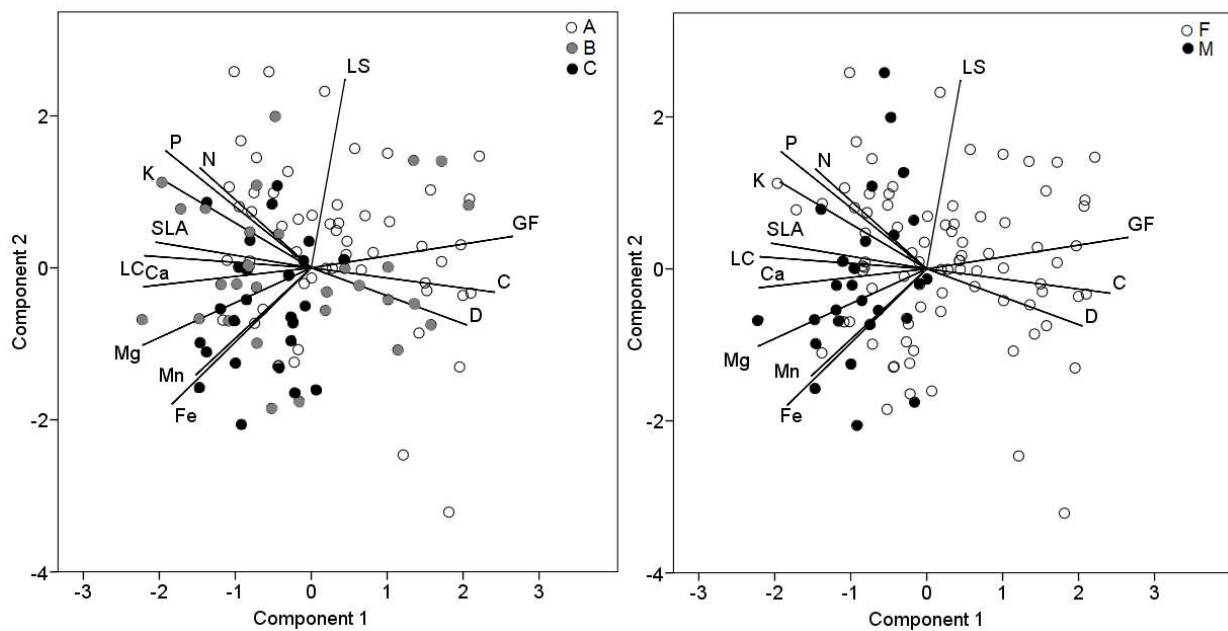


Fig. 5. Principal components analysis of species in coastal dunes, ordinated according to leaf functional traits. Legend. A (P.N. del Estrecho), B (M.N. Artola-Cabopino), F (Fixed dunes), M (Mobile semi-fixed dunes); D (deciduousness), GF (growth forms), LC (Leaf consistence), LS (leaf size), SLA (specific leaf area), C (Leaf [C]), Ca (Leaf [Ca]), Fe (Leaf [Fe]), K (Leaf [k]), Mg (Leaf [Mg]), Mn (Leaf [Mn]), N (Leaf [N]), P (Leaf [P]).

Atlantic dunes (M-oceanic dunes in P.N. del Estrecho) the poorest leaves (the lowest values of leaf [Fe], [Mg] and [Mn] have been found in these dunes). This difference is explained by the distribution of major functional groups, because the majority of evergreen sclerophyll species, which are expected to show lower leaf N and other nutrients content (Westoby et al., 2002; Wright et al. 2005; He et al. 2006), are located on P.N. del Estrecho. However, soil composition is also relevant in this result, because soil conditions exert an important and direct influence on nutrients concentration in leaves (e.g. Rode et al. 1992; Thompson et al. 1997), and these soils are indeed the poorest in [Mn].

4.6. Different leaf patterns of specialization among the dune sectors

This study has demonstrated that dune sectors show contrasting leaf traits. The exception was P.N. Cabo de Gata-Níjar, where no significant difference was found between fixed and mobile semi-fixed dunes.

Fixed dunes are closer to the result obtained in previous studies in Mediterranean ecosystems (e.g. Ackerly et al. 2002). These are the typically stress-tolerant strategists which are predominant in coastal dunes.

However, mobile semi-fixed dunes show closer leaf patterns than those found in M-subdesert dunes (P.N. Cabo de Gata-Níjar). They are dominated by xerophytic malacophyllous species of small size (herbs and small shrubs). The high leaf nutrient content in this dune sector may be related to the dominance of deciduous/semi-deciduous species (He et al, 2006). Particularly

relevant is the leaf Ca content, even higher than leaf [N], and whose enrichment could be explained by the higher Ca content in these soils. Coastal soils are known to receive large annual inputs of nutrients in the form of salt spray (Clayton 1972; Woodhouse and Hanes 1966; Van der Valk 1974), rich in [K], [Mg] and [Ca] (Riley and Tongudai, 1967; Clayton, 1972).

5. Acknowledgements

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Appendix. Leaf traits of perennial species in coastal dunes in S Spain. Maximum and minimum values are indicated in bold. GF (Growth forms): H (herbs), SS (small shrubs), LS (large shrubs), T (trees); D (deciduousness): E (evergreen), D (deciduous), (SD) semideciduous; LC (leaf consistence): M (malacophyllous), S (sclerophyllous).

	Family	GF	LH	LC	LCR	LS cm ²	SLA cm ² g ⁻¹	Leaf nutrient content (%)							
								C	N	Ca	Fe	K	Mg	Mn	P
P.N. del Estrecho. Fixed dunes															
<i>Adenocarpus telonensis</i>	Fabaceae	LS	D	M	G	0.1	111.5	.	.	1.6	0.040	1.32	0.32	0.013	0.12
<i>Calamintha nepeta subsp. nepeta</i>	Lamiaceae	H	D	M	G	1.23	134.74	42.43	2.07	1.02	0.026	3	0.23	0.004	0.3
<i>Calicotome villosa</i>	Fabaceae	LS	D	M	G	0.22	57.2	46.09	4	0.76	0.014	1.04	0.18	0.009	0.18
<i>Calluna vulgaris</i>	Ericaceae	SS	E	S	G	0.01	4.77	52.62	1.33	0.77	0.062	0.35	0.18	0.005	0.04
<i>Cistus albidus</i>	Cistaceae	LS	S	M	GR	3.88	49.31	44.67	1.35	1.77	0.028	0.64	0.24	0.002	0.14
<i>Cistus crispus</i>	Cistaceae	SS	S	M	G	1.43	94.43	42.43	2.48	1.68	.	0.79	0.2	0.004	0.17
<i>Cistus ladanifer</i>	Cistaceae	LS	S	M	G	6.95	49.5	46.98	1.45	0.93	0.026	0.52	0.23	0.013	0.09
<i>Cistus monspeliensis</i>	Cistaceae	SS	S	M	G	1.88	69.4	43.61	1.69	0.65	0.008	0.37	0.2	0.007	0.07
<i>Cistus salvifolius</i>	Cistaceae	LS	S	M	G	1.99	74.12	41.67	2.07	1.5	0.054	0.58	0.43	0.004	0.16
<i>Corema album</i>	Empetraceae	SS	E	S	G	0.53	390.5	55.6	0.87	0.42	0.014	0.54	0.13	0.002	0.06
<i>Cytisus striatus</i>	Fabaceae	LS	D	M	G	0.03	40.24	51.98	3.99	0.36	0.013	1.16	0.15	0.010	0.23
<i>Chamaerops humilis</i>	Palmae	LS	E	S	G	12.04	15.12	44.97	1	0.19	0.005	0.92	0.13	0.002	0.11
<i>Daphne gnidium</i>	Thymelaeaceae	LS	E	M	G	0.6	75.4	43.62	1.55	1.9	0.038	0.79	0.11	0.003	0.08
<i>Dianthus broteri</i>	Caryophyllaceae	SS	D	S	G	1.3	74.35	44.42	1.44	2.44	0.011	1.94	0.35	0.005	0.16
<i>Erica scoparia</i>	Ericaceae	SS	E	S	G	0.04	75.4	53.15	1.22	0.67	0.025	0.43	0.23	0.010	0.04
<i>Fumana thymifolia</i>	Cistaceae	SS	S	M	G	0.06	69.5	39.91	1	2.29	0.043	0.62	0.32	0.005	0.12
<i>Galium tricornutum</i>	Rubiaceae	SS	D	S	G	2.71	272.28	41.51	3.28	1.12	0.016	0.92	0.07	0.002	0.1
<i>Halimium halimifolium</i>	Cistaceae	LS	S	M	G	0.87	43.7	46.16	1.13	0.46	0.015	0.37	0.24	0.004	0.16
<i>Juniperus oxycedrus subsp. macrocarpa</i>	Cupressaceae	T	E	S	G	0.2	36.27	46.51	0.81	2.02	0.035	0.66	0.13	0.005	0.12
<i>Juniperus phoenicea subsp. turbinata</i>	Cupressaceae	T	E	S	G	1.05	16.17	52.16	1.07	0.89	0.014	0.47	0.21	0.003	0.09
<i>Lavandula stoechas</i>	Lamiaceae	SS	S	M	G	0.14	55.83	48.05	1.09	0.85	0.031	1.51	0.34	0.013	0.1
<i>Lonicera implexa</i>	Caprifoliaceae	LS	E	M	G	2.7	54.41	44.46	0.99	1.8	0.004	1.35	0.24	0.005	0.1
<i>Marrubium vulgare</i>	Lamiaceae	SS	S	M	G	8.95	107	41.94	3.43	1.8	0.022	3.3	0.23	0.004	0.3
<i>Myrtus communis</i>	Myrtaceae	LS	E	S	G	1.13	57.32	46.25	1.11	1.11	0.023	0.73	0.18	0.001	0.05
<i>Olea europaea var. sylvestris</i>	Oleaceae	T	E	S	G-GR	1.32	47.5	47.93	1.47	1.17	0.009	0.91	0.18	0.002	0.13
<i>Osyris lanceolata</i>	Santalaceae	LS	E	S	GR	0.95	47.23	47.74	1.01	1.32	0.020	1.33	0.16	0.002	0.2
<i>Phillyrea angustifolia</i>	Oleaceae	T	E	M	G	2.69	37.85	49.4	0.99	0.67	0.006	0.54	0.32	0.003	0.06
<i>Phlomis purpurea</i>	Lamiaceae	LS	S	M	G	1.78	112.01	44.44	2.99	0.96	0.010	1.85	0.13	0.002	0.14
<i>Pistacia lentiscus</i>	Anacardiaceae	T	E	S	G	10.47	30.06	49.79	1.13	0.79	0.008	0.71	0.19	0.002	0.07
<i>Quercus coccifera</i>	Fagaceae	T	E	S	G	3.68	43.66	48.21	1.34	0.97	0.010	0.36	0.15	0.003	0.07
<i>Rhamnus alaternus</i>	Rhamnaceae	LS	S	M	G	4.2	63.49	45.64	1.8	2.31	0.004	1.26	0.12	0.004	0.07
<i>Rhamnus lycioides subsp. oleoides</i>	Rhamnaceae	LS	S	S	G	0.65	69.26	45.97	1.75	1.88	0.039	1.01	0.22	0.006	0.11
<i>Ruscus aculeatus</i>	Liliaceae	LS	E	S	G	3.24	58.25	50.75	1.62
<i>Ruta chalepensis</i>	Rutaceae	SS	D	M	G	1.57	65.67	42.2	1.61	1.87	0.037	3.7	0.18	0.004	0.26
<i>Sideritis arborescens subsp. perezlarae</i>	Lamiaceae	SS	S	M	G	1.23	105.2	42.47	2.77	1.98	0.049	1.32	0.22	0.005	0.16
<i>Stauracanthus boivinii</i>	Fabaceae	LS	E	S	G	0.18	38.2	47.49	1.8	0.33	0.012	0.22	0.17	0.006	0.04
<i>Teucrium fruticans</i>	Lamiaceae	LS	S	M	G-GR	0.6	57.05	45.69	1.62	1.95	0.057	1.19	0.15	0.001	0.06
<i>Ulex australis</i>	Fabaceae	LS	E	S	G	0.5	18.66	48.64	1.68	0.57	0.028	0.38	0.13	0.002	0.08
<i>Viola arborescens</i>	Violaceae	SS	S	M	G	0.73	119.13	40.9	3.77	1.24	0.020	2.13	0.64	0.004	0.15
Mean						2.15	75.43	46.28	1.78	1.24	0.024	1.09	0.22	0.005	0.12

Anexo Capítulo 3

130

	Family	GF	LH	LC	LCR	LS cm ²	SLA cm ² g ⁻¹	Leaf nutrient content (%)							
								C	N	Ca	Fe	K	Mg	Mn	P
<i>Asteriscus maritimus</i>	Asteraceae	SS	S	M	G	1.14	60.9	30.82	1.27	6.09	0.015	1.18	0.4	0.007	0.11
<i>Crucianella maritima</i>	Rubiaceae	SS	S	S	GR	0.05	183.78	38.38	2.92	3.45	0.009	1.69	0.19	0.003	0.23
<i>Eryngium maritimum</i>	Umbelliferae	H	D	M	GR	36.39	54.67	41.39	2.58	1.74	0.009	1.17	0.26	0.004	0.28
<i>Euphorbia paralias</i>	Euphorbiaceae	H	D	M	G	0.58	72.1	45.83	1.28	1.54	0.030	1.69	0.19	0.003	0.21
<i>Frankenia laevis</i>	Frankeniaceae	SS	D	M	G	0.16	34.5	41.55	1.36	2.81	0.051	0.78	0.78	0.008	0.41
<i>Helichrysum picardii</i>	Asteraceae	SS	S	M	GR	0.2	61.69	49.11	1.92	1.06	0.027	1.78	0.22	0.007	0.08
<i>Limonium emarginatum</i>	Plumbaginaceae	SS	S	M	G	0.76	37.5	40.95	1.28	0.57	0.012	0.82	0.75	0.004	0.1
<i>Limonium sinuatum</i>	Plumbaginaceae	SS	S	M	G	1.45	56.5	41.21	1.61	0.57	0.005	1.67	0.58	0.004	0.21
<i>Lotus creticus</i>	Fabaceae	H	D	M	GR	0.12	82.64	37.95	2.04	2.96	0.052	0.58	0.4	0.009	0.2
<i>Malcolmia littorea</i>	Brassicaceae	H	D	M	GR	0.53	69.4	35.91	1.8	4.86	0.008	0.88	0.27	0.005	0.22
<i>Medicago marina</i>	Fabaceae	H	D	M	GR	0.36	61	41.42	2.25	1.48	0.009	0.87	0.13	0.006	0.13
<i>Ononis natrx</i> subsp. <i>ramosissima</i>	Fabaceae	SS	S	M	G	0.07	79.54	43.57	2.38	3.37	0.112	0.48	0.32	0.004	0.13
<i>Phagnalon saxatile</i>	Asteraceae	SS	S	M	G	1.2	171.85	44.07	2.33	0.84	0.035	1.09	0.41	0.014	0.08
Mean						3.31	78.93	40.94	1.92	2.41	0.029	1.13	0.38	0.006	0.18
M.N. Artola-Cabopino. Fixed dunes															
<i>Asparagus aphyllus</i>	Liliaceae	SS	S	S	G	0.07	50.5	42.02	1.46	0.5	0.027	1.46	0.1	0.004	0.08
<i>Calicotome villosa</i>	Fabaceae	LS	D	M	G	0.18	70.9	44.52	2.71	0.72	0.071	1.31	0.31	0.009	0.15
<i>Cistus monspeliensis</i>	Cistaceae	SS	S	M	G	0.55	55.62	47.71	1.65
<i>Cistus salviifolius</i>	Cistaceae	LS	S	M	G	3.11	71.1	47.38	1.17	1.47	0.067	0.47	0.32	0.005	0.11
<i>Chamaerops humilis</i>	Palmae	LS	E	S	G	32.41	53.8	45.21	1.32
<i>Daphne gnidium</i>	Thymelaeaceae	LS	E	M	G	0.88	83	46.4	1.77	1.19	0.079	0.63	0.26	0.009	0.14
<i>Dianthus broteri</i>	Caryophyllaceae	SS	D	S	G	0.85	115.21	42.42	1.9	2.8	0.138	1.41	0.42	0.018	0.16
<i>Euphorbia terracina</i>	Euphorbiaceae	H	D	M	G	0.99	235.81	35.77	2.35
<i>Genista umbellata</i>	Fabaceae	SS	E	M	G	0.41	160.82	46.2	3.57	0.75	0.047	1.22	0.36	0.024	0.19
<i>Halimium calycinum</i>	Cistaceae	LS	S	M	G	0.22	51.8	48.58	2.56	0.91	0.041	0.45	0.26	0.002	0.11
<i>Halimium halimifolium</i>	Cistaceae	LS	S	M	G	1.82	60.1	47.38	1.17	0.78	0.055	0.51	0.25	0.004	0.15
<i>Juniperus phoenicea</i> subsp. <i>turbinata</i>	Cupressaceae	T	E	S	G	1.36	22	48.04	0.98	1.38	0.028	0.63	0.26	0.008	0.15
<i>Lavandula multifida</i>	Lamiaceae	SS	S	M	G	2.33	157.7	40.92	2.24	1.75	0.242	3.51	0.38	0.009	0.36
<i>Lavandula stoechas</i> subsp. <i>stoechas</i>	Lamiaceae	SS	S	M	G	0.44	112.22	44.6	1.07	1.24	0.227	0.64	0.4	0.012	0.08
<i>Myrtus communis</i>	Myrtaceae	LS	E	S	G	2.24	65.5	45.97	1.07	0.99	0.030	0.53	0.24	0.007	0.11
<i>Olea europaea</i> var. <i>sylvestris</i>	Oleaceae	T	E	S	G-GR	1.17	49.82	48.01	2.12	1.83	0.035	0.61	0.22	0.006	0.13
<i>Phillyrea angustifolia</i>	Oleaceae	T	E	S	G	2.65	48.79	.	.	0.7	0.017	0.69	0.13	0.002	0.07
<i>Phlomis purpurea</i>	Lamiaceae	LS	S	M	G	12.58	79.8	42.73	1.31	1.43	0.341	1.85	0.33	0.008	0.26
<i>Pistacia lentiscus</i>	Anacardiaceae	T	E	S	G	1.49	33.1	47	1.28	1.07	0.020	0.47	0.23	0.008	0.06
<i>Quercus coccifera</i>	Fagaceae	T	E	S	G	11.83	112.45	.	.	0.45	0.015	0.65	0.15	0.004	0.11
<i>Rhamnus lycioides</i> subsp. <i>oleoides</i>	Rhamnaceae	LS	S	S	G	0.96	114.8	46.18	2.21	1.88	0.070	1.21	0.17	0.002	0.08
<i>Rubia peregrina</i>	Rubiaceae	SS	D	S	G	1.21	176.19	41.24	2.41	2.73	0.085	1.88	0.53	0.007	0.18
<i>Ruta chalepensis</i>	Rutaceae	SS	D	M	G	1.43	66.1	44.13	2.49
<i>Ulex australis</i>	Fabaceae	LS	E	S	G	0.18	54.7	43.6	1.35	0.41	0.056	0.55	0.23	0.004	0.08
Mean						3.39	87.58	44.82	1.82	1.25	0.084	1.03	0.28	0.008	0.14
M.N. Artola-Cabopino. Mobile semi-fixed dunes															
<i>Crucianella maritima</i>	Rubiaceae	SS	S	S	GR	0.16	109.8	32.86	1.25	4.12	0.082	1.84	0.68	0.007	0.23
<i>Eryngium maritimum</i>	Umbelliferae	H	D	M	GR	31.78	43.6	43.72	1.75	1.51	0.009	1.44	0.23	0.010	0.28
<i>Helichrysum stoechas</i>	Asteraceae	SS	S	M	GR	0.22	89.7	47.2	1.02	1.42	0.080	0.79	0.27	0.013	0.06
<i>Lotus creticus</i>	Fabaceae	H	D	M	GR	0.36	112.9	42.98	1.76	3.26	0.038	0.53	0.34	0.008	0.12

	Family	GF	LH	LC	LCR	LS cm ²	SLA cm ² g ⁻¹	Leaf nutrient content (%)							
								C	Family	GF	LH	LC	LCR	LS cm ²	
<i>Malcolmia littorea</i>	Brassicaceae	H	D	M	GR	0.5	61.1	37.75	1.98	5.49	0.129	0.83	0.31	0.004	0.19
<i>Medicago marina</i>	Fabaceae	H	D	M	GR	0.57	104.58	41.52	2.96
<i>Ononis natrix</i> subsp. <i>ramosissima</i>	Fabaceae	SS	S	M	G	0.81	123.2	42.53	2.74	1.9	0.065	0.91	0.56	0.005	0.22
<i>Phagnalon saxatile</i>	Asteraceae	SS	S	M	G	1.4	239.51	43.58	2.02	1.07	0.058	0.91	0.3	0.029	0.17
<i>Scrophularia canina</i>	Scrophulariaceae	SS	S	M	G	2	102.94	47.87	2.37	1.51	0.056	0.43	0.26	0.006	0.23
<i>Silene niceensis</i>	Caryophyllaceae	H	D	M	G	1.15	89.5	34.23	2.51	2.32	0.319	2.81	1.17	0.016	0.16
Mean						3.89	107.68	41.42	2.03	2.51	0.093	1.17	0.46	0.011	0.18
P.N. Cabo Gata-Níjar. Fixed dunes															
<i>Asparagus albus</i>	Liliaceae	SS	S	S	G	0.07	87.8	44.09	1.95
<i>Asparagus horridus</i>	Liliaceae	SS	E	S	G
<i>Launaea arborescens</i>	Asteraceae	LS	E	M	G	1.45	169	40.21	2.84
<i>Launaea nudicaulis</i>	Asteraceae	SS	E	M	G	2.18	252.5	.	.	3.73	0.147	1.48	0.88	0.009	0.11
<i>Lycium intricatum</i>	Solanaceae	LS	D	M	G	0.64	94.27	29.36	1.87
<i>Teucrium hieronymi</i>	Lamiaceae	SS	S	M	GR	0.45	158.7	48.24	1.3	1.91	0.077	1.38	0.14	0.001	0.1
<i>Thymelaea hirsuta</i>	Thymelaeaceae	SS	E	M	G	0.03	160.4	48.03	0.84	1.07	0.051	1.08	0.22	0.006	0.12
<i>Thymus hyemalis</i>	Lamiaceae	SS	D	M	G	0.03	55.3	42.8	0.69	1.94	0.113	1.47	0.22	0.003	0.09
<i>Withania frutescens</i>	Solanaceae	LS	D	S	G	3.35	116.4	43.23	2.6	1.96	0.063	3.02	0.67	0.003	0.1
<i>Ziziphus lotus</i>	Rhamnaceae	LS	E	S	G	2.31	99.8	45.55	2.47	1.26	0.037	0.76	0.29	0.018	0.18
Mean						1.17	132.69	42.69	1.82	1.98	0.081	1.53	0.40	0.007	0.12
P.N. Cabo Gata-Níjar. Mobile semi-fixed dunes															
<i>Asteriscum maritimum</i>	Asteraceae	SS	S	M	G	0.81	76.1	30.82	1.59	4.89	0.198	0.54	0.92	0.009	0.08
<i>Crucianella maritima</i>	Rubiaceae	SS	S	S	GR	0.53	255.2	35.71	1.25
<i>Helichrysum stoechas</i>	Asteraceae	SS	S	M	GR	0.15	83.2	47.44	0.94	1.01	0.090	1.31	0.21	0.005	0.16
<i>Limonium lobatum</i>	Plumbaginaceae	SS	S	M	G	6.34	67	38.3	1.61	1.2	0.073	0.81	0.84	0.003	0.18
<i>Lotus creticus</i>	Fabaceae	H	D	M	GR	0.37	136.9	43.64	2.21	1.82	0.074	0.8	0.53	0.009	0.13
<i>Medicago marina</i>	Fabaceae	H	D	M	GR	0.54	113.8	42.57	2.78	2.46	0.086	1	0.33	0.006	0.07
<i>Ononis natrix</i>	Fabaceae	SS	S	M	G	0.19	258	41.27	2.14	3.2	0.119	0.59	0.52	0.007	0.15
<i>Othantus maritima</i>	Asteraceae	SS	S	M	GR	0.6	90.78	40.72	1.44	1.41	0.090	1.8	0.52	0.003	0.16
<i>Phagnalon saxatile</i>	Asteraceae	SS	S	M	G	0.45	168.8	33.61	1.04	1.62	0.061	1.32	0.28	0.015	0.17
<i>Plantago albicans</i>	Plantaginaceae	H	D	M	G	0.96	55.1	39.58	1.25
<i>Salsola oppositifolia</i>	Chenopodiaceae	SS	E	M	G	0.37	71.6	30.83	1.94	4.11	0.092	4.02	.	0.020	0.07
<i>Salsola vermiculata</i>	Chenopodiaceae	SS	E	M	G	0.03	.	.	.	1.75	0.060	2.59	0.66	0.009	0.1
<i>Teucrium dunense</i>	Lamiaceae	SS	S	M	GR	0.27	105.3	49.66	1.13	1.28	0.114	1.45	0.33	0.002	0.11
Mean						0.89	123.48	39.51	1.61	2.25	0.096	1.48	0.51	0.008	0.13



Conclusiones

Conclusiones

1. *Relacionado con los caracteres funcionales fenológicos.* Los sistemas costeros de dunas del sur de España presentan patrones e índices fenológicos similares a los encontrados en regiones mediterráneas cálidas y secas. Predominan las especies secuenciadoras, que permanecen activas fenológicamente durante gran parte del año y con dominio de la fenofase vegetativa sobre la reproductiva. La floración es temprana (final de invierno-principios de primavera) y puede extenderse hasta el verano, periodo de mayor inactividad. Durante estos meses tiene lugar la fructificación y la dispersión, siendo entonces el crecimiento vegetativo mínimo y mantenido por braquiblastos. Mediante estas adaptaciones fenológicas se evitan la competición por los recursos y el periodo de máxima sequía, favoreciendo la supervivencia de la planta.

2. *Relacionado con la dispersión y regeneración.* Los caracteres de dispersión y regeneración de la vegetación de dunas costeras del sur de España se asemejan a los observados en ecosistemas áridos. Las diásporas que predominan son semillas de pequeño tamaño y carentes de estructuras facilitadoras de la dispersión en el espacio. Son mayoritariamente semacoras, con dispersión espacial restringida y mecanismos de supervivencia (antitelecóricos). Los caracteres de dispersión y regeneración muestran variaciones entre las formas de crecimiento, encontrándose la mayor variación de estos en los arbustos de pequeño tamaño.

3. *Relacionado con los caracteres funcionales de la hoja.* Las hojas con mayor representación en sistemas de dunas costeras del sur de España son de pequeño tamaño (nanófilas), con bajos valores de área específica de la hoja (SLA) y de concentración de nutrientes. Los resultados muestran correlaciones positivas entre los nutrientes foliares, así como entre estos y el SLA, confirmándose las co-variaciones establecidas por Wright (2004). La concentración foliar de potasio presenta fuertes correlaciones con los caracteres del espectro económico foliar, siendo incluso más significativas que las obtenidas para el nitrógeno. Las variaciones de los caracteres de la hoja entre los grupos funcionales de especies es acorde con lo establecido en trabajos previos sobre el espectro económico foliar; las hierbas y pequeños arbustos de hoja decidua/semidecidua y malacófila, presentan los valores más altos de SLA y de concentración de nutrientes. Además, se ha encontrado variación significativa de estos caracteres entre familias taxonómicas; Amaranthaceae, Caryophyllaceae y Fabaceae presentan las máximas concentraciones de nutrientes.

4. *Relacionado con la variación de los caracteres funcionales en el área de estudio.* Los caracteres funcionales estudiados (fenología, espectro económico foliar, dispersión y regeneración) en sistemas de dunas costeras muestran diferencias significativas tanto entre dunas con diferente variante climática dentro del macroclima Mediterráneo (Mediterráneo-oceánico, M-subtropical, M-subdesértico) como entre sectores de duna (duna fija y duna móvil y semi-fija).

Las dunas de clima M-subdesértico (P.N. Cabo de Gata-Níjar) presentan una mayor duración de la floración y características de dispersión más próximas a lo observado previamente en estudios desarrollados en sistemas áridos (ej. mayor presencia de mecanismos antitelecóricos y de especies con dispersión anemócora). Las diferencias entre caracteres foliares son especialmente patentes entre las dunas M-subdesérticas (P.N. Cabo de Gata) y las M-oceánicas (P.N. del Estrecho). En esta última los valores de SLA y nutrientes como el hierro y el manganeso fueron significativamente inferiores. Dichas diferencias no son sólo debidas al clima, sino también a la composición del suelo.

Entre sectores dunares, las dunas móviles muestran una mayor concentración de sus fenofases en el periodo favorable (primavera). Las duras condiciones ambientales que se alcanzan en verano implican la imposibilidad de mantener crecimiento de dolicoblastos y la necesidad de acortar los periodos de fructificación y dispersión. Esta última es llevada a cabo por diásporas de menor tamaño que en dunas fijas y con menos adaptaciones a la supervivencia (mecanismos antitelecóricos). Además, las dunas móviles y semi-fijas albergan a la mayoría de las especies con dispersión aérea y a todas las especies cuyas diásporas pueden ser transportadas por el agua de mar. En cuanto a los caracteres foliares, en P.N. Cabo de Gata-Níjar no existen diferencias entre duna fija y duna móvil y semi-fija, mientras que en las otras dos dunas estudiadas, estos caracteres diferencian claramente entre sectores de duna, encontrándose en la duna fija mayor porcentaje de especies siempre-verdes de hoja esclerófila y con menor concentración de nutrientes (especialmente calcio y magnesio).

5. *Relacionado con los patrones recurrentes de especialización ecológica.*

En sistemas de dunas costeras se han diferenciado cuatro patrones fenológicos, que ponen de manifiesto la importante diversidad fenológica de estos ecosistemas. Estos están basados fundamentalmente en variaciones en la superposición de las fenofases, la duración de la floración y del ciclo fenológico a lo largo del año. La mayoría de las especies presentan el patrón típicamente mediterráneo.

Los caracteres funcionales de dispersión y regeneración diferencian entre estrategias de colonización (dispersión aérea, vehiculada por animales o por el agua de mar) y de supervivencia, lo cual se consigue mediante la capacidad de rebrotar y/o clonar, y mediante mecanismos antitelecóricos que posibilitan la formación de un banco de semillas tanto cerca de la planta (semacoría) como sobre las estructuras de la planta (bradisporía). De este modo, se consigue el mantenimiento *ex situ* e *in situ* de la vegetación en sistemas de dunas costeras.

Los caracteres funcionales foliares diferencian entre dos patrones de especialización: el de resistencia al estrés (predominante en especies siempre-verdes y esclerófilas, con bajos valores de área específica de la hoja y bajas concentraciones de nutrientes) y el de especies competidoras (mayoritario entre especies deciduas/semideciduas y malacófilas, con mayores valores de área específica y concentración de nutrientes).