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ORIGINAL ARTICLE

Interaction between plants growing together from germination to 2 years: A test of competition and phylogenetic closeness for Northeastern Mexico

Interacción entre plantas coexistiendo desde la germinación hasta los 2 años: un experimento de competencia y cercanía filogenética en el noreste de México

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ABSTRACT

Competition and facilitation are important factors affecting seedling survival. These factors probably affect plant distribution and abundance. Interactions between species relate to phylogeny, in that closely related species are likely to compete more for resources and facilitation is expected between more distantly related species. We tested for Tamaulipan thornscrub plants, grown with close and distant relatives if they differed in survival, length and weight of shoots and roots, assuming that closely related species would compete more than distant ones. We also explored whether seed mass was associated with plant size from 1-24 months after germination. We grew plants from Tamaulipan thornscrub, with a sibling or with one individual from other species from 1-24 months. Seedling survival was similar for all species when their seedlings grew alone or under competition, at 1, 6 and 12 months. At 24 months seedling survival of *Vachellia farnesiana* was lower when grown with *Havardia pallens*. There was no evidence of stronger competition or facilitation for phylogenetically closer species. Seedling size correlated with seed mass one month after germination but not after 6 months. Maximum and mean adult plant height did not correlate with seed mass or with plant height in our trials. We found no evidence of phylogeny explaining nearest neighbors in competition during germination for Tamaulipan thornscrub.

Keywords: phylogeny, seed mass, seedling, shoot/root ratio, Tamaulipan thornscrub.

RESUMEN

La competencia y la facilitación son factores importantes que afectan la supervivencia de las plántulas y probablemente afectan la distribución y abundancia de las plantas. Las interacciones entre especies se relacionan con la filogenia, es probable que las especies estrechamente relacionadas compitan más por recursos y que en las menos emparentadas ocurra facilitación. Se investigó si plantas de matorral tamaulipeco creciendo junto a parientes cercanos y lejanos diferían en supervivencia, longitud y peso de tallos y raíces, asumiendo que las especies estrechamente relacionadas competirían más que las lejanas. También se exploró si el peso de semillas se asoció con el tamaño de la planta entre 1 y 24 meses de edad. Se pusieron a crecer plantas de matorral tamaulipeco, con un hermano o con un individuo de otras especies, de 1-24 meses. La supervivencia de plántulas fue similar para todas las especies cuando éstas crecieron solas o en competencia, a los 1, 6 y 12 meses. A los 24 meses, la supervivencia de plántulas de *Vachellia farnesiana* fue menor cuando creció con *Havardia pallens*. No hubo evidencia de una competencia o facilitación fuerte para especies filogenéticamente más cercanas. El tamaño de la plántula se correlacionó con el peso de la semilla únicamente al mes de germinadas. La altura máxima y promedio de la planta adulta no se correlacionó con el peso de semillas o con la altura de la planta. La filogenia no explicó la competencia con los vecinos más cercanos durante la germinación de especies del matorral tamaulipeco.

Palabras clave: filogenia, matorral tamaulipeco, peso de semillas, plántula, proporción vástago/raíz.

INTRODUCTION

Knowledge on seed germination, seedling emergence and growth could help better understand relationships between plant species and their environment (Armas & Pugnaire 2005). This could contribute to predict vegetation dynamics (Scholze *et al.* 2006, Bhadouria *et al.* 2017). Authors usually study such traits separately and only few studies determine effects of competition during germination and seedling establishment (Bhadouria *et al.* 2017).

Seed germination and seedling growth are influenced by environmental triggers (Flores *et al.* 2004), which are in turn affected by other plants, since seeds and seedlings compete for light, water and nutrients with other seedlings as well as with established individuals (Arora & Boer 2006, Purves & Pacala 2008, Xiang & Xiaodong 2014, Melton & Arora 2016). In arid environments with harsh environmental conditions seeds, more often germinate under the canopy of the mother plant, as this is already located in a site compatible with plant growth (Ellner & Shmida 1981). Seeds often germinate near other seedlings of the same or other species (McMurray *et al.* 1997) which often implies competition but also facilitation (Flores & Jurado 2003). Differences in early seedling development could help explain why some species dominate landscapes (Woods *et al.* 2014).

Some studies have found phylogeny to influence plant species distribution and abundance (Lososová 2016). Authors consider phylogenetically closely related species to be ecologically similar (Burns & Strauss 2011) and therefore have similar environmental requirements and be strong competitors (Violle 2011). Distantly related species in turn, promote high plant diversity by reducing competition (Gravel *et al.* 2006, Adler *et al.* 2007, Van der Putten 2009, Valiente-Banuet & Verdú 2013). Both competition and facilitation very likely influence plant distribution and abundance (Goldberg *et al.* 1999). Because closely related species are considered to exploit resources similarly (Schwartz *et al.* 2016), they are expected to compete more strongly than distantly related ones. Since Darwin authors consider phylogeny to affect plant distribution and abundance in that, plants will grow closer to more distantly related species. Some evidence for this has been found for plant species associations in nurse-protégé interactions (Valiente-Banuet & Verdú 2007), but not for nearest neighbors of adult plants (Marroquín *et al.* 2019), or seed germination (Jurado *et al.* 2020).

Some plants allocate more resources to shoots or roots depending on environmental variations and competition (Bush 2008). Competition is likely to be stronger for water than for light in arid and semiarid environments (Noy-Meir 1973), hence competition might promote stronger roots. Competition has caused low numbers of *Prosopis glandulosa* seedlings in environments with high density from grasses and adult trees (Bush & Van Auken 1990).

In here, we aim at determining possible effects of plant competition at the early stages of growth. Response variables were seedling emergence, survival, shoot, and root length and weight for plants grown on their own, competing with a sibling or with a plant from another species from one to 24 months after germination for common woody species of thornscrub.

We also explored for associations of seed mass and plant size, seed mass for instance, has been associated with plant size in that larger plants across species produce heavier seeds (Thompson & Rabinowitz 1989, Aarssen & Eriksson 2005, Rees & Venable 2007, Wright *et al.* 2007) and these produce heavier seedlings Jurado & Westoby 1992. For our species, we tested whether seeds of taller species were heavier and if 1 to 24 months after germination plants of larger seeded species were heavier.

Our hypotheses were: (i) Seedling competition would inhibit seedling survival and growth, resulting in lower survival and lower seedling mass and length, for phylogenetically closer species grown together. (ii) Seedling mass would be correlated with seed mass and with adult plant height at least during the early stages of growth.

MATERIALS AND METHODS

The study site was at the nursery of the School of Forest Sciences from the Universidad Autónoma de Nuevo León close to remnant fragments of native Tamaulipan thornscrub. This vegetation has a closed canopy with about half of the species thorny and about half shedding their leaves, either during the cold or during the dry season (Reid *et al.* 1990, Jiménez *et al.* 2009). The area (24° 47' N; 99° 32' W) is flat with an elevation of 350 m above sea level, a mean annual temperature of 22 °C and a mean rainfall of 805 mm (López-Hernández *et al.* 2013).

We collected seeds from 13 species, *Cordia boissieri* A.DC. and *Ehretia anacua* (Terán & Berland.) I.M. Johnst. (Boraginaceae); *Celtis pallida* Torrey (Cannabaceae); *Ebenopsis ebano* (Berland.) Barneby & J.W.Grimes, *Erythrostemon mexicana* (A.Gray 1861) E. Gagnon & G. P. Lewis 2016, *Havardia pallens* (Berl.) Britton & Rose, *Parkinsonia aculeata* L., *Prosopis laevigata* (Humb. et Bonpl. ex Willd) M.C. Johns, *Senegalia greggii* (A. Gray) Britton & Rose, *Vachellia farnesiana* (L.) Wight et Arn., *Vachellia rigidula* (Benth.) Seigler & Ebinger, and *Vachellia schaffnerii* (S. Watson) Seigler & Ebinger (Fabaceae), and *Condalia hookeri* (Rhamnaceae).

Seeds were collected from at least 20 mother plants, and then mixed, air dried and separated from pods or flesh. We kept seeds at room temperature in paper bags, in the dark for up to 8 weeks until the trials started. Before germination, we scarified seeds with hard teguments and physical dormancy (Martínez *et al.* 2006), with sandpaper in the area next to where the radicle emerges (Flores & Jurado 1998). Only healthy-looking seeds were set to germinate.

We measured and analyzed seedling emergence from the soil, survival, length and weight of shoots and roots in two experiments. For the first experiment seeds from 13 species (Table 1), germinated within the same 24 hours were planted in soil from the region (vertisol) in black plastic bags (1.9 l in volume: 10 cm in diameter by 25 cm deep). Germinated seeds were covered by 0.5 cm of soil. There were 14 treatments. Each germinated seed was planted at the center of the bag, alone or next to a germinated seed of the same species or, to each one of other 12 species. There were ten replicates per treatment; inside each one, plant combinations were randomly allocated. Bags were watered every other day to keep the soil moist. Plants were harvested after 30 days; they were separated from the soil by cutting away the plastic bag and washing out soil under gentle running water over a metal grid. Length of seedlings, shoots and roots were measure to the nearest mm. Roots were manually extended to measure maximum length as bags with soil were often shorter than roots. Harvested plants were set to dry in an oven at 80 °C until constant weight, to determine shoot and root biomass to the nearest 0.001 mg. A similar experiment was run for five legume species (Table 1), in which plant harvesting were measured 6, 12 and 24 months after germination. For this, plastic bags were 20 cm in diameter by 50 cm deep (15.7 l in volume). Plants were watered weekly after the first month. Seedling survival was measured daily for both experiments.

Phylogenetic distance between species (Fig. 1) was determined in millions of years since a common ancestor using Timetree (Kumar *et al.* 2017). To determine if seed mass correlated with plant size at 1, 6, 12 and 24 months after germination, we made correlation analyses using seed mass as the independent variable and length and weight of plants, shoots, and roots as dependent variables. Weight of seeds was obtained from a former study in the region (Jurado *et al.* 2001). Seed mass was tested for correlation with data on maximum plant height from the literature (Estrada *et al.* 2017). Maximum and mean adult plant height were also tested for correlation with height of plants at 1, 6, 12 and 24 months grown on their own.

Statistical analysis

ANOVAs and Tukey tests ($\alpha = 0.05$) were used to determine differences between days to seedling emergence, seedling mass and length. Seedling survival in days was analyzed using Kruskal-Wallis test for equal medians. Spearman correlation analyses ($\alpha=0.05$) were used to determine relationships between seed mass and plant weight and length. We used R 3.4.2 (R Core Team 2017) for statistical analyses.

RESULTS

On average seedling emergence started after four days of planting (Table 1) and did not differ between species ($p > 0.05$). Seedling survival was similar ($P > 0.05$) for all species when their seedlings were grown alone or under competition at 1, 6 and 12 months. At 24 months seedling survival of *Vachellia farnesiana* was lower (10% survival) when grown with *Havardia pallens* than when grown alone or with another *V. farnesiana* seedling (90%) or with other species (80%) ($H(2) = 16.18$, $P < 0.001$).

Table 1. Taxonomic species list and the experiment in which species were used. Length and weight (mean ± standard deviation) of seedlings' roots and shoots one month after germination. Different letters indicate differences between species ($P < 0.05$). Except for the root of *Vachellia schaffnerii* that was shorter (7.0 ± 1.7 cm) growing with *Ebenopsis ebano* than when grown alone or with seedlings from other species (See text for results) there were no differences between treatments. * Data from Jurado *et al.* (2001). ** Data from Estrada *et al.* (2017). / Lista de especies taxonómicas y el experimento en el que se utilizaron las especies. Longitud y peso (media ± desviación estándar) de las raíces y brotes de las plántulas un mes después de la germinación. Letras diferentes indican diferencias entre especies ($P < 0.05$). No hubo diferencias entre tratamientos, excepto por la raíz de *Vachellia schaffnerii* que fue más corta (7.0 ± 1.7 cm) al crecer con *Ebenopsis ebano* que cuando se cultivó sola o con plántulas de otras especies (Ver texto para resultados).

Family Species	**Experiment**	**Shoot length (cm)**	**Root length (cm)**	**Shoot weight (mg)**	**Root weight (mg)**	**Days to emerge**	**Seed weight** (mg)**	**Adult plant max height (cm) ****
Boraginaceae								
Cordia boissieri A.DC.	1	11.1±1.7 a	8.4±0.6 c	0.11±0.32 b	0.06±0.01 a	5.8 a	591.46	800
Ehretia anacua (Terán & Berland.) I.M.Johnst.	1	7.9±2.1 b	8.3±1.1 b	0.03±0.01 c	0.03±0.01 b	4.0 a	67.46	1,500
Cannabaceae								
Celtis pallida Torrey	1	4.1±2.0 c	7.4±2.1 c	0.03±0.04 c	0.07±0.01 a	5.5 a	46.83	500
Fabaceae								
Ebenopsis ebano (Berland.) Barneby & J.W.Grimes	1&2	10.6±0.6 a	16.5±3.4 a	0.20±0.04 a	0.03±0.00 b	4.6 a	597.63	1,200
Erythrostemon mexicana (A.Gray) E. Gagnon & G. P. Lewis	1	11.7±1.4 a	12.6±2.0 b	0.12±0.03 a	0.04±0.03 b	4.7 a	46.83	500
Havardia pallens (Berl.) Britton & Rose	1&2	7.6±1.4 b	12.8±6.0 ab	0.04±0.02 c	0.01±0.01 c	5.4 a	42.79	1,200
Parkinsonia aculeata L., Sp. Pl.	1	11.7±5.2 a	10.4±1.6 b	0.11±0.08 b	0.04±0.03 ab	4.9 a	112.07	700
Prosopis laevigata (Humb. et Bonpl. ex Willd) M.C. Johns	1&2	8.9±2.1 b	10.74±2.1 b	0.05±0.02 c	0.03±0.05 a	4.0 a	54.78	1,300
Senegalia greggii (A. Gray) Britton & Rose	1	12.0±5.3 a	14.0±6.3 ab	0.06±0.02 bc	0.02±0.01 b	4.3 a	63.18	600
Vachellia farnesiana (L.) Wight et Arn.	1&2	10.9±4.3 a	10.4±1.8 b	0.05±0.03 bc	0.05±0.09 a	4.4 a	61.45	700
Vachellia rigidula (Benth.) Seigler & Ebinger	1	6.1±2.8 b	9.8±3.8 b	0.03±0.03 c	0.01±0.01 b	4.9 a	82.06	800
Vachellia schaffnerii (S. Watson) Seigler & Ebinger	1&2	8.6±1.2 ab	9.9±1.8 b	0.06±0.03 bc	0.02±0.02 b	5.6 a	24.97	500
Rhamnaceae								
Condalia hookeri M. C. Johnst	1	8.1±1.4 b	10.1±4.2 b	0.03±0.01 c	0.02±0.02 ab	4.8 a	17.11	600

Between species, root and shoot weight and length varied between species from one to 24 months of growth (Tables 1 - 4). Within treatments, seed length and mass differed at 1, 6, 12 and 24 months for some species, but not following our prediction of greater effect on closely related species.

At one month after germination, seedling weight and length varied between species (Table 1) but not for species within treatments (*P* > 0.05), except for the root of *Vachellia schaffnerii* that was shorter (7.0 ± 1.7 cm) growing with *Ebenopsis ebano* than when grown alone or with seedlings from other species (10.1 ± 1.6 cm) (*P* = 0.031). This result does not coincide with our prediction of greater competition effects on closely related species, as *E. ebano* and *V. schaffnerii* are not closely related (Fig. 1).

Six months after germination, except for *V. schaffnerii*, the length of shoots differed across combinations. Shoots were taller for plants grown alone, in competition with the same and at least one more species (Table 2). For three species (*V. farnesiana*, *V. schaffnerii* and *H. pallens*) roots were longer for plants grown alone, with a conspecific and at least with one other species, but for two species (*E. ebano* and *Prosopis laevigata*) roots had similar length in all combinations (Table 2). For all but one species (*V. schaffnerii*) shoot mass differed between treatments. Shoots were heavier for plants without competition or when grown with a plant from the same species. *Vachellia farnesiana* also had heaviest shoots when grown with *E. ebano* (Table 2), this is perhaps evidence of facilitation. For four species (*V. farnesiana*, *H. pallens*, *E. ebano* and *P. laevigata*) root mass was heavier when grown alone, but for *V. schaffnerii* it was also heavier when grown with a plant from the same and two other species (Table 2).

Shoot and root length and root mass after 12 months from germination, were greater for most species when grown alone and in many cases similar to those of plants grown with a plant from the same or other species. For four species (*V. farnesiana*, *H. pallens*, *E. ebano* and *P. laevigata*), root length was similar across treatments. In no cases, values of shoot and root length or mass were lower for plants grown on their own (Table 3).

At 24 moths, shoot length for *V. farnesiana* was similar across treatments (except when grown with *H. pallens*, for which there was only one replicate surviving). For *V. schaffnerii*, *H. pallens* and *Prosopis laevigata* shoots were shorter when grown with *E. ebano* (Table 4). Shoots of *E. ebano* and *P. laevigata* were taller when grown alone. Shoots of *V. farnesiana* were heavier when grown with *E. ebano*, less so when grown alone and less so, when grown with a plant form the same species and from *V. schaffnerii* and *P. laevigata* (Table 4). Shoots of *V. schaffnerii* were lighter when grown with *E. ebano* and *P. laevigata*. Shoots of *H. pallens* were heavier when grown alone. Shoots of *E. ebano* were lighter when grown with its closest relative, *H. pallens*. Roots of *V. farnesiana* were equally long across combinations. Roots of *V. schaffnerii* were longer when grown with *E. ebano*, *P. laevigata* and *H. pallens*. *H. pallens* had longer roots for plants grown alone. Roots of *P. laevigata* were longer for plants grown alone, with *V. farnesiana* and with *V. schaffnerii*. Roots of *E. ebano* were longer when grown alone, with *P. laevigata* and with *V. schaffnerii*. Roots of *V. farnesiana* were heavier for plants grown alone. Roots of *V. schafnerii* were heavier for plants grown alone and with plants of *V. farnesiana* and *H. pallens*. Roots of *H. pallens* were heavier for plants grown alone. Roots of *P. laevigata* had similar weight across treatments. Roots of *E. ebano* were heavier for plants grown on their own, with another *E. ebano* plant or with *V. farnesiana* and *V. schaffnerii*. For four species (*V. farnesiana*, *H. pallens*, *E. ebano* and *P. laevigata*) root mass was heavier when grown alone, but for *V. schaffnerii* it was also heavier when grown with a conspecific and two other species.

Seed mass correlated with seedling mass at 1 month for all 13 species (*r* = 0.7991, F = 19.44, *P* = 0.001) but not for plant mass for any of the five species for the second experiment at 6, 12 or 24 months (*P* > 0.05). Maximum and mean adult plant height did not correlate with seed mass or with plant height at 1, 6, 12 and 24 months (*P* > 0.05).

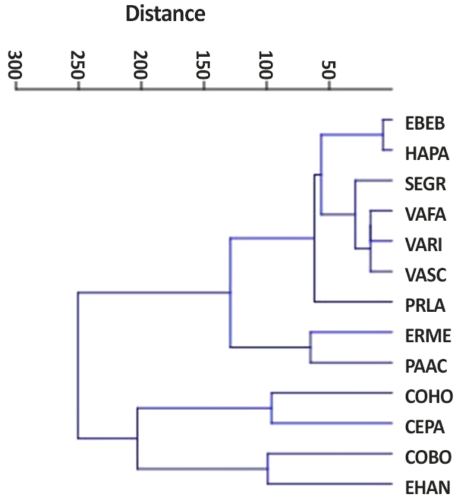

Figure 1. Distance in million years since a common ancestor between species. Made from Timetree (Kumar *et al.* 2017). CEPA = *Celtis pallida*, COBO = *Cordia boissieri*, COHO = *Condalia hookeri*, EBEB = *Ebenopsis ebano*, EHAN = *Ehretia anacua*, ERME = *Erythrostemon mexicana*, HAPA = *Havardia pallens*, PAAC = *Parkinsonia aculeata*, PRLA = *Prosopis laevigata*, SEGR = *Senegalia greggii*, VAFA = *Vachellia farnesiana*, VARI = *Vachellia rigidula*, VASC = *Vachellia schaffnerii*. / Distancia en millones de años de un ancestro común entre especies. Realizado en Timetree (Kumar *et al.* 2017). CEPA = *Celtis pallida*, COBO = *Cordia boissieri*, COHO = *Condalia hookeri*, EBEB = *Ebenopsis ebano*, EHAN = *Ehretia anacua*, ERME = *Erythrostemon mexicana*, HAPA = *Havardia pallens*, PAAC = *Parkinsonia aculeata*, PRLA = *Prosopis laevigata*, SEGR = *Senegalia greggii*, VAFA = *Vachellia farnesiana*, VARI = *Vachellia rigidula*, VASC = *Vachellia schaffnerii*.

Table 2. Shoot and root length and weight (mean ± standard deviation) for plants six months after germination. Bags were only 50 cm deep, so root length is the result of maximum root extension after extraction from the soil. Different lowercase letters are for different means ($P < 0.05$) for each species and its combinations in columns. Differences between species are presented with capital letters inside parentheses. / Longitud y peso de los tallos y raíces (media ± desviación estándar) de las plantas seis meses después de la germinación. Las bolsas tenían solo 50 cm de profundidad, por lo que la longitud de la raíz es el resultado de la extensión máxima de la raíz después de la extracción del suelo. Diferentes letras minúsculas son para diferentes medias ($P < 0.05$) para cada especie y sus combinaciones en columnas. Las diferencias entre especies se presentan con letras mayúsculas entre paréntesis.

Species	Growing with	Shoot length (mm) ± SE at 6 months	Shoot mass (g) ± SE at 6 months	Root length (mm) ± SE at 6 months	Root mass (g) ± SE at 6 months
Ebenopsis ebano		F=855.09, P<0.0001	F=220.01, P<0.0001	F=295963.30, P<0.0001	F=260.57, P<0.0001
	Alone	52.27±3.58 a (B)	8.48±1.12 a (A)	80.30±7.42 a (A)	6.34±0.67 a (B)
	Ebenopsis ebano	38.50±2.69 ab	5.03±1.04 ab	59.80±5.87 a	2.81±0.46 b
	Havardia pallens	35.60±4.32 b	4.70±0.78 b	59.00±7.85 a	3.38±0.42 b
	Prosopis laevigata	41.60±1.97 ab	4.05±0.47 b	72.90±8.01 a	2.39±0.37 b
	Vachellia farnesiana	38.20±4.14 ab	3.88±0.92 b	81.95±5.33 a	2.57±0.61 b
	Vachellia schaffnerii	38.45±3.17 ab	4.94±0.58 ab	67.45±7.39 a	2.78±0.46 b
Havardia pallens		F= 351.43, P<0.0001	F=118.44, P<0.0001	F=762.36, P<0.0001	F=186.69, P<0.0001
	Alone	63.57±8.99 a (B)	9.84±2.24 a (A)	76.33±6.53 a (A)	5.85±0.88 a (B)
	Ebenopsis ebano	31.94±3.88 b	3.88±0.92 b	46.83±4.73 b	1.90±0.24 b
	Havardia pallens	58.55±8.15 a	6.39±1.38 ab	64.95±5.84 ab	2.06±0.33 b
	Prosopis laevigata	39.00±4.80 ab	3.47±0.91 b	60.45±6.02 ab	1.25±0.19 b
	Vachellia farnesiana	47.27±5.92 ab	3.56±0.53 b	58.44±3.68 ab	2.78±0.43 b
	Vachellia schaffnerii	50.00±4.49 ab	3.43±0.82 b	72.05±5.93 a	1.92±0.29 b
Prosopis laevigata		F= 460.15, P<0.0001	F=109.77, P<0.0001	F=620.28, P<0.0001	F=191.48, P<0.0001
	Alone	70.35±4.86 a (B)	10.35±2.06 a (A)	66.35±4.41 a (A)	6.88±0.77 a (A,B)
	Ebenopsis ebano	46.16±3.64 b	3.69±0.67 b	72.90±8.01 a	2.64±0.46 b
	Havardia pallens	47.44±4.78 ab	4.93±0.58 b	61.61±8.12 a	2.91±0.38 b
	Prosopis laevigata	53.23±7.16 ab	7.75±1.41 ab	69.45±6.13 a	3.66±0.63 b
	Vachellia farnesiana	45.20±7.06 b	3.46±0.72 b	61.65±6.10 a	3.04±0.58 b
	Vachellia schaffnerii	36.58±4.98 b	3.47±0.91 b	48.27±2.49 a	2.81±0.78 b
Vachellia farnesiana		F=1544.49, P<0.0001	F=226.62, P<0.0001	F=1077.80, P<0.0001	F=351.07, P<0.0001
	Alone	74.36±3.33 a (A)	7.75±0.75 a (A)	88.05±4.32 a (A)	11.38±1.10 a (A)
	Ebenopsis ebano	67.87±3.90 a	5.03±1.04 ab	81.95±5.33 ab	7.16±0.90 b
	Havardia pallens	57.27±4.05 b	3.71±0.51 b	70.14±5.56 ab	5.28±1.04 bc
	Prosopis laevigata	48.85±5.28 b	2.69±0.69 b	61.65±6.10 b	3.01±0.54 c
	Vachellia farnesiana	73.45±3.83 a	5.39±0.55 ab	78.45±5.57 ab	6.48±0.64 b
	Vachellia schaffnerii	59.66±2.74 ab	2.70±0.53 b	66.26±6.16 ab	6.72±0.80 b
Vachellia schaffnerii		F=1112.80, P<0.0001	F=113.67, P<0.0001	F=549.54, P<0.0001	F=178.75, P<0.0001
	Alone	53.77±5.75 a (B)	4.64±1.30 a (A)	86.72±6.61 a (A)	7.19±0.98 a (A,B)
	Ebenopsis ebano	51.77±4.81 a	2.70±0.53 a	66.8±9.47 ab	4.04±0.84 ab
	Havardia pallens	43.27±4.25 a	3.46±0.72 a	73.3±7.26 ab	3.32±0.98 b
	Prosopis laevigata	43.44±4.43 a	4.70±0.78 a	48.28±2.49 b	4.07±0.94 ab
	Vachellia farnesiana	42.87±4.23 a	3.46±0.58 a	55.29±5.27 b	3.10±0.33 b
	Vachellia schaffnerii	47.65±4.44 a	1.87±0.21 a	61.27±5.92 ab	4.245±0.43 ab

Table 3. Shoot and root length and weight (mean ± standard deviation) for plants 12 months after germination. Bags were only 50 cm deep, so root length is the result of maximum root extension after extraction from the soil. Different lowercase letters are for different means ($P < 0.05$) for each species and its combinations in columns. Differences between species are presented with capital letters inside parentheses. / Longitud y peso de tallos y raíces (media ± desviación estándar) para plantas 12 meses después de la germinación. Las bolsas tenían solo 50 cm de profundidad, por lo que la longitud de la raíz es el resultado de la extensión máxima de la raíz después de la extracción del suelo. Diferentes letras minúsculas son para diferentes medias ($P < 0.05$) para cada especie y sus combinaciones en columnas. Las diferencias entre especies se presentan con letras mayúsculas entre paréntesis.

Species	Growing with	Shoot length (mm) ± SE at 12 months	Shoot mass (g) ± SE at 12 months	Root length (mm) ± SE at 12 months	Root mass (g) ± SE at 12 months
Ebenopsis ebano		*F*=7.11, *P*<0.0001	*F*=7.22, *P*<0.0001	*F*=2.22, *P*=0.06	*F*=11.93, *P*<0.0001
	Alone	93.97±4.85 a (B)	29.08±1.99 a (A,B)	87.54±6.17 a (A)	16.75±1.30 a (A)
	Ebenopsis ebano	56.27±5.75 b	14.38±1.48 ab	70.90±3.41 a	4.95±0.91 c
	Havardia pallens	67.10±4.69 b	12.05±1.89 b	75.19±5.00 a	6.74±0.98 bc
	Prosopis laevigata	68.88±6.49 b	14.57±3.53 ab	91.52±8.84 a	8.32±1.63 b
	Vachellia farnesiana	77.00±5.01 ab	17.81±3.70 ab	92.62±6.16 a	10.54±2.02 b
	Vachellia schaffnerii	83.81±3.60 a	23.78±2.23 a	81.28±5.24 a	12.70±0.73 ab
Havardia pallens		*F*=15.27, *P*<0.0001	*F*=13.58, *P*<0.0001	*F*=0.51. *P*=0.76	*F*=13.75, *P*<0.0001
	Alone	127.44±17.72 b	18.94±3.76 b	67.34±5.00 a	10.40±1.60 b
	Ebenopsis ebano	93.66±11.79 bc	13.25±1.39 b	62.13±9.03 a	5.69±1.02 b
	Havardia pallens	182.83±9.30 a (A)	36.55±2.55 a (A,B)	74.82±6.71 a (B)	18.88±1.57 a (A)
	Prosopis laevigata	103.947.37 b	11.67±1.41 b	64.85±6.59 a	7.02±1.22 b
	Vachellia farnesiana	126.67±7.63 b	18.80±2.17 b	65.00±3.18 a	8.55±0.91 b
	Vachellia schaffnerii	61.05±6.10 c	16.53±1.84 b	69.57±6.62 a	10.25±1.11 b
Prosopis laevigata		*F*=6.14, *P*<0.0001	*F*= 13.69, *P*<0.0001	*F*=2.10, *P*=0.08	*F*=7.44, *P*<0.0001
	Alone	105.93±6.31 a (B)	29.41±2.16 a (A,B)	77.70±5.22 a (B)	16.18±1.31 a (A)
	Ebenopsis ebano	68.88±6.49 b	18.08±2.51 b	78.45±8.50 a	10.89±1.47 ab
	Havardia pallens	74.98±4.76 b	10.75±1.98 bc	71.6±7.48 a	7.92±1.27 b
	Prosopis laevigata	79.22±5.12 b	13.62±3.09 bc	75.60±3.54 a	9.05±2.40 b
	Vachellia farnesiana	63.52±8.06 b	8.86±0.76 bc	55.87±4.04 a	5.55±0.75 b
	Vachellia schaffnerii	68.28±7.14 b	7.31±1.70 c	63.60±5.07 a	4.34±0.87 b
Vachellia farnesiana		*F*=5.68, *P*=0.0003	*F*=11.94, *P*<0.0001	*F*=0.88, *P*=0.50	*F*=5.97, *P*=0.0002
	Alone	111.16±3.15 a (B)	17.41±1.74 a (B,C)	67.22±3.02 a (B)	14.81±2.15 a (A)
	Ebenopsis ebano	94.77±6.75 ab	10.31±2.17 b	72.27±5.82 a	9.10±2.25 a
	Havardia pallens	79.95±4.98 b	5.10±0.77 b	68.20±5.87 a	5.90±0.79 b
	Prosopis laevigata	68.16±3.53 b	4.00±0.79 c	67.27±5.86 a	3.64±0.58 b
	Vachellia farnesiana	87.03±10.08 ab	9.55±1.13 b	62.11±6.72 a	9.74±1.51 a
	Vachellia schaffnerii	88.80±5.45 ab	9.10±1.31 b	77.38±5.94 a	9.06±1.28 a
Vachellia schaffnerii		*F*=0.62, *P*=0.68	*F*=28.12018, *P*<0.0001	*F*=4.42, *P*=0.002	*F*=22.97, *P*<0.0001
	Alone	64.32±7.75 a (C)	15.45±1.30 a (C)	88.37±5.93 a (B)	13.15±1.20 a (A)
	Ebenopsis ebano	52.30±3.51 a	3.00±0.54 b	54±5.16 b	2.97±0.62 b
	Havardia pallens	60.26±4.60 a	5.11±0.79b	66.37±6.02 ab	4.81±0.63 b
	Prosopis laevigata	54.05±5.77 b	5.27±0.97 b	56.38±5.69 b	4.18±0.73 b
	Vachellia farnesiana	61.05±6.10 a	4.525±0.67 b	56.02±4.53 b	3.67±0.61 b
	Vachellia schaffnerii	58.30±6.01 a	6.39±0.54 b	65.2±8.29 ab	5.60±0.74 b

Table 4. Shoot and root length and weight (mean ± standard deviation) for plants 24 months after germination. Bags were only 50 cm deep, so root length is the result of maximum root extension after extraction from the soil. Different lowercase letters are for different means ($P < 0.05$) for each species and its combinations in columns. Differences between species are presented with capital letters inside parentheses. / Longitud y peso de tallos y raíces (media ± desviación estándar) para plantas 24 meses después de la germinación. Las bolsas tenían solo 50 cm de profundidad, por lo que la longitud de la raíz es el resultado de la extensión máxima de la raíz después de la extracción del suelo. Diferentes letras minúsculas son para diferentes medias ($P < 0.05$) para cada especie y sus combinaciones en columnas. Las diferencias entre especies se presentan con letras mayúsculas entre paréntesis.

Species	**Growing with**	**Shoot length (mm) ± SE at 24 months**	**Shoot mass (g) ± SE at 24 months**	**Root length (mm) ± SE at 24 months**	**Root mass (g) ± SE at 24 months**
Ebenopsis ebano		*F*=4.019, *P*=0.003	*F*=4.19, *P*=0.003	*F*=2.80, *P*=0.027	*F*=5.567, *P*=0.005
	Alone	160.77±11.09 a (B)	74.15±9.96 a (A,B)	101.03±11.95 a (A)	41.59±5.49 a (A)
	Ebenopsis ebano	108.36±13.4 b	62.38±8.66 a	75.58±8.79 b	29.64±5.45 ab
	Havardia pallens	122.99±19.83 b	25.87±5.69 b	65.58±3.30 b	15.24±3.78 b
	Prosopis laevigata	109.14±10.63 b	54.66±9.84 a	81.74±5.95ab	23.63±4.11 b
	Vachellia farnesiana	112.81±6.95 b	62.93±7.14 a	73.40±7.83 b	36.11±2.41 a
	Vachellia schaffnerii	121.17±8.93 b	67.57±6.34 a	90.37±7.87 a	32.00±3.47 a
Havardia pallens		*F*=3.02, *P*=0.02	*F*=6.697, *P*=0.0004	*F*=4.21, *P*=0.004	*F*=2.482, *P*=0.047
	Alone	249.16±24.66 a (A)	206.18±34.22 a (A)	106.91±15.31 a (A)	77.65±9.61 a(A)
	Ebenopsis ebano	152.2±27.22 b	53.34±8.68 b	61.62±6.88 b	45.60±9.52 b
	Havardia pallens	176.3±24.48 a	106.02±36.95 b	61.17±8.35 b	35.72±10.35 b
	Prosopis laevigata	224.28±24.1 a	75.53±19.25 b	54.48±5.26 b	26.46±5.47 b
	Vachellia farnesiana	234.42±9.5 a	93.38±12.53 b	67.15±6.15 b	42.14±5.30 b
	Vachellia schaffnerii	202.08±14.24 a	89.86±13.66 b	74.60±2.52 b	38.80±4.54 b
Prosopis laevigata		*F*=3.54, *P*=0.008	*F*=5.03, *P*=0.012	*F*=2.42, *P*=0.049	*F*=70.76, *P*=0.58
	Alone	140.48±6.05 a (B)	67.91±8.95 a (B,C)	94.22±9.68 ab (A)	16.85±3.05 a (B)
	Ebenopsis ebano	78.11±15.62 b	23.17±5.41 b	58.65±8.17 b	11.89±2.75 a
	Havardia pallens	124.84±8.41 a	36.93±6.27 b	66.76±5.20 b	19.16±4.02 a
	Prosopis laevigata	102.63±12.22 a	37.77±10.41 b	67.55±8.98 b	12.20±3.05 a
	Vachellia farnesiana	93.18±12.95 a	38.89±4.43 b	75.43±9.91ab	14.84±2.42 a
	Vachellia schaffnerii	95.81±14.54 a	28.05±5.42 b	104.91±9.80 a	14.25±2.76 a
Vachellia farnesiana		*F*=1.32, *P*= 0.28	*F*=24.55, *P*<0.0001	*F*=2.00, *P*=0.114	*F*=27.56, *P*<0.0001
	Alone	120.8±9.13 a (B)	32.63±3.81 b (C,D)	89.61±5.87 a (A)	30.33±2.67 a (B)
	Ebenopsis ebano	95.83±10.28 a	62.93±7.14 a	84.21±8.48 a	9.28±1.61 b
	Havardia pallens	Not available	Not available	Not available	Not available
	Prosopis laevigata	89.48±9.17 a	11.19±3.14 c	73.74±8.26 a	6.44±1.69 b
	Vachellia farnesiana	103.75±12.11 a	13.06±1.82 c	67.28±4.01 a	10.25±1.55 b
	Vachellia schaffnerii	104.44±11.85 a	13.42±3.37 c	65.55±9.45 a	11.19±0.61 b
Vachellia schaffnerii		*F*=3.628, *P*=0.01	*F*=4.31, *P*=0.05	*F*=2.77, *P*=0.03	*F*=12.18, *P*<0.0001
	Alone	89.15±6.09 a (C)	23.12±3.42 a (D)	69.50±7.15 b (A)	15.85±1.76 a(B)
	Ebenopsis ebano	44.66±1.66 b	3.09±1.14 b	99.80±9.13 a	1.10±0.45 b
	Havardia pallens	93.4±9.53 a	22.93±3.86 a	75.14±7.40 ab	15.83±2.45 a
	Prosopis laevigata	79.87±8.45 ab	9.01±3.23 b	75.55±9.90 ab	2.59±0.36 b
	Vachellia farnesiana	75.85±6.83 ab	16.31±1.46 a	56.37±5.37 b	12.49±1.48 a
	Vachellia schaffnerii	90.93±4.90 a	19.85±3.65 a	67.38±12.41 b	6.82±2.14 b

DISCUSSION

We found no support for our hypothesis that seedling competition would inhibit seedling survival and growth, resulting in lower survival and lower seedling mass and length, for phylogenetically closer species grown together. No evidence that a stronger competition effect for closer relatives was detected, in the only effect found in plant survival, as *H. pallens* and *V. farnesiana* were not the closest relatives (Fig. 1). Competition between two species has been found for thornscrub species in that seedlings of one species were heavier and seedlings of another were lighter when grown competing with each other, but not when competing against seedlings from their own species (Van Auken & Bush 1987, Van Auken & Bush 1990a, 1990b). Our findings agree with Watanabe & Maesako (2021), who found that closely related tree species often coexist even at the finest spatial scale.

Differences for plant length or weight occurred only in few combinations and some not until after 12 months. Out of 1,088 mean values of seedling measurements (from 1 to 24 mo), there were 12 instances in which one or two species combinations resulted in differences in root or shoot length or weight. For six of them, seedling parts were smaller (weight or length) when grown with another species, as expected by the effect of competition (Tables 1 to 4). This coincides with Jurado *et al.* (2020) testing seed germination under competition of phylogenetic close and distant species and with Marroquín *et al.* (2019) studying adult plant, nearest neighbors and germination inhibition were unrelated to phylogenetic distance. This competition effect did not coincide with the expectation of phylogenetically closest species. Only in four cases, the smallest seedling parts occurred when seedlings grew with a conspecific, or a phylogenetically closest species (Tables 3 and 4) as expected by our hypothesis. In two cases (Table 4), seedling parts were bigger (heavier or longer) when grown with a seedling from another species as expected by facilitation, although not with the phylogenetically more distant species as proposed in other studies (Valiente-Banuet & Verdú 2013).

We mostly found no evidence that growing next to another plant affects plant survival or growth, this could be a result of experimental conditions such as watering and competition restricted to one plant. Perhaps under natural conditions, with more stressors, the presence of another seedling competing or facilitating could tip the balance of seedling survival. However, the structure of thornscrub includes many adult plants with overlapping stems and crowns (Reid *et al.* 1990, Marroquín *et al.* 2019). Maybe competition in thornscrub is not a strong driving force for (i) light as in forests (Laurans *et al.* 2014), (ii) water as in more arid ecosystems (Montaña *et al.* 1995) and nutrients as in poor soils (Wilson & Tilman 1991). This coincides with Jurado *et al.* (2020) testing seed germination under competition of phylogenetic close and distant species and with Marroquín *et al.* (2019) study of adult plant nearest neighbor's not related to phylogenetic distance.

Our hypothesis that seedling mass would be correlated with seed mass at least during the early stages of growth was accepted. Seed mass correlated with seedling mass at 1 month (cotyledon-stage seedlings), but not for plant mass (leaf stage) for five species at 6, 12 or 24 months. Similarly, Quero *et al.* (2007) found a correlation between seed mass and seedling mass for seedlings growing under low light, suggesting that seedlings growing in shade depend more upon their seed reserves. In addition, seedling mass was positively related to seed mass in five *Psychotria* species in the shaded forest, but only in two *Psychotria* species in gaps (Paz & Martínez-Ramos 2003). Seed mass has also been associated with seedling survival in shaded environments, Saverimuttu & Westoby (1996) found that seed mass was a predictor of seedling longevity in the shade for cotyledon-stage seedlings but not for seedlings grown to first-leaf stage in the light but then transferred to shade, after deploying reserves in cotyledons and the seedling has embarked fully on self-supporting growth.

In conclusion, plant size correlated with seed mass one month after germination but not after six months. Seedling survival was similar for all species when their seedlings were growing alone or under competition, at 1, 6 and 12 months after germination. At 24 months seedling survival of *V. farnesiana* was lower when grown with *H. pallens* than when growing alone or with another *V. farnesiana* seedling or with a seedling from other species. Seed mass and seedling mass were correlated at 1 month for all 13 species. Maximum and mean adult plant height did not correlate with seed mass or with plant height at 1, 6, 12 and 24 months ($p > 0.05$). There was no evidence that competition or facilitation related with phylogeny, this could be a result of experimental conditions such as watering and competition restricted to one plant. It is possible that under natural stressors, the occurrence of another seedling competing or facilitating could tip the stability of seedling survival; however, the structure of thornscrub includes many adult plants growing together with overlapping stems and crowns.

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