

Ontogenetic shifts in plant–plant interactions in a rare cycad within angiosperm communities

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Abstract Gymnosperms and angiosperms can co-occur within the same habitats but key plant traits are thought to give angiosperms an evolutionary competitive advantage in many ecological settings. We studied ontogenetic changes in competitive and facilitative interactions between a rare gymnosperm (*Dioon sonorensis*, our target species) and different plant and abiotic neighbours (conspecific-cycads, heterospecific-angiosperms, or abiotic-rocks) from 2007 to 2010 in an arid environment of northwestern Mexico. We monitored survival and growth of seedlings, juveniles, and adults of the cycad *Dioon sonorensis* to evaluate how cycad survival and relative height growth rate (RHGR) responded to intra- and interspecific competition, canopy openness, and nearest neighbour. We tested spatial associations among *D. sonorensis* life stages and angiosperm species and measured ontogenetic shifts in cycad shade tolerance. Canopy openness decreased cycad survival while intraspecific competition decreased survival and RHGR during early ontogeny. Seedling survival was higher in association with rocks and heterospecific neighbours where intraspecific competition was lower. Shade tolerance decreased with cycad ontogeny reflecting the spatial association of advanced stages with more open canopies. Interspecific facilitation during early ontogeny of our target species may promote its persistence in spite of increasing interspecific

competition in later stages. We provide empirical support to the long-standing assumption that marginal rocky habitats serve as refugia from angiosperm competition for slow-growing gymnosperms such as cycads. The lack of knowledge of plant–plant interactions in rare or endangered species may hinder developing efficient conservation strategies (e.g. managing for sustained canopy cover), especially under the ongoing land use and climatic changes.

Keywords Competition · Facilitation · Habitat tracking · Tropical dry forest · Water use efficiency

Introduction

The interplay between competitive (negative) and facilitative (positive) interactions among neighbouring plants can have complex effects on the long-term persistence of the interacting species (Callaway and Walker 1997; Goldberg et al. 1999). For example, facilitative interactions can increase species local abundance and extend species regional distributions into less suitable areas (Brooker 2006; Freestone 2006), while competitive interactions may lead to local or regional competitive exclusion of those species that are weak competitors (Choler et al. 2001). Competitive interactions may shift to facilitation with increasing environmental stress [stress gradient hypothesis (Bertness and Callaway 1994; Maestre et al. 2009; Fajardo and McIntire 2011)]. However, the balance between competitive and facilitative interactions may also depend on ontogeny of interacting plants (Goldberg et al. 2001; Schiffers and Tielbörger 2006; Armas and Pugnaire 2009; Soliveres et al. 2010). Facilitation has most often been described as occurring during early stages of plant development when appropriate conditions for germination and early survival may

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require amelioration of physical stress [nurse effect (Niering et al. 1963; McAuliffe 1984)]. In advanced plant life stages, facilitation tends to shift to interspecific or intraspecific competition as the nutritional and space requirements of interacting plants increase (Chapin et al. 1994; Maestre et al. 2001). Plant shade tolerance also tends to change with ontogenetic stage (Givnish 1988; Kitajima 1994; Craine and Reich 2005) and species with high shade tolerance during their early ontogenetic stages are more likely to benefit from facilitation by canopy shade (Gómez-Aparicio et al. 2006).

Competitive or facilitative interactions among plants can strongly affect spatial associations and consequently the structure and dynamics of populations and communities (Tewksbury and Lloyd 2001; McIntire and Fajardo 2009). Spatial patterning of plant communities influences plant survival and growth since spacing between individual plants is related to distribution of resources (Sprugel et al. 2009; Boyden et al. 2012). Spatial association patterns of individual life stages and species can inform us about the underlying mechanisms (e.g. competitive or facilitative interactions) that structure plant populations and communities through their ontogeny (Dovčiak et al. 2001; Comita et al. 2007). Facilitative interactions that ameliorate microclimate (heat and drought stress) are particularly important in arid areas (cf. Tewksbury and Lloyd 2001) where they may play an increasing role in the persistence of rare and endangered species (such as cycads) as regional aridity may become amplified by global climate change.

Cycads are one of the most threatened gymnosperm groups; they evolved ~300 million years ago, became widespread during the Jurassic, and dramatically declined during the mass extinction at the end of the Cretaceous when they contracted to marginal (i.e. rocky or nutrient-poor) habitats where it has been proposed that the competition from the more evolutionary advanced angiosperms was limited (Bond 1989; Norstog and Nicholls 1997; Becker 2000). Cycads usually occur in small isolated populations in tropical and subtropical regions (Donaldson 2003) where their ability to symbiotically fix atmospheric nitrogen provides them with a competitive advantage in marginal rocky habitats over most angiosperms (Vovides 1990; Lindblad and Costa 2002). In addition to limiting competing vegetation, rocks on the ground surface can facilitate seedling establishment by providing suitable microsites, particularly for plant species that are less sensitive to low soil nutrient content (Parker 1989; Peters et al. 2008), such as cycads. Since nurse objects such as rocks do not compete for resources with a facilitated plant, they can have stronger facilitative effects than nurse plants (Munguía-Rosas and Sosa 2008). However, circumstantial evidence suggests that cycad seedling establishment and survival can be facilitated also by tree canopies [including those of angiosperm

species (Pérez-Farrera and Vovides 2004; Pérez-Farrera et al. 2006)], perhaps reflecting a more general trend where evolutionarily modern plant species have been suggested to facilitate ancient (Tertiary) drought-intolerant lineages by creating shaded microsites in comparatively arid contemporary climate (Valiente-Banuet et al. 2006). Thus, the persistence of cycads within the communities dominated by angiosperms may hinge on a subtle interplay between competitive and facilitative interactions and it provides a unique study system to investigate how plant–plant interactions and especially facilitation may lead to species persistence and coexistence.

We studied survival and growth rates of three ontogenetic stages (seedlings, juveniles, and adults) of an endangered cycad, *D. sonorensis*, in its natural habitat at the southern edge of the Sonoran Desert Region over a period of 4 years in order to evaluate how facilitative and competitive interactions may affect the persistence of this apparently declining species (Álvarez-Yépiz et al. 2011). *D. sonorensis* occurs in fragmented low-density populations in northwestern Mexico and its long-term persistence appears to be threatened by small adult population sizes, low-quality habitat, and the combination of low fecundity and poor recruitment (Álvarez-Yépiz et al. 2011). We expected that facilitation and competition at the intra- and interspecific level will vary with ontogeny with contrasting effects on *D. sonorensis* survival and growth. We tested the following two hypotheses:

Hypothesis 1. Facilitation occurs at early ontogeny (seedling stage) when higher canopy shading increases cycad seedling survival and growth rates. These positive effects of shade decline at more advanced cycad life stages when establishment has been assured and stress amelioration is no longer needed.

Hypothesis 2. Abiotic neighbours (rocks) provide both safe microsites that facilitate cycad seedlings as well as refugia from (inter- and intraspecific) competition at later ontogenetic stages; thus all cycad life stages are positively associated with rocks.

Materials and methods

Study species and area

Dioon sonorensis (Zamiaceae; previously known as *Dioon tomasellii* var. *sonorensis*) is an endemic endangered cycad of Mexico (IUCN 2012; SEMARNAT 2002). An estimated total population size of 500–1,000 adult individuals in the wild places it among the rarest plant species in the world but the real number of total individuals and populations is highly uncertain (Donaldson 2003). It occurs only

in central and southern Sonora, in northwestern Mexico, in fragmented low-density populations with a high degree of between-population genetic differentiation (González-Astorga et al. 2008). *D. sonorensis* is a dioecious understory species with stems usually ≤ 2 m tall at maturity. Seed dispersal in *Dioon* species is limited and occurs mainly by gravity and small mammals (Vovides 1990). The longevity of our target species is unknown but is probably similar to that of other *Dioon* species (e.g. *Dioon edule*) which are known to grow very slowly (<0.5 cm year $^{-1}$ on average) and some individuals can reach a considerable age [$>1,000$ years (Vovides 1990)].

The study sites are located in the Sierra de Alamos-Rio Cuchujaqui Biosphere Reserve, a 93,000-ha protected area located at the south of the State of Sonora, Mexico (27°12' to 26°53'N, 109°03' to 108°29'W). The climate is warm, semi-arid with mean annual precipitation of 712 mm and marked seasons; dry season from November to June and wet season from June to October when ~ 80 % of the annual precipitation occurs. The lowest temperatures can dip below freezing in winter, while the highest summer temperatures can be >40 °C, with a mean annual temperature of 24.3 °C (CNA, San Bernardo Meteorological Station). The three main vegetation types are tropical dry forest, oak forest, and pine-oak forest. Elevation ranges from 300 to 1,800 m a.s.l. and shallow lithosols predominate in the mountainous portions of the Biosphere Reserve where steep slopes prevail (INEGI 1985). In this landscape, most *D. sonorensis* populations are restricted to an elevation between 500 and 1,200 m a.s.l. on sheltered steep slopes (10°–50°) near seasonally dry streams (i.e. arroyos).

Data collection and processing

Growth and survival of *D. sonorensis* life stages

We monitored 4 years of annual growth and survival of 214 individuals of *D. sonorensis* in total across three different populations (one large population with >50 adults, and two small populations with <30 adults each). Three 20 \times 20-m permanent monitoring plots were placed within each population to contain ≥ 90 % of all *D. sonorensis* individuals in each population and all individuals within the plots were tagged. Their survival and height growth was measured annually between 2007 and 2010, at the end of each growing season. For all subsequent analyses, we followed a previously used classification of *D. sonorensis* individuals into three life stages based on height and reproductive characteristics: seedlings (<50 cm tall), juveniles (≥ 50 but <100 cm tall), and adults (≥ 100 cm tall). Seedlings included new individuals likely to experience high mortality rates, juveniles included well established, but non-reproductive individuals, and adults were potentially reproductive mature

individuals (Álvarez-Yépez et al. 2011). We calculated relative height growth rate (RHGR) = $\ln(h_2) - \ln(h_1)/(t_2 - t_1)$, where $\ln(h_t)$ is the ln-transformed plant height at time t (Hoffmann and Poorter 2002). We calculated separate competition indices for conspecifics (Hegyi competition index; HCI_{Intra}) and heterospecifics (HCI_{Inter}) to account for their potentially different effects on focal plants (i.e. intra- vs. interspecific competition). Intraspecific and interspecific competition indices were calculated using a density-dependent HCI (Hegyi 1974; Fajardo and McIntire 2011), which takes into account the Euclidean distance between the focal plant (i.e. *D. sonorensis*) and its potential competitors (conspecific or heterospecific) within each local neighbourhood (see “Mapping spatial associations” below) while including the size of the individual competitors relative to the focal plant:

$$HCI_i = \sum_{j \neq i} \left(\frac{h_j/h_i}{D_{ij}} \right)$$

where HCI_i is the HCI for the focal plant i , h_j is the height of the potential competitor j , h_i is the height of the focal plant i , and D_{ij} is the distance between the focal plant i and competitor plant j .

Canopy openness and photosynthetic light curves

To estimate canopy openness directly above each tagged *D. sonorensis* individual, we took a 180° hemispherical (fish-eye) photograph with a digital camera (Nikon Coolpix 4500), equipped with a fish-eye converter, in June and July 2010. The camera was mounted and levelled on a tripod and oriented to geographic north. We calculated canopy openness above each individual plant by analysing the hemispherical photographs with the program Gap Light Analyser (GLA) version 2.0 (Frazer et al. 2000). To construct photosynthetic light response curves, we randomly selected three individual plants per life stage from the large *D. sonorensis* population. Measurements of net CO $_2$ assimilation rates were performed on leaves exposed to solar radiation (one leaf per plant) in August 2011 at ambient temperature and CO $_2$, and varying photosynthetic photon flux densities (PPFD) using an LCpro+ Portable Photosynthesis System (ADC BioScientific, Great Amwell, Hertfordshire, UK). We modelled individual photosynthetic response curves as a function of light (PPFD) using a non-rectangular hyperbola (Cannell and Thornley 1998) and obtained two key photosynthetic traits related to plant shade tolerance [i.e. light compensation point (LCP), and light saturation point (LSP) (Givnish 1988; Kitajima 1994; Craine and Reich 2005)]. LCP and LSP represent physiologically important light-level thresholds in the photosynthetic response curve where CO $_2$ assimilation and respiration rates are in

equilibrium for LCP (zero C gain), and where photosynthesis becomes light saturated for LSP (maximum net C gain).

Mapping spatial associations

To calculate indices of intra- and interspecific competition (see “Data analysis” below), and independently from the other spatial analyses, we established circular neighbourhoods ($n = 214$) centred on each monitored *D. sonorensis* individual from the three studied populations [$r = 4$ m for juveniles and adults; $r = 2$ m for seedlings (cf. Dovčiak et al. 2001)]. These neighbourhood sizes were supported by our spatial point pattern analyses using Ripley’s cross- K for the largest population (see methods below and “Results”). Within each neighbourhood, we measured the distance from its central *D. sonorensis* individual to all woody plants within the neighbourhood and we recorded their identity and height. This included conspecific (all *D. sonorensis* individuals) and heterospecific plants (all angiosperm individuals). The nearest neighbours were identified as the closest plants (conspecific or heterospecific) with diameter at breast height (DBH) ≥ 2.0 cm (basal diameters for conspecifics) or rocks ≥ 20 cm tall. In addition, we established a 100×100 -m plot that completely included the largest *D. sonorensis* population and we fully mapped the spatial locations of all: (1) *D. sonorensis* seedlings, juveniles, and adults ($n = 129$); (2) individuals of other woody species with DBH ≥ 2.0 cm ($n = 1,020$ individuals from 13 species); and (3) rocks ≥ 20 cm tall ($n = 26$). All mapping was performed with accuracy to the nearest centimetre using a Topcon total station (Topcon Positioning Systems, Tokyo).

Data analysis

Models of survival and growth of *D. sonorensis* life stages

We used mixed-effects models to analyse the effects of intraspecific and interspecific competition (HCI_{Intra} , HCI_{Inter}), canopy openness, and nearest neighbour identity (conspecific, heterospecific, rock) on the final survival and RHGR of *D. sonorensis* life stages (seedlings, juveniles, adults). Logistic and linear regression models were used for survival (binomial variable) and RHGR, respectively, with random effects for plots nested within sites and fixed effects for HCI_{Intra} , HCI_{Inter} , canopy openness, and nearest neighbour identity (categorical). For each response variable and life stage (except for adult survival which was $\sim 100\%$), we constructed a set of all 15 possible models using all combinations of the four predictor variables given above. We tested for possible multicollinearity among variables in the full models by estimating the variance inflation factor (VIF; available for general linear models). In all cases, VIF was < 3 , well below the

threshold of $VIF = 5$ which is generally considered to indicate multicollinearity. Pearson correlation among predictor variables was also very low ($r < 0.3$). Therefore, all predictors remained in the full models. All models were run in R (R Development 2009), using the lme4 package for model fitting (Bates and Maechler 2011). We employed an information-theoretic approach for model selection based on Akaike’s information criterion corrected for small sample size (AICc) using the difference in AICc values between a tested model and the model with the lowest AICc ($\Delta AICc$) and Akaike weights (w_i ; the measure of the evidence in favour of model i being the best model based on its proportional likelihood) (Burnham and Anderson 2002). In addition, we compared LCP and LSP among life stages using one-way ANOVA followed by Tukey honest significant difference tests ($\alpha = 0.05$ in both tests).

Spatial association

We studied spatial associations of *D. sonorensis* life stages at a range of scales (every 2 m up to 10 m and thus not just for the nearest neighbours) by analysing the fully mapped large *D. sonorensis* population (100×100 m) using Ripley’s cross- K function, the bivariate form of Ripley’s K -function (Ripley 1979; Goreaud and Pélissier 2003). For two point types distributed in space (e.g. plant stems of different species or life stages or rocks), Ripley’s K -function is given as $K_{12}(h) = \lambda_2^{-1}E$, where λ is the density of events and E is the expected number of points of type 2 within the distance h of an arbitrary point type 1. We tested the null hypothesis of spatial independence between *D. sonorensis* life stages (point type 1) and each of the 13 other woody species (with DBH ≥ 2 cm) and rocks (≥ 20 cm tall) (point type 2) on this site. We square-root transformed the $K(h)$ -function to linearize it, stabilize its variance, and centred its expected value at 0 at all distances h ; this scaled form $[L(h)]$ is easier to interpret than $K(h)$ (Bailey and Gatrell 1995). We performed 1,000 Monte Carlo randomizations to calculate the 95 % upper and lower simulation envelopes for the $L(h)$ function keeping the relative spatial arrangements within point types 1 and 2, but randomly displacing the locations of type 2 relative to type 1 [i.e. toroidal shift (Bailey and Gatrell 1995)]. The observed values of $L(h)$ above the simulated upper envelope indicate a positive spatial association of two point types at distance h ; $L(h)$ function below the lower envelope indicates a negative spatial association; and $L(h)$ within the two simulation envelopes indicates spatial independence of the two point types (Bailey and Gatrell 1995). Spatial point pattern analysis was performed in MATLAB (Mathworks 2009a; Mathworks, USA).

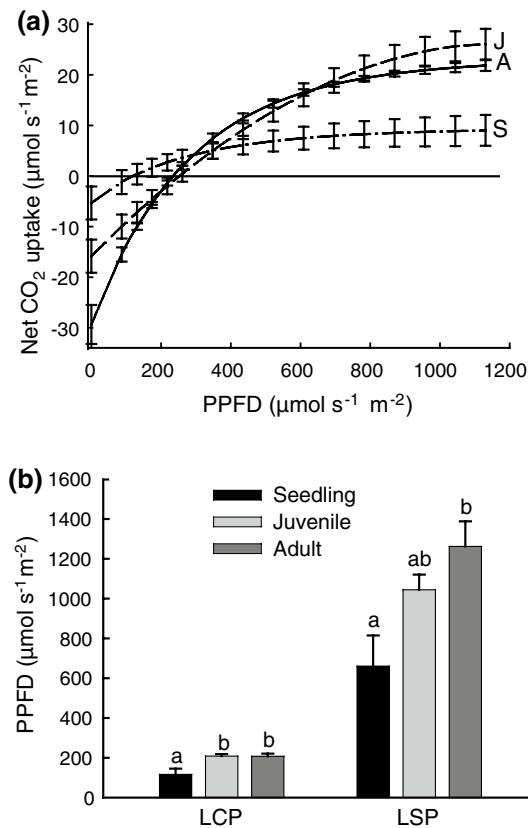


Fig. 1 Variation among life stages in **a** photosynthetic light curves and **b** light compensation (LCP) and light saturation (LSP) points obtained from field measurements of *Dioon sonorensis* individuals in August 2011 (mean \pm SE are shown). **b** Different letters indicate significant differences among life stages with Tukey tests ($P < 0.05$). A Adult, J juvenile, S seedling, PPFD photosynthetic photon flux density

Results

Responses of life stages to light

Advanced *D. sonorensis* life stages were less shade tolerant than seedlings (Fig. 1a, b). Compared to juveniles or adults, seedlings had significantly lower light compensation point (116 ± 29 compared to 208 ± 10 or 207 ± 13 $\mu\text{mol s}^{-1} \text{m}^{-2}$, $F_{2,6} = 7.45$, $P = 0.02$; Fig. 1b). The LSP tended to increase from seedling to adult stage (also suggesting a decrease in shade tolerance with ontogeny). Seedlings and adults differed significantly (660 ± 154 vs. 1262 ± 126 $\mu\text{mol s}^{-1} \text{m}^{-2}$, $F_{2,6} = 6.10$, $P = 0.03$), with juvenile LSP approaching that of adults (Fig. 1b). The response of life stages to light conditions is consistent with the increase in canopy openness above cycad individuals and with the higher frequency of negative associations with angiosperms at advanced ontogenetic stages (compared to seedlings), suggesting an increasing avoidance of interspecific competition at advanced ontogenetic stages.

Effects of neighbours and canopy openness on the performance of the target species

The best model for seedling survival included canopy openness, intraspecific competition and nearest neighbour (Table 1). Seedling survival sharply decreased as intraspecific competition (HCI_{Intra}) and canopy openness increased, and it was lower near conspecific nearest neighbours compared to heterospecific or rock nearest neighbours (Fig. 2a–c). Intraspecific competition was driven by same-cohort (i.e. seedling) aggregation, at short distances (fine scales)

Table 1 Top three candidate models for survival and relative height growth rate (RHGR) for each life stage

Survival was not modelled for adult *Dioon sonorensis* because it was constant (100 %). Best model was ranked by Akaike weights (w_i)

AICc Akaike information criterion corrected for small sample size, ΔAICc differences in AICc values between the individual models and the best model, R^2 explained deviance, CO canopy openness, HCI_{Intra} intraspecific Hegyi competition index, HCI_{Inter} interspecific HCl, NN nearest neighbour (conspecific, heterospecific, or rock)

Response and life stage	Model rank	Parameters	AICc	ΔAICc	w_i	R^2
Survival						
Seedling	1	HCI_{Intra} , CO, NN	68.39	0	0.93	0.36
	2	HCI_{Intra} , CO	75.63	7.2	0.02	0.22
	3	HCI_{Intra} , HCI_{Inter} , CO	75.74	7.3	0.02	0.25
Juvenile	1	HCI_{Inter}	40.73	0	0.45	0.10
	2	HCI_{Intra} , HCI_{Inter}	43.49	2.8	0.11	0.10
	3	HCI_{Intra} , NN	44.01	3.3	0.09	0.14
RHGR						
Seedling	1	HCI_{Intra}	-72.96	0	0.99	0.38
	2	HCI_{Intra} , CO	-61.99	11.0	0.00	0.38
	3	HCI_{Intra} , NN	-58.81	14.2	0.00	0.38
Juvenile	1	HCI_{Inter}	-148.03	0	0.93	0.05
	2	HCI_{Intra}	-141.56	6.5	0.03	0.02
	3	CO	-140.36	7.7	0.02	0.01
Adult	1	HCI_{Inter}	-198.45	0	0.70	0.01
	2	NN	-191.57	2.6	0.19	0.01
	3	CO	-194.51	3.9	0.09	0.01

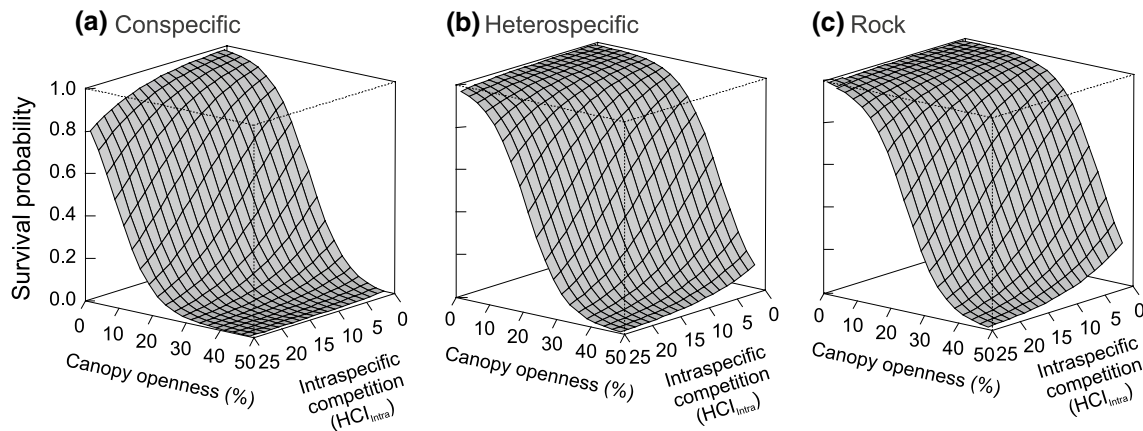


Fig. 2 Predicted seedling survival probability as a function of canopy openness (%), intraspecific Hegyi competition index (HCl_{intra}), and nearest neighbour (categorical), for three neighbour categories: **a** con-

specific, **b** heterospecific and **c** rock. Model specifications are given in Table 1 (best model for seedling survival)

while canopy openness (inverse of canopy shading; unaffected by short seedlings) represented a broader-scale measure of overall canopy effects on seedlings. Compared to seedlings associated with conspecific neighbours, the odds of surviving were about nine times greater for seedlings associated with heterospecifics and 17 times greater for seedlings associated with rocks (cf. Fig. 2a–c). Seedling growth (RHGR) was also negatively affected by intraspecific competition, which was the single most important variable in the best model of seedling growth (Table 1). In contrast, interspecific (not intraspecific) competition was the only explanatory factor in the best model for juvenile survival and juvenile and adult growth (RHGR; Table 1). The negative effect of intraspecific competition at early ontogeny (seedling stage) thus shifted to the negative effects of interspecific competition with other species at later ontogenetic stages; however, the effects of interspecific competition were weaker as suggested by the low explanatory power of models dealing with RHGR in juveniles and adults (Table 1).

Spatial interactions of life stages

In the large fully mapped population, *D. sonorensis* seedlings and juveniles were positively associated with conspecific adults (at all distances examined; Fig. 3a), but the only consistent positive heterospecific associations were with the endemic evergreen palm *Brahea aculeata* (out of 13 species present and tested; Fig. 3b). The associations of juvenile and adult *D. sonorensis* with the palm were weaker compared to those of seedlings, especially at fine spatial scales (<2–4 m; Fig. 3b). All *D. sonorensis* life stages were negatively spatially associated with the legume *Lysiloma watsonii* (Fig. 3c) and *Bursera stenophylla* (data not shown) at spatial scales <10 m, and juvenile and adult

stages showed additional spatial repulsion from other three drought-deciduous species (*Acacia pennatula*, *Diphysa suberosa*, and *Eysenhardtia orthocarpa*; data not shown). The higher frequency of negative associations in advanced ontogenetic stages compared to seedlings is consistent with the expected increase in interspecific competition with ontogeny. Positive spatial associations with the palm *B. aculeata* at short distances observed in seedlings but not in advanced ontogenetic stages (Fig. 4b) are consistent with the facilitative effects at the seedling stage. Positive fine-scale spatial associations with rocks were maintained throughout all *D. sonorensis* life stages (Fig. 3d) as we hypothesized.

Discussion

In this study we used a suite of spatial, demographic and physiological approaches to assess the co-occurrence between different ontogenetic stages of a rare cycad and its neighbours. Several previous studies have addressed ontogenetic shifts on plant–plant interactions within semi-arid environments before (e.g. Miriti 2006; Armas and Pugnaire 2009; Soliveres et al. 2010). However, our study links the fate of these different ontogenetic stages with their shade-tolerance and with the presence of different biotic (intra- and inter-specific) and abiotic (rocks) nurses, and moreover it deals with a rare endemic species of high conservation concern.

Several lines of evidence from our study support hypothesis 1 that canopy shading can facilitate the initial cycad seedling survival. First, shade tolerance in cycad seedlings was higher compared to that in juveniles and adults, suggesting that the shade-tolerant seedlings could benefit from the positive facilitative effects of nurse-plant associations

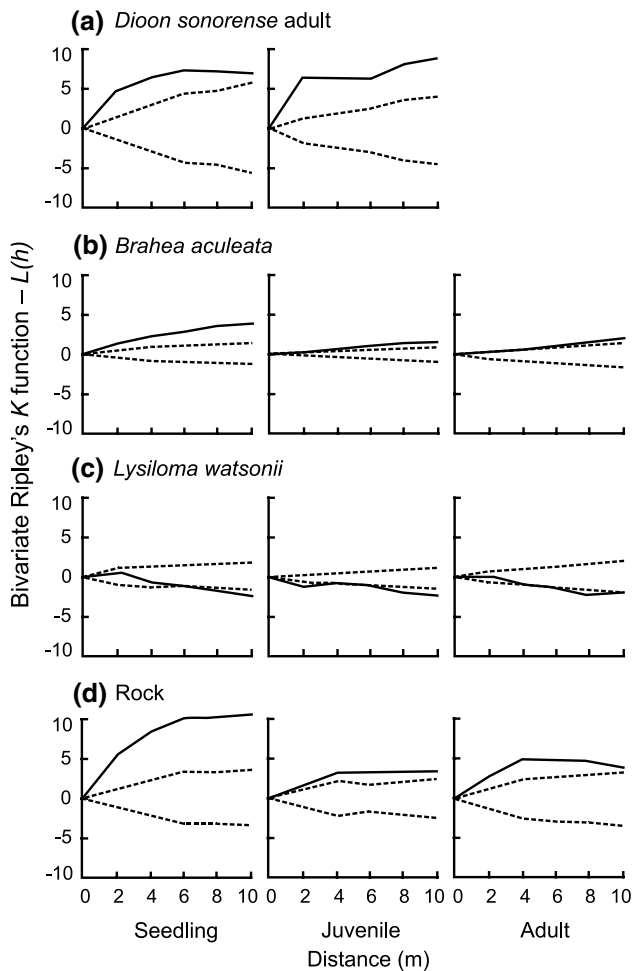


Fig. 3 Scale-dependent spatial associations of *D. sonorensis* life stages with **a** conspecific adults, **b** evergreen palm *Brahea aculeata*, **c** legume *Lysiloma watsonii*, and **d** rocks in the largest *D. sonorensis* population studied in northwestern Mexico. $L(h)$ function (solid line) relative to the 95 % random simulation envelope (dashed lines). $L(h)$ above the simulation envelope indicates positive spatial association, $L(h)$ within the simulation envelope indicates random association, and $L(h)$ below the simulation envelope indicates negative association

while tolerating the negative effects of canopy shading that can affect the distribution of advanced ontogenetic stages (Gómez-Aparicio et al. 2006). Shade-tolerant plants can survive and grow even in low light conditions under conspecific or heterospecific canopies (Walters and Reich 1996) and canopy shading (a proxy for many correlated microclimatic variables) seems to drive positive plant–plant associations in arid environments (McAuliffe 1984; Valiente-Banuet and Ezcurra 1991; Tewksbury and Lloyd 2001). Second, the importance of facilitation of *D. sonorensis* during the initial ontogenetic (seedling) stage is further strengthened by our analyses of spatial patterns of natural populations of this species; *D. sonorensis* seedlings were strongly positively spatially associated particularly

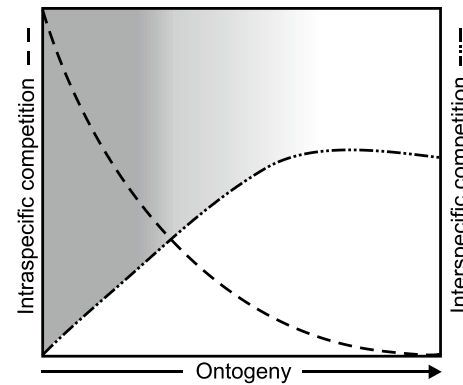


Fig. 4 Simplified conceptual model of ontogenetic shifts in plant–plant interactions in the rare long-lived cycad *D. sonorensis*. Intraspecific competition is largest in the seedling stage and it declines asymptotically with ontogeny following an inverse- J curve especially in sheltered microsites densely colonized by cycad seedlings. Interspecific competition gradually asymptotically increases as seedlings recruit into more advanced stages. The initial importance of facilitation (shaded area) by angiosperms is overridden by interspecific competition as ontogeny progresses

with evergreen plants (i.e. *B. aculeata* and conspecific adults) which provide shading during the most stressful time of the year—the dry season when the predominant drought-deciduous canopy provides little protection against solar radiation. A similarly high nurse-effect potential of an endemic evergreen palm species has been documented also in arid environments in India where the diversity of woody plant species was enhanced due to abiotic amelioration by a persistent canopy (Kinhil and Parthasarathy 2010). It is noteworthy that *B. aculeata* and *D. sonorensis* were the only evergreen species present in our study sites, which suggests that drought-deciduous species are unable to provide a comparable degree of shading during the dry season when most seedlings succumb to drought due to increased water stress (see McDowell et al. 2008). Third, and most important, our models of cycad seedling survival suggested that seedlings survived better under shaded conditions, probably due to amelioration of physical stress. For example, seedling survival probability was negligible at canopy openness >40 % while seedling survival was 80–100 % on average under more shaded conditions).

In a related study, cycad seedlings exhibited a considerably lower water use efficiency compared to juveniles and adults, especially during the dry season when seedling average net C assimilation was negative (Álvarez-Yépiz et al., unpublished data). Cycad juveniles and adults can produce more sclerophyllous leaves with waxy coatings that are more resistant to mechanical damage and drought compared to new seedlings (Nobel 2009; Lopez Bujanda et al., unpublished data). Dense shade ameliorates drought especially among drought-intolerant and shade-tolerant

plants (Holmgren et al. 2012), two major characteristics of *D. sonorensis* seedlings. Thus, multiple lines of evidence suggest that seedlings exhibit a drought-avoidance strategy (via facilitation) as opposed to a drought-tolerance strategy of advanced life stages such as juveniles and adults. Similar effects of canopy shade on the survival and recruitment of seedlings have been suggested for both cacti and trees in arid or semiarid environments (e.g. deserts or drought-prone grasslands) where high solar radiation combined with low soil moisture can lead to heat and water stress (e.g. Turner et al. 1966; Dovčiak et al. 2005). In addition to the well-documented case of the saguaro-nurse association (Niering et al. 1963; Turner et al. 1966; McAuliffe 1984), our study suggests that facilitation may be an important mechanism that promotes the persistence of slow-growing long-lived plant species in stressful arid environments (such as the Sonoran Desert Region).

D. sonorensis individuals were strongly and positively associated with rocks in all life stages, consistent with our hypothesis 2 that rocks provide safe microsites for both seedling establishment and their recruitment into more advanced ontogenetic stages. Recent studies have shown that abiotic elements such as rocks can act as nurse objects by ameliorating microclimatic conditions and acting as seed traps (Munguía-Rosas and Sosa 2008; Peters et al. 2008). In addition, rocks in our study system seem to be important in structuring competitive and facilitative environments by affecting levels of plant competition. In our study, only rocks provided microsites with low competition at the intra- and inter-specific levels. At the population level, *D. sonorensis* and other cycad species seem mostly restricted to sheltered steep slopes near seasonally dry streams (Preece et al. 2007; Álvarez-Yépiz et al. 2011). Similarly, at the individual level cycad seedlings appear to recruit in sheltered habitats and microsites that facilitate their survival and represent milder environmental conditions to which they generally appear evolutionarily pre-adapted [viz sheltered and relatively mesic sites (Preece et al. 2007)]. Cycads that occur in arid habitat such as *D. sonorensis* may be possibly tracking the environmental factors such as low heat and drought stress [cf. habitat tracking (Ackerly 2003)], for which they may exhibit narrow physiological tolerances (Marler and Willis 1997; this study), and especially so during the regeneration stage when cycad seedlings are most sensitive to physical stress such as desiccation due to their higher transpiration rates and lower water use efficiency (Álvarez-Yépiz et al., unpublished data).

Seedlings established under the tree canopy shading are inferred to have experienced high levels of intraspecific competition that negatively affected their survival and growth rates. How can the positive effects of canopy shading and the negative effects of competition be reconciled?

Our results suggest that such effects are scale dependent with the latter occurring at short distances (<2 m) and the former over longer distances. Intraspecific competition seems to be driven by same-cohort (i.e. seedling) aggregation while canopy shading represents a more integrative measure (i.e. 360° plant's view) of the influence of taller plants. Seedlings in favourable microsites can compete for resources because they exploit the same niche and might not provide significant shade to one another since they normally have one composite leaf as opposed to multiple composite leaves from *D. sonorensis* juveniles and adults, and from other higher stature plants from different species that ameliorate stress from solar radiation. Limited seed dispersal (such as in cycads) can lead to seedling aggregation over very short distances and thus to particularly high levels of intraspecific competition within the same cohort, which preferentially establish within spatially restricted favourable microsites (Pacala and Levin 1997).

The processes behind *D. sonorensis* persistence and coexistence with the rest of the community can leave strong spatial patterns that can be tracked and linked to spatial analyses, but our methods are correlative and while they might suggest causality they do not demonstrate it. For example, the occurrence of interspecific competition may be due to dispersal limitation, habitat sharing, or the reduction of intraspecific competition with the aging of individuals involved. However, we used a blend of different independent analyses that altogether provided key insights into the mechanisms underlying plant–plant interactions in our target species. In the case of *D. sonorensis*, and considering that dispersal of cycad seeds occurs by gravity or small mammals (Hall and Walter 2013), we identified at least three classes of ‘preferred’ microsites: under the canopy of maternal plants (i.e. the conspecific neighbours), where intraspecific competition is high during the seedling stage due to seedling aggregation; under the canopy of angiosperms such as the palm *B. aculeata* (i.e. the heterospecific neighbour), where intraspecific competition is low but interspecific competition is higher especially at advanced juvenile and adult ontogenetic stages; and next to rocks (i.e. the abiotic neighbours), where competition at the intra- and inter-specific levels is low at all ontogenetic stages.

Ontogenetic shifts in plant–plant interactions: implications for cycad persistence

The strong negative effects of intraspecific competition and the positive effects of facilitation by the overstory canopy on cycad seedling survival and growth during early ontogeny shifted in our study to mainly negative (but weaker) effects of interspecific competition at more advanced juvenile and adult stages. We previously found in a *D. sonorensis* demographic analysis that the combined effect of low

fecundity and seedling recruitment is one of the intrinsic factors threatening the long-term viability of *D. sonorensis* populations (Álvarez-Yépiz et al. 2011). Thus, our previous and present findings taken together suggest that seedling facilitation might be a critical mechanism for cycad species persistence in arid environments. We would like to advance a conceptual model in which cycads such as *D. sonorensis* persist within angiosperm communities due to facilitative effects of the overstory canopy (especially so from evergreen angiosperms) and due to stronger intraspecific than interspecific competition during early ontogeny (Fig. 4). Although facilitation and competition (both intra- and inter-specific) can operate simultaneously, the negative effects of interspecific competition seem to gradually increase with ontogeny and (at least partly) override the initially dominant positive facilitative effects at early ontogenetic stages, in agreement with other studies on interspecific plant–plant interactions (e.g. Miriti 2006; Soliveres et al. 2010). Facilitation through canopy shading reduces heat and drought stress and thus increases seedling survival in arid environments (e.g. Turner et al. 1966) and it can also provide additional avenues of facilitation related to canopy cover such as protection from herbivores or wind and hydraulic lift (Valiente-Banuet and Ezcurra 1991). In advanced ontogeny, the importance of facilitation can be expected to decrease as cycad juveniles and adults have to compete with neighbours for resources such as space and light or simply because establishment has been assured and stress amelioration is no longer needed. We found a progressive decrease in cycad shade tolerance with ontogeny as cycad individuals grew into canopy positions where they experienced spatial disassociation from angiosperms and higher tolerance to desiccation due to lower transpiration rates and higher water use efficiency. Thus, while strong intraspecific competition and facilitation affect early survival and growth, interspecific competition can limit later cycad recruitment to areas such as canopy or rocky refugia where competition tends to be lower (see Runkle 1981; Dovčiak et al. 2003).

Conclusion

For the first time, we documented in detail plant–plant interactions between a cycad (gymnosperm) species and more evolutionarily modern angiosperms. Interspecific facilitation during early (and most sensitive) stages of our target species may promote its persistence in spite of increasing interspecific competition in later life stages. We also provide empirical support to the long-standing assumption that cycads establish in marginal habitats where competition from angiosperms is lower. At the population and individual level, our target species appears to be tracking the sheltered environment for which they exhibit

narrow physiological tolerance (e.g. in transpiration rates and water use efficiency) to avoid heat and drought stress during their regeneration phase but at the cost of higher intraspecific competition during early ontogeny due to seedling aggregation within favourable microsites. Facilitation as a general mechanism promoting the persistence of other cycad species, especially from dry environments, remains to be tested. The lack of knowledge of plant–plant interactions in rare or endangered species may hinder the development of efficient conservation strategies (e.g. managing for persistent canopy cover to increase seedling survival), especially under the ongoing global land use and climatic changes.

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