

Ontogenetic shifts in interactions of two dominant shrub species in a semi-arid coastal sand dune system

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Abstract

Question: How does the interaction between two dominant shrub species in a coastal sand dune community change during their life history? Does this interaction influence their population dynamics?

Location: A semiarid coastal sand dune system in south-east Spain.

Methods: For 3 years we monitored physiological status, growth and reproductive effort of *Juniperus phoenicea* and *Pistacia lentiscus*, the dominant shrub species, growing either alone or in close spatial association. We also recorded adult mortality patterns and characterized seedling survival, soil properties and microclimate conditions beneath canopies and in bare ground.

Results and conclusions: There was a strong bi-directional interaction between the two studied species, with a net balance that changed in sign with increasing plant development. While mature individuals facilitated the establishment of seedlings of both species, adult mortality patterns suggested asymmetric competition at later life stages. The interaction with *Pistacia* negatively affected growth of juniper and contributed to its high mortality rates, while juniper had almost no effect on mature *Pistacia* individuals. Physiological data suggested that *Pistacia* had a competitive advantage over juniper, most likely because of differences in rooting patterns and tolerance to salinity, which may determine the source of water available for each species. Community dynamics are governed by facilitation at the seedling stage and shaped by differences in physiological traits in adult plants. Plant-plant interactions, which are strongly affected by environmental gradients, are important drivers of community dynamics in this system.

Keywords: Competition; Facilitation; Nurse plants; Rooting depth; Salinity; Water stress.

Nomenclature: Castroviejo et al. (1986–)

Abbreviations: ψ = pre-dawn stem water potential; A = leaf photosynthesis; F_v/F_m = maximum photochemical efficiency of photosystem II; g_s = leaf conductance to water vapour; RWC = relative water content; OM = organic matter.

Introduction

Plant interactions play a critical role in the structure of plant communities in dry conditions (Aguiar & Sala 1999; Brooker et al. 2008). In particular, facilitation influences community dynamics by increasing recruitment of less stress-tolerant species (Bertness & Callaway 1994; Walker & del Moral 2003; Valiente-Banuet et al. 2006), which are often unable to colonize open spaces because their regeneration niche requires more mesic conditions (Valiente-Banuet et al. 2006). Several authors have shown how many woody species in such habitats become established under standing vegetation (Herrera et al. 1994; Barnes & Archer 1999; Flores & Jurado 2003), and “nursing” by shrubs is a pivotal feature of the community (Callaway & Walker 1997; Gómez-Aparicio et al. 2004; Padilla & Pugnaire 2006). However, less is known about how these beneficiary species interact with the nurses as they mature. Such considerations are relevant to colonization processes because nurse species not only promote recruitment, but may also increase the fitness of beneficiary species (Rousset & Lepart 2000). Conversely, beneficiary species may place nurse species at a competitive disadvantage at later growth stages (Chapin et al. 1994), leading to their competitive exclusion (Callaway 1992; Flores-Martínez et al. 1994) or turning them into subordinate species (Chapin et al. 1994; Gasque & García-Fayos 2004). Consequently, these interactions may have large impacts on community structure and dynamics.

Community dynamics are often inferred from spatial distribution patterns, population structure or

by monitoring populations through the different life stages of the species involved. Another important, yet less frequently used, tool in understanding these dynamics is physiology; repeated physiological measurements over extended periods of time are crucial to reveal interaction mechanisms and their consequences for community dynamics (Shumway 2000; Forseth et al. 2001; Armas & Pugnaire 2005). Plant interactions depend on environmental severity (Bertness & Callaway 1994; Brooker & Callaghan 1998), its temporal variability (Tielbörger & Kadmon 2000; Kikvidze et al. 2006), and ontogeny of the interacting species (Armas & Pugnaire 2005; Schiffers & Tielbörger 2006). Therefore, measuring interaction intensity at only one point in time, during one life stage or using only one response variable is insufficient for drawing valid conclusions about long-term effects on population dynamics (Schiffers & Tielbörger 2006) or community responses to changing conditions (Tielbörger & Kadmon 2000; Brooker 2006; Brooker et al. 2008).

In order to understand plant community dynamics in a semiarid coastal sand dune system, we monitored the interaction between two dominant shrub species at different life stages. The dune system is structured into discrete patches of vegetation in a matrix of bare ground. Plant patches are dominated by Phoenician juniper, *Juniperus phoenicea* subsp. *turbinata* Guss. (Cupressaceae, juniper hereafter) and lentisc, *Pistacia lentiscus* L. (Anacardiaceae, lentisc hereafter). This juniper species is a colonizer of coastal dunes in the Mediterranean basin (Alcaraz & Peinado 1987), while lentisc is characteristic of mature communities in Mediterranean environments (Tomaselli 1981).

Our objectives were to use physiological measurements to identify interaction mechanisms and their effects on population dynamics. We hypothesized that facilitation and competition would determine establishment success and plant performance, with important consequences for community structure and dynamics. We expected interactions to be shaped by the physiological traits of the two species. We measured seedling survival and adult mortality rates and monitored gas exchange, water relations, growth and reproductive effort of adult plants as either isolated individuals or growing with the other species during 3 years of variable precipitation.

Methods

Study site and species

The study was conducted in a coastal dune system in the Punta Entinas-Sabinar Nature Reserve,

Almería, Spain (36°41'N, 2°42'W; 0–8 m elevation). Local climate is typically dry Mediterranean with a mean annual rainfall of 220 mm. Mean monthly temperatures range between 12 and 30°C, with high relative air humidity (around 70%). Sand dunes between 3 and 8 m in height over quaternary fossil beaches are stabilized by plants and dissected by slacks with salty, wet soils (hereafter referred to as dune slacks). The northern limit of the dunes is delimited by a system of lagoons and semi-natural salt pans where the water table surfaces. Seawater intrusion into the groundwater is generalized (ITGME & Junta de Andalucía 1998).

On dune tops, vegetation is distributed in discrete patches dominated by juniper and lentisc and separated by bare or low-cover gaps (Armas 2004). In this habitat, individuals of both species can grow alone or in clumps, either in pairs of the two species or in diverse, large (> 50 m²) patches, in which other smaller shrubs, annual grasses, forbs and bryophytes coexist. Communities in salty dune slacks are comprised of halophytic species and scattered lentisc; juniper is absent (Supporting Information, Appendix S1).

Juniperus phoenicea subsp. *turbinata* is a monoecious evergreen shrub up to 6 m tall, generally found in western Mediterranean coastal dune systems. Fruits ripen in the second summer, producing three to nine seeds (Castroviejo et al. 1986–). Seeds are dispersed by birds and by some mammals. *Pistacia lentiscus* is a dioecious evergreen shrub 3–4 m tall. Females produce many one-seeded drupes, which ripen in autumn and are mainly bird-dispersed (Herrera 1984; Castroviejo et al. 1986–).

On the top of a stabilized dune, we randomly selected 24 mature individuals of each species with similar heights (1.8–2.0 m) and canopy cover (approximately 50 and 12 m² for lentisc and juniper, respectively). For each species, 12 plants were growing alone (i.e. with no other associated plants) and 12 were in close association with the other species (hereafter referred to as clumps). Measurements were taken on clumps that had only one lentisc and one juniper individual. All measurements were performed within this group of 48 mature individuals.

Microclimate and soil properties

Air temperature and relative humidity 10 cm above the soil surface were recorded every 5 min for 2 weeks in 2002 in February, March, June, August, October and December. Three microclimate sensors (HOBO H8, Onset Computers, Pocasset, MA, USA) were placed in each of four microhabitats:

beneath the canopy of isolated juniper and lentisc, under the canopy of clumps, and on bare dune tops (gaps, hereafter).

Cylindrical soil samples of $\sim 200 \text{ cm}^3$ were collected in August 2000 from the upper 10 cm of soil in the four microhabitats. Samples from under a plant canopy were taken 40 cm NW and SE of the main trunk of each shrub (under the canopy). The two soil samples from each plant were mixed thoroughly and analysed as a composite sample ($n = 9$ per microhabitat). Soils were air-dried, sieved through a 2-mm mesh, and analysed by wet digestion to determine soil organic matter (Porta et al. 1986), total soil nitrogen (N) by Kjeldahl analysis in a semi-automatic analyser (Velp Científica s.r.l., Italia) and soluble phosphorus (P) extracted by the Watanabe & Olsen (1965) method and measured by colorimetry with a spectrophotometer (Bausch & Lomb, Rochester, NY, USA).

Juvenile transplants and adult mortality

We tested seedling survival in five microhabitats: under isolated adult juniper shrubs, under isolated adult lentisc shrubs, under clumps, in bare soil on the top of the dune (gaps) and in bare soil in dune slacks. One-year-old juniper and lentisc seedlings were transplanted in December 2002 ($n = 20\text{-}36$ seedlings per species and microhabitat). Plants were watered once with 0.25 L and survival was monitored for two growing seasons. Plants that died within the first month ($< 1\%$) were excluded from analyses. We also selected an 11-ha plot in the field site, identified each mature juniper and lentisc plant and recorded if it was dead or alive. Mature individuals selected for other measurements were inside this 11-ha plot.

Adult physiological status

We monitored the physiological status of adult shrubs ($n = 6$ per species and situation) in February, March, July, October and December between July 2000 and December 2002. Pre-dawn water potential (ψ) was determined on terminal shoots using a pressure chamber (SKPM 1400, Skye Instruments Ltd., Llandrindod Wells, UK). Pre-dawn relative water content (*RWC*) was calculated following Barrs & Weatherley (1962). Maximum photochemical efficiency of photosystem II (F_v/F_m) was measured at dawn with a portable fluorimeter (PEA, Hansatech, Kings Lynn, UK) in leaves previously dark-adapted for 30 min. Early in the morning (7:00-8:30 solar time) we measured leaf conductance to water va-

pour (*gs*) and daily maximum photosynthesis (*A*) on mature, fully sunlit leaves or green twigs at a similar height ($\sim 1.2 \text{ m}$). Measurements were performed using a portable infrared gas analyser (LCi; Analytical Development Co. Ltd., Hoddesdon, UK) under ambient CO_2 concentrations; results were expressed on a projected leaf area basis, obtained from scanned images of leaves or twigs using an image area analyser (Midebmp, Almería, Spain). For juniper, we used Cregg's (1992) correction for cylindrical leaves/twigs.

Growth and reproductive effort

In 2002 we measured growth of new shoots on mature plants of both species growing alone or with the other species ($n = 9$ growing in each situation; six of these were used for the physiological determinations described in the previous section). At the beginning of the growing season (January for juniper, April for lentisc), we marked the base of five growing terminal twigs on each aspect at a similar height in the canopy ($\sim 1.5 \text{ m}$) in each plant. We harvested one twig on five different dates, the first being when twigs were marked (January for juniper, September for lentisc) then in April, June, July and December for both species. All twigs were dried at 70°C for 72 h and weighed.

In September 2000, 2001 and 2002, we measured fruit production per volume of canopy in the same shrubs as measured above ($n = 9$). A rigid 0.04 m^2 quadrat was randomly placed at each cardinal aspect of the canopy and the number of fruits in the column underneath the quadrat, the column height and its distance to the main trunk were recorded.

In August (juniper) and November (lentisc) each year we collected 30 ripe fruits per individual plant and randomly selected 10 undamaged fruits to obtain fresh mass; we then extracted the seeds. These seeds and another 10 fruits were labelled and placed in an oven for 72 h at 70°C to obtain seed and fruit dry mass.

Statistical analyses

Mortality of mature plants in each situation (isolated versus clump) was tested by χ^2 . Seedling survival was analysed by binary logistic regressions. Status (alive or dead) was considered the response variable, and species and situation the predictor variables.

Physiological data, reproductive effort and growth of adult plants were tested by ANOVA at a

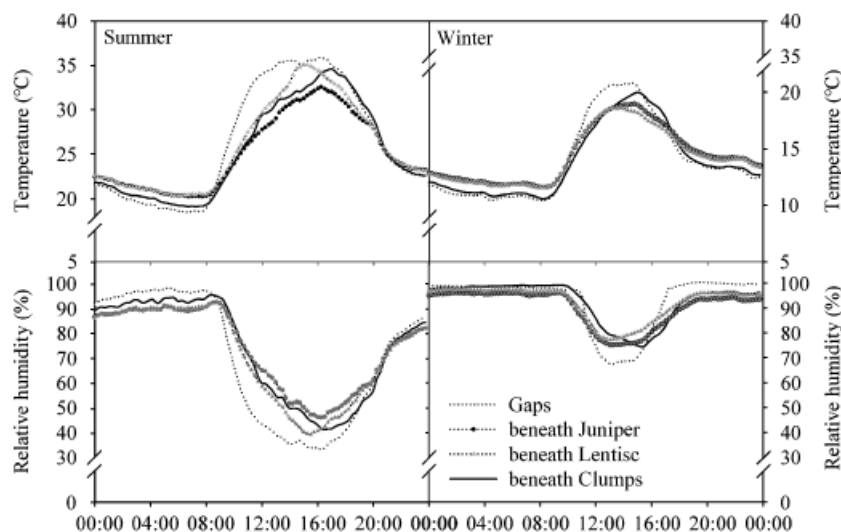


Fig. 1. Air temperature and relative humidity beneath vegetation canopies and in gaps in August and December 2002 (mean values; $n = 3$, measured on 10 sunny days).

Table 1. Soil properties of gaps and under juniper, lentisc and plants of both species growing together (mean \pm 1 SE; $n = 9$, except soil conductivity and pH where $n = 5$). Values in the same line with different letters are significantly different at $P < 0.05$.

	Gap	Juniper	Lentisc	Clump
pH	7.69 \pm 0.05 ^a	7.36 \pm 0.04 ^b	7.46 \pm 0.07 ^{ab}	7.50 \pm 0.07 ^{ab}
Soil conductivity (dS m ⁻¹)	0.36 \pm 0.04 ^a	2.34 \pm 0.15 ^b	1.13 \pm 0.08 ^c	1.67 \pm 0.10 ^d
Organic matter (mg g ⁻¹)	3.80 \pm 2.1 ^a	34.23 \pm 4.63 ^b	15.88 \pm 2.08 ^c	33.98 \pm 2.88 ^b
Nitrogen (mg g ⁻¹)	0.21 \pm 0.07 ^a	0.66 \pm 0.08 ^b	0.29 \pm 0.04 ^a	0.88 \pm 0.06 ^b
Phosphorus (μ g g ⁻¹)	2.12 \pm 0.63 ^a	5.74 \pm 0.65 ^b	5.21 \pm 0.46 ^{ab}	10.27 \pm 1.42 ^c

significance of 0.05. One-way ANOVA was used for individual measurements, and MANOVA or RMANOVA for time-repeated measurements. We checked the homogeneity of variances using Levene's test, evaluated the homogeneity of variances/covariances matrices with the Box M test and checked the sphericity and compound symmetry prior to performing RMANOVA. Post-hoc differences were examined with Scheffé's tests. Differences in fruit production between isolated plants and plants growing in clumps were tested using a Generalized Linear Model with a Poisson distribution.

Data were analysed with the SPSS 12.0 software (SPSS Inc., Chicago, IL, USA). Results are presented as mean values \pm 1 SE throughout the text.

Results

Microclimate and soil properties

Microclimatic conditions were less severe beneath plant canopies than in gaps, with differences

of up to 12°C in summer. Mean and maximum temperatures were lower under juniper than in gaps ($F_{1,23} = 3.2$ and 9.1, mean and maximum values, respectively; $P < 0.05$, Fig. 1), with the other microhabitats being intermediate. Juniper has a thicker canopy than lentisc, leading to slightly lower temperatures and higher relative humidity beneath juniper during summer ($P < 0.07$). In winter there were no significant differences among shrub microhabitats.

In this dune system soils are neutral or slightly alkaline, and low in organic matter and nutrients, especially soluble phosphorus (Table 1). Surprisingly, dune soils have very low salinity in contrast to dune slacks (0.4 versus 8.0 dS m⁻¹), suggesting that salt is washed out from the top of the dune. The presence of shrubs strongly modified soil properties, increasing organic matter (OM) by five- to 10-fold as well as increasing nutrient content and salinity compared with gaps. The two species modified soil in different ways. Soils under juniper had double the OM and N content and almost double the salinity of soils under lentisc, while nutrient content under clumps had the highest values for these variables (Table 1).

Seedling survival and adult mortality

Survival of transplanted seedlings was very different and dependent on microhabitat ($\chi^2 = 22.5$ for lentisc and 69.8 for juniper; $df = 4$, $P < 0.001$). Lentisc survival was highest beneath juniper (70%) and in dune slacks (60%) and lowest (10%) in gaps (Fig. 2a). Two years after planting, nearly all juniper seedlings in dune slacks and gaps had died, while survival rates beneath canopies were high, especially in clumps (73%, Fig. 2a). More than half the junipers planted in these salty dune slacks, despite the higher water availability, while lentisc seedlings are more tolerant.

A total of 658 lentisc and 1603 juniper mature individuals were recorded in the 11-ha plot. The number of juniper and lentisc individuals in clumps was 1.7- and 6.6-times greater, respectively, than isolated individuals (1001 versus 602 plants for juniper; 572 versus 86 plants for lentisc, $\chi^2 = 99.3$ and 359.0, respectively, $df = 1$, $P < 0.001$ in both cases). There were dead individuals of both species in at least 25% of the clumps. The incidence of dead junipers in clumps was almost eight-times higher than dead isolated juniper, whereas in lentisc the proportion of dead individuals was similar in both situations (Fig. 2b). The frequency of dead junipers in clumps increased with the number of lentisc and other shrub species in the clump (data not shown).

Adult physiological status

Water relations and overall physiological responses of juniper were highly dependent on rainfall regime and position, with seasonal ups and downs, whereas the responses were less affected in lentisc (Fig. 3, Table 2, Appendix S2). Overall, juniper water potentials were much lower than those of lentisc, and even in periods of high water availability, the water potentials in juniper were twice as negative as in lentisc (e.g. -0.4 to -0.8 MPa in juniper versus -0.1 to -0.5 MPa in lentisc). Only in December 2002 were the values similar in both species (around -0.5 MPa). Generally, junipers reflected summer water shortage by lowering water potentials below -8.0 MPa, whereas lentisc did not seem to be affected by water deficits even in periods of strong drought when water potentials were above -2.2 MPa (Fig. 3).

Juniper individuals growing with lentisc consistently had more negative water potentials than isolated individuals, especially in the dry season (Fig. 3, Table 2). Their low ψ in summer and fast recovery after autumn rains suggest that junipers mainly used rainwater stored in the dune profile. By contrast, the ψ of isolated lentiscs only occasionally differed from those of lentiscs growing with juniper, when isolated plants had slightly higher ψ (Fig. 3, Table 2).

Gas exchange rates in lentisc were higher than in juniper (Fig. 4), a difference that was more pronounced during periods of water deficit. Overall,

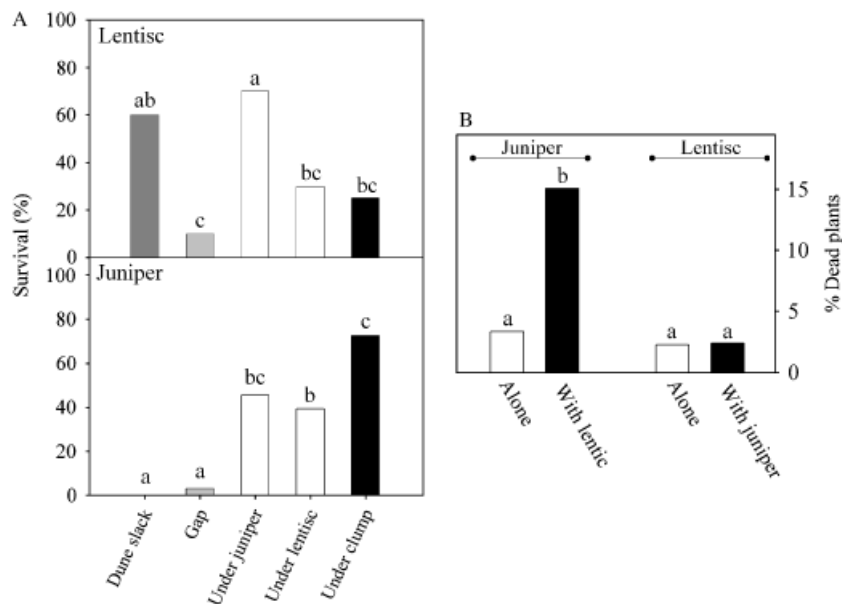


Fig. 2. Seedling survival in different microhabitats (a) and percentage of dead mature individuals that were either growing alone or with the other species (b). Within each panel, bars with different letters are statistically significant at $P < 0.05$.

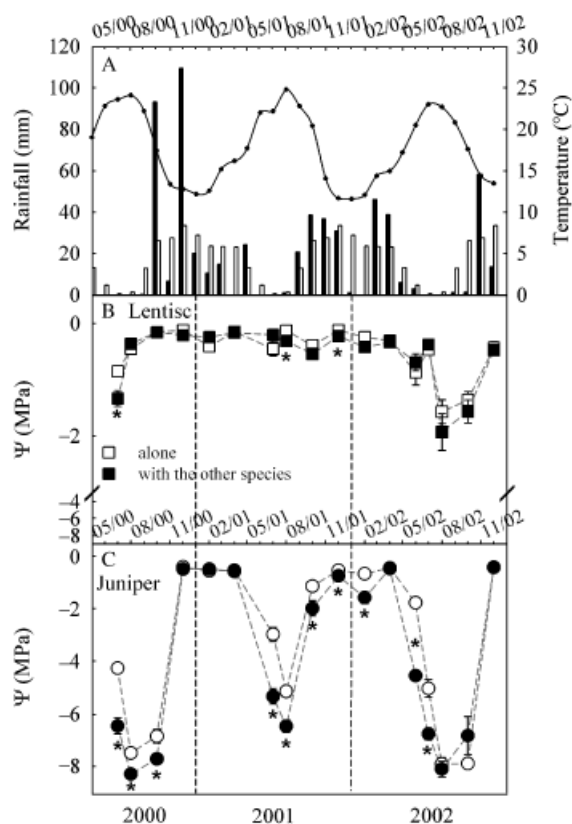


Fig. 3. (a) Monthly precipitation (solid bars) and temperature (line) during the measuring period, and mean monthly rainfall (open bars) over 52 years. (b) Predawn stem water potential of mature lentisc and (c) juniper growing alone or in clumps containing both species (mean \pm 1 SE; error bars only visible if larger than symbol; $n = 6$). Monthly values with an asterisk are significantly different at $P < 0.05$.

seasonal patterns in the two species depended on water availability, especially in juniper, which may cease gas exchange during a prolonged drought period (e.g. October 2002; Fig. 4a).

Differences in g_s between isolated or clumped plants appeared only occasionally, when isolated plants tended to have higher g_s values than those in clumps (Fig. 4a, Table 2). In lentisc, differences in g_s were significant in February (flowering) and October (fruit maturation) but did not depend on rainfall.

Differences in photosynthesis between plants growing alone and in clumps were significant in both species (Table 2). When there were differences, isolated plants had higher A than those in clumps. In juniper, differences occurred mainly at the beginning of the drought season and when the winter months were unusually dry (December 2001 and February 2002, Fig. 4b). Isolated lentisc had slightly

Table 2. F values from MANOVA and significance (*, **, ***, at $P < 0.05$, 0.01, 0.001, respectively, all values in bold; n.s. = non-significant) of differences between individuals growing alone and in clumps for shrubs of juniper (a) and lentisc (b). Variables are stem predawn water potential (ψ_{pd}), stem relative water content (RWC), leaf photosynthesis (A), leaf conductance to water vapour (g_s), predawn photochemical efficiency of PSII (F_v/F_m) and leaf nitrogen pool (N pool). Species were analysed separately.

	a			b		
	JUNIPER			LENTISC		
	2000	2001	2002	2000	2001	2002
Df	$F_{3,8}$	$F_{5,6}$	$F_{5,6}$	$F_{3,8}$	$F_{5,6}$	$F_{5,6}$
ψ_{pd}	19.6***	12.64**	16.19**	7.59**	2.20 ^{n.s.}	0.64 ^{n.s.}
RWC	2.71 ^{n.s.}	10.56**	4.33 ^{n.s.}	0.59 ^{n.s.}	13.91*	7.60*
g_s	0.50 ^{n.s.}	1.56 ^{n.s.}	3.60 ^{n.s.}	1.08 ^{n.s.}	1.77 ^{n.s.}	3.13 ^{n.s.}
A	36.60***	7.84*	43.00**	1.29 ^{n.s.}	5.22*	5.79*
F_v/F_m	10.42**	1.32 ^{n.s.}	1.05 ^{n.s.}	2.02 ^{n.s.}	6.79*	3.82 ^{n.s.}

higher A than those in clumps, but significant differences occurred once in 2001 (Table 2) or when the drought season was unusually long (2002, Fig. 4b).

In periods of high water availability, both species had values of photochemical efficiency of PSII (F_v/F_m) around 0.81 (Fig. 4c), which is close to the ecological optimum (sensu Maxwell & Johnson 2000). Again, the main differences in F_v/F_m values between species appeared during periods of water deficit. While F_v/F_m values were generally above 0.73 in lentisc, in juniper they were as low as 0.45–0.50 in August and October 2002. Compared to other physiological measures, F_v/F_m values in juniper were relatively steady, decreasing only when water stress was high. At this time, significant differences between solitary junipers and those in clumps did occur. Lentiscs growing in clumps had slightly higher values of F_v/F_m than those solitary individuals, but differences were significant only in 2001 (Table 2) and were unrelated to water status (Fig. 4c versus Fig. 3, Appendix S2).

Growth and reproductive output

Twig growth in mature junipers was higher in isolated plants than in clumps, with heavier twigs by the end of the growing season in clumps (0.60 ± 0.04 versus 0.48 ± 0.03 g in isolated and in clumps, respectively; $F_{1,15} = 6.11$, $P < 0.03$). There were no differences in twig growth in lentisc (2.10 ± 0.12 g, average twig mass of lentisc at the end of the growing season; $F_{1,17} = 1.12$, $P = 0.29$).

Fruit production varied substantially with year in both species, and between isolated plants and

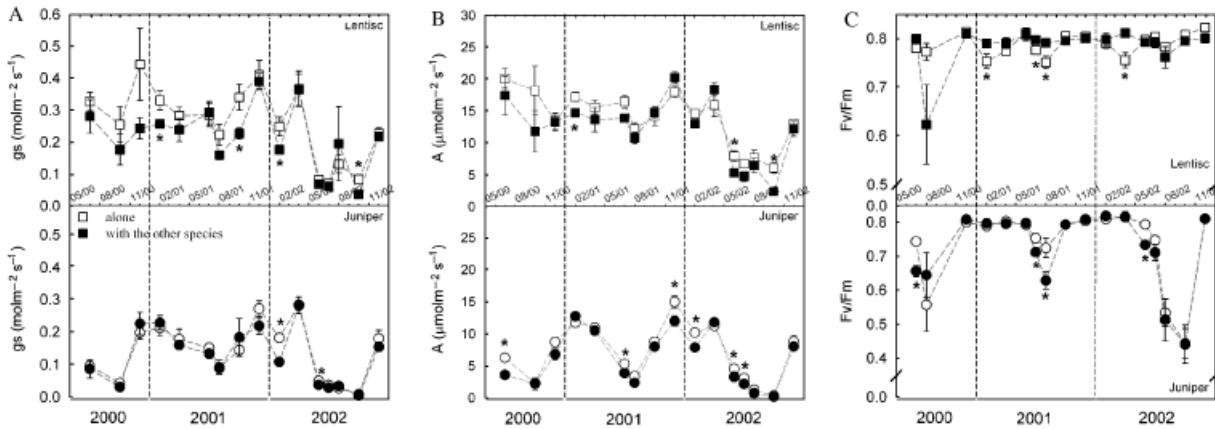


Fig. 4. Conductance to water vapour (a); photosynthesis (b) and predawn photochemical efficiency of photosystem II (c) of leaves of mature lentisc and juniper growing alone or in clumps containing both species (mean \pm 1 SE; error bars only visible if larger than symbol; $n = 6$). Monthly values with an asterisk are significantly different at $P < 0.05$.

Table 3. Number of fruit per m^3 of canopy, fruit and seed dry mass (fresh mass for lentisc) and seed number per fruit (mean \pm 1 SE; $n = 9$) for juniper and lentisc. Numbers with different letters in the “Mean” column indicate significant differences among years at $P < 0.05$. P values result from comparison within each year between plants growing alone or in clumps. Values in bold indicate significant differences between treatments at $P < 0.05$.

	Year	JUNIPER				LENTISC			
		Mean	Alone	Clumps	P	Mean	Alone	Clumps	P
Fruit number per volume of canopy (m^3)	2000	–	–	–	–	4792 \pm 903 ^a	5926 \pm 1462	3657 \pm 995	0.00
	2001	471 \pm 271 ^a	868 \pm 520	75 \pm 37	0.00	–	–	–	–
	2002	730 \pm 97 ^b	915 \pm 161	544 \pm 71	0.00	16 541 \pm 1842 ^b	15 494 \pm 1446	17 588 \pm 3484	0.00
Fruit mass (g)	2000	0.36 \pm 0.02 ^a	0.39 \pm 0.02	0.33 \pm 0.03	0.08	57.66 \pm 3.49 ^a	58.80 \pm 5.66	56.52 \pm 4.50	0.76
	2001	0.40 \pm 0.03 ^a	0.47 \pm 0.03	0.33 \pm 0.02	0.01	64.16 \pm 2.58 ^a	66.94 \pm 4.51	61.39 \pm 2.43	0.30
	2002	0.42 \pm 0.03 ^a	0.44 \pm 0.05	0.40 \pm 0.02	0.65	63.89 \pm 2.67 ^a	66.81 \pm 3.25	60.97 \pm 4.18	0.29
Seed dry mass (mg)	2000	20.03 \pm 1.17 ^{ab}	22.62 \pm 1.32	17.43 \pm 1.41	0.02	13.96 \pm 1.10 ^a	12.64 \pm 0.90	15.27 \pm 1.96	0.27
	2001	17.88 \pm 1.24 ^a	20.52 \pm 1.93	15.24 \pm 0.74	0.02	12.32 \pm 0.32 ^a	12.47 \pm 0.40	12.18 \pm 0.52	0.63
	2002	21.46 \pm 1.26 ^b	25.32 \pm 1.22	17.59 \pm 0.63	0.00	16.94 \pm 0.85 ^b	17.31 \pm 1.01	16.56 \pm 1.43	0.60
Seed number per fruit	2000	4.51 \pm 0.22 ^a	4.41 \pm 0.39	4.60 \pm 0.23	0.69	–	–	–	–
	2001	5.61 \pm 0.17 ^b	5.73 \pm 0.33	5.49 \pm 0.14	0.50	–	–	–	–
	2002	5.70 \pm 0.26 ^b	5.71 \pm 0.41	5.69 \pm 0.35	0.96	–	–	–	–

those growing in clumps (Table 3). In juniper, isolated plants always produced more fruits than those in clumps, whereas for lentisc fruit production depended on the year (Table 3). Overall, fruit dry mass and seed dry mass were clearly higher in isolated juniper than in clumps, while the mean number of seeds per fruit was similar. In 2002, seed mass of lentisc was significantly higher than in the other 2 years (Table 3).

Discussion

Here, we have shown that plant interactions in an arid environment are very dynamic and strongly affect the physiological responses of the species involved and thereby their population dynamics. Our results revealed strong bi-directional interactions between juniper and lentisc, showing measurable

variations on a seasonal scale, with a net balance that changed in sign with increasing plant development. While mature individuals of either species facilitated the survival of seedlings of the opposite species, physiological and productivity responses in adults point to asymmetric competition, lentisc being the stronger competitor. Their interaction negatively affected the physiological status, growth and reproductive effort of juniper and contributed to its mortality. Overall, the interactions between the two species had an important bearing on community structure and dynamics.

Seedling stage: nurse effect of adults and mechanisms controlling seedling survival

The two species showed differential survival rates among microhabitats but, overall, survival on the top of dunes was mainly confined to the under-

storey of adult plants that acted as nurses. As adult shrubs form multi-stemmed canopies lying on or emerging from the soil surface, they act as effective protection against wind and its consequences – increased transpiration, burial by sand or uprooting of seedlings (Holmgren et al. 1997; Perumal & Maun 2006). Shade may be another factor responsible for enhanced seedling survival under shrubs. In these particular environments, plants growing in open areas are subject to potentially lethal soil temperatures and intense water loss by transpiration and evaporation (Shumway 2000; Flores & Jurado 2003). Shading by shrubs reduces soil water evaporation and decreases thermal stress and transpiration in understory plants (Moro et al. 1997; Domingo et al. 1999; Pugnaire et al. 2004), although shrubs may also impair the performance of understory plants through competition for water (Fowler 1986; Casper & Jackson 1997) or by reducing light availability (Holmgren et al. 1997; Valladares & Pearcy 2002). However, overall, our results show that the positive effects of shrubs on seedlings offset the negative effects of competition for water or light.

Survival of juniper seedlings was enhanced beneath shrubs, especially under clumps and juniper compared to gaps on bare dune tops, while their survival was inhibited in dune slacks. Soil beneath clumps was particularly high in P, a limiting nutrient in sandy ecosystems (Lammerts et al. 1999; Martínez 2003). Soils under juniper and clumps were also high in N and OM, which are important for securing seedling survival and growth (Shumway 2000; Martínez 2003; Riginos et al. 2005; Armas et al. 2008). In addition, mycorrhizal infections may be more likely beneath shrubs (Moora & Zobel 2009; but see Bashan et al. 2000; Carrillo-García et al. 2002), a factor that may be critical for establishment. In contrast to juniper, lentisc survival seemed to be minimally affected by soil nutrient levels or OM content. The highest survival rates of lentisc seedlings was on dune slacks, which are saturated by salty water all year round, and in the understory of juniper, where summer temperatures and daily thermal amplitudes tend to be lower than elsewhere. Moreover, the litter layer under adult juniper plants is usually thick and dense, whereas it is thinner and sparse under lentisc and clumps (personal observation). The juniper litter layer may reduce water evaporation from soil, thus probably enhancing water availability for seedlings. All these factors suggest that improved water relations and microclimate amelioration are the most important factors for establishment of lentisc in this system, which agrees with previous reports of Verdú & García-Fayos (1996) and

Maestre et al. (2003). On the top of the dunes, microclimatic conditions and soil humidity (data not shown) were improved under juniper, but not lentisc, thus stressing the importance of the nurse effect of juniper over that of lentisc.

Ontogenetic shifts in the interaction. Physiological effects of competition between mature plants

While mature individuals of either species facilitated the survival of seedlings of the opposite species, the effect of the interaction between adults was negative for juniper and almost neutral for lentisc. Our physiological data suggest that mature individuals of the two species competed for water, with very negative consequences for juniper. The water status of juniper clearly governed its physiological status and performance; juniper individuals growing in clumps had lower A and F_v/F_m than those growing in isolation. In addition, junipers growing in clumps produced smaller twigs, fewer fruits and smaller seeds than isolated plants, which again may be a consequence of the long-term competition for water (Venable 1992). Lentisc, in contrast, was virtually unaffected by the presence of juniper. Only occasionally was its water status and photosynthetic rate lower in clumps than in isolated plants, and neither its growth nor its reproductive output was affected by the interaction with juniper.

Adult physiological responses suggest the mechanisms underlying the interaction

The root system of *Juniperus phoenicea* is shallow, with most roots in the top 50 cm of the soil (Martínez García & Rodríguez 1988; Castillo et al. 2002). Juniper ψ values in our field site were similar to those measured by Castillo et al. (2002) in SW Spain, and much lower than those measured in other Mediterranean coastal systems (Berger & Heurteaux 1985). Castillo et al. (2002) and Martínez-Ferri et al. (2000) suggest that this juniper species displays a drought tolerance strategy. They found no daily changes in water potential under severe water deficits, and ψ recovered immediately after rain, as in our site, which is a typical response of shallow-rooted species (Gucci et al. 1997). Juniper probably cannot reach the salty groundwater 6–7 m below the top of a dune. In addition, the high mortality of juniper seedlings and the absence of mature plants in dune slacks suggest that this species does not tolerate salty water, a fact related to its high osmotic potential (around -1.6 MPa, F. I. Pugnaire, unpublished data). Hence, the evidence suggests that

juniper is able to use only rainwater stored in the dunes. Similarly, Muñoz-Reinoso & García Novo (2005) demonstrated that, in another coastal system, Phoenician juniper is mainly confined to sand dunes where rainfall is the only source of water.

Lentisc had completely different behaviour; water potential was always well above -2.2 MPa, although this species has summer values of around -5.0 MPa in other coastal sites (Ain-Lhout et al. 2001; Filella & Peñuelas 2003). *A* and *gs* in lentisc were also, on average, higher in our study site than in other higher rainfall sites (Flexas et al. 2001). In addition, lentisc in our site does not seem to be dependent on rainfall, and only under a long drought period (2002) did the water potential drop slightly, with no effect on gas exchange. This behaviour could be due to the presence of a dual root system, with both surface roots and roots reaching below 5 m (Martínez-García & Rodríguez 1988), and its ability to use salty water (Valentini et al. 1992) because of its low osmotic potential (around -3.0 MPa, Vilagrosa et al. 2003). All these data point to permanent access to the groundwater table in lentisc, which may explain its high and steady physiological performance and its independence of the precipitation regime in this arid environment.

Plant interactions and population dynamics

It has been shown that early-successional nurse species may be replaced by beneficiary species (McAuliffe 1986; Flores-Martínez et al. 1994; Callaway & Walker 1997) that may then later become dominant (Chapin et al. 1994; Gasque & García-Fayos 2004). Although we do not have strong evidence to conclude that juniper is replaced by lentisc on the top of the dunes, the stronger competitive ability of lentisc may contribute to the mortality patterns observed in adult junipers, because there were more dead juniper individuals associated with lentisc than in isolation. This suggests that lentisc has a large impact in the juniper adult population because junipers growing in clumps are probably eventually replaced by lentisc.

In conclusion, plant-plant interactions play a crucial role in the population dynamics of this coastal community. Facilitation by adult plants enhances seedling survival on the top of the dunes. The facilitation effect of juniper on lentisc seedlings may be of special importance because it promotes the formation of patches of both species, which, in turn, enables the establishment of other species in this semiarid coastal community. Mature junipers and lentiscs compete for water, but lentisc seems to be

able to use saline water from the aquifer, while juniper definitely does not. As a result, juniper reflects in its physiology, productivity and mortality patterns the effect of competition with lentisc. Community dynamics in this arid sand dune system seem to be triggered by the facilitation effect of juniper and shaped by the different abilities of the two species to tolerate water salinity and to access the saline water. Plant-plant interactions, which are strongly affected by environmental gradients, are important drivers of the dynamics of this community.

Acknowledgements. We thank the Junta de Andalucía environmental department, and particularly Juan Carlos Nevado, for funding and support. This work was also funded by the Spanish Ministry of Education and Science (grant number RNM2001-1544/GLO). C. A. is supported by an I3P CSIC contract. We thank Olga Corona, Bartolome Manobel and Reyes Tirado for field assistance, and Harriet Whitehead, Juan de Dios Miranda, Francisco M. Padilla, Amy Symstad and two anonymous reviewers for their help with an early draft of this manuscript.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Plant density in stabilized dunes.

Appendix S2. Correlation values (r) between different physiological variables measured in juniper and lentisc.

Supporting Information may be found in the online version of this article.

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Received 5 August 2008;

Accepted 12 December 2008.

Co-ordinating Editor: Amy Symstad