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Growth and ecophysiology of succulent seedlings under the protection of nurse plants in the Southern Chihuahuan Desert

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Abstract. In arid zones, light and water are two important factors that limit seedling development. The shade provided by nurse plants can reduce overheating, excessive transpiration, and photoinhibition in protégé seedlings. The difference that a nurse plant microenvironment may provide on the physiological performance of succulent desert seedlings could be tested by measuring plant growth and photosynthesis. Specifically, in this study we measured the variables related to chlorophyll fluorescence: Quantum yield of photosystem II photochemistry (Φ_{PSII}) and electron transport rate (ETR), as well as relative growth rate (RGR) and its components (net assimilation rate, NAR, and leaf area rate, LAR), root to shoot (R/S) ratio, and relative water content (RWC) for seedlings transplanted under nurse plants and seedlings transplanted under direct sunlight. We tested whether Φ_{PSII}, ETR, LAR, R/S ratio, and RWC, were lower, and RGR and NAR were higher for seedlings of seven succulent species common to the Southern Chihuahuan Desert (*Agave lechuguilla, A. salmiana, Echinocactus platyacanthus, Ferocactus histrix, Myrtillocactus geometrizans, Stenocactus coptonogonus* and *Yucca filifera*) grown under direct sunlight than for those grown under nurse Mesquite trees. Although species responded differently to treatments, in general we found that seedlings grown under nurse plants had higher Φ_{PSII} and lower ETR than those grown under direct sunlight. RWC, R/S ratio, and RGR and its components varied in response to microenvironments for some species but not consistently. The ecophysiology variables tested here were more clearly affected by solar radiation than the morphology variables. These results are the first field study including the ecophysiological and morphological mechanisms of seedlings of succulent species under nurse plants.

Key words: Asparagaceae; Cactaceae, Mimosaceae; nurse-protégé; seedling ecophysiology; seedling growth; Southern Chihuahuan Desert.

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Introduction

Early stages of plant growth are crucial in plant population dynamics, as seedlings are not as tolerant as seeds or as sturdy as mature plants (Kitajima and Fenner 2000). During this vulnerable stage young plants should grow as fast as possible; establish roots for rapid water uptake; compete for light, nutrients and space with other plants; and develop chemical and mechanical defenses for protection against herbivores (Kitajima and Fenner 2000, Fenner and Thompson 2005).

In arid and semiarid zones light and water are two of the most important physical factors that limit seedling development (Flores and Jurado 2003). Shade in places with abundant vegetation can induce stress by limiting photosynthesis and arrest seedling development (Kitajima and Fenner 2000), but it can also be beneficial by reducing overheating, excessive transpiration, and photoinhibition that seedlings growing in open areas may experience (Valladares and Pearcy 1997, Flores and Jurado 2003, Valladares 2004, Yang et al. 2009).

Photoinhibition is defined as any downregulation of the photosynthetic apparatus in response to excess light when more sugar is produced in leaves than can be utilized by the rest of the plant and/ or more light energy is harvested than can be utilized by the chloroplasts for the fixation of carbon dioxide into sugars (Adams et al. 2013). Stress caused by drought or extreme temperatures increases the risk and severity of photoinhibition in arid environments (Cornic 1994, Flexas and Medrano 2002, Valladares 2004).

Most studies done on desert seedling establishment have focused on evaluating survival (Turner et al. 1966, Ibáñez and Schupp 2001, Flores et al. 2004, Munguía-Rosas and Sosa 2008, García-Chávez et al. 2014); little research has been conducted on the mechanisms related to desert seedling growth and light and water stress, and most has been done in greenhouse conditions (Martínez-Berdeja and Valverde 2008, Miquelajáuregui and Valverde 2010, Delgado-Sánchez et al. 2013, Romo-Campos et al. 2013).

Allometry is very often used to test hypotheses regarding facilitation under nurse plants (Martınez-Berdeja and Valverde 2008, Miquelajáuregui and Valverde 2010). Often, if no differences in morphology or mass are found, it is assumed that other variables such as grazing or trampling affect seedling growth (Flores et al. 2004).

Here we argue that, at least for succulent protégé species, physiology is often overlooked (Romo-Campos et al. 2013). However, it is possible that seedlings are responding to elevated radiation in ways different to morphology. For instance, physiological changes can occur at least in the early stages, without detectable growth changes (Delgado-Sánchez et al. 2013).

Some studies have shown higher survival but similar or lower relative growth rate for seedlings grown under shade, than for those grown under direct sunlight (Martínez-Berdeja and Valverde 2008, Romo-Campos et al. 2013). This has been interpreted as a result of a lower photosynthesis rate for shaded seedlings (Franco and Nobel 1989, Martínez-Berdeja and Valverde 2008, Romo-Campos et al. 2013). In a greenhouse study, Romo-Campos et al. (2013) found higher net assimilation rate (NAR), the physiological component of RGR, and lower leaf (or photosynthetic) area ratio (LAR), the morphological component of RGR, for cactus seedlings (*Opuntia jaliscana* and *O. streptacantha*) located in high solar radiation than for those in the shade. NAR is a physiological component because it is a measure of whole-plant daily net photosynthetic rate weighted by the rate of change in plant carbon content (Delgado-Sánchez et al. 2013). Because solar radiation affects temperature and temperature affects moisture, higher survival of seedlings under nurse plants could result from higher soil moisture and not from reduced light.

It is possible that the microenvironment under nurse plants improves the physiological performance of succulent desert seedlings, which could be tested by measuring chlorophyll fluorescence on the leaves or photosynthetic structures (Maxwell and Johnson 2000). If the microenvironment under nurse plants reduces stress, seedlings beneath them would show higher effective quantum yield of photosystem II (Φ_{PSII}) values than seedlings of the same species at higher solar radiation.

Because electron transport rate (ETR) is related to the flow of electrons through PSII to PSI eventually to form $NADPH_2$ which is used to fix CO_2, lower ETR values indicate reduced photosynthetic performance in plants (Ritchie and Bunthawin 2010*a*, *b*, Aragón-Gastélum et al. 2014). Hence, if environmental conditions of open spaces negatively affect the performance of seedlings, those located under nurse plants should display higher electron transport rate (ETR) values.

Specifically, in this study we determined the variables related to chlorophyll fluorescence: Φ_{PSII} and ETR, as well as the RGR and their components (NAR and LAR) for seedlings under nurse plants and for those under direct sunlight. We tested whether Φ_{PSII}, ETR, LAR, root to shoot (R/S) ratio, and relative water content (RWC), were lower, and RGR and NAR were higher for seedlings grown under direct sunlight than for those grown under nurse plants. We used seven species, including both cacti and rosette succulents.

Methods

Study site

A field experiment was carried out in San Juanico Chico in the municipality of San Luis Potosí, S.L.P., Mexico, at 1870 m above sea level (22°14′07.5″ N, 100°59′48.3″ W). Vegetation includes microphyllous, rosetophyllous and crassicaule desert scrub, the area has a mean annual rainfall from 300 to 450 mm and mean temperatures from 18°C to 25°C (INEGI 2002).

Studied species

We studied seven species in two families; four belong to Cactaeae (*Echinocactus platyacanthus* Link & Otto, *Ferocactus histrix* (DC) G.E.Linds., *Myrtillocactus geometrizans* (Mart. ex Pfeiff.) Console. and *Stenocactus coptonogonus* (Lem.) A.Berger ex A.W.Hill.) and three to Asparagaceae (*Agave lechuguilla* Torrey, *Agave salmiana* Otto ex Salm-Dick and *Yucca filifera* Chabaud). These species are common in the area and are used by people for their fiber and fruit and/or in ornamental uses (Pérez-Sánchez et al. 2011). The nurse plant selected was mesquite (*Prosopis laevigata* (Humb. & Bonpl. ex Willd.) M.C. Johnst.; Mimosaceae).

Seed collection

Seeds of the studied species were collected in the Southern Chihuahuan Desert in San Luis Potosi, Mexico. We collected mature fruits from at least 10 individuals for each species. Seeds were mixed and stored in paper–bags at room temperature.

Seedling growth

Species were set to germinate in such a way as to have sufficient seeds germinated within the same 24 h period and limit variation in seedling growth due to germination speed (Jurado and Westoby 1992, Flores and Jurado 1998). Prior assays were carried out to determine germination rate (Pérez-Sánchez et al. 2011).

Germination and seedling transplant were carried out in the greenhouse at the Instituto Potosino de Investigación Científica y Tecnológica (IPICYT). Seeds were set to germinate in trays using peat moss as substrate; trays were watered every day until seedling emergence. Seedlings were transplanted individually into biodegradable cups (295 ml) using field soil as substrate with weekly irrigation. Age of transplanted seedlings was between four and five weeks.

Experimental design

Permanent plots were set at the start of the 2012 rainy season (September), when germination and seedling establishment are more likely to occur. *Prosopis laevigata* (mesquite) trees were used as nurse plants, as they are common nurse trees in the Chihuahuan Desert (Muro-Pérez et al. 2012). Trees from 2.5 to 3 m height and a canopy of 2–2.5 m in diameter were selected.

For each one of the seven studied species, five replicates were made for two conditions: (1) under direct sunlight (open spaces) and (2) under the shade of a mesquite tree. A total of 41 seedlings were used for each replicate in each treatment (30 were used for morphological destructive measurements using five replicates in each one of six dates, five for chlorophyll fluorescence evaluations and six to allow for incidental losses). Only three species fitted under each mesquite, so a total of 12 trees were used for the experiment.

Environmental variables.—Under direct sunlight and under nurse plants (six replications per microenvironment), soil surface temperature and moisture as well as photosynthetic flux density (PFD) were recorded 7, 21, 35, 49, 77 and 105 d after planting. Soil temperature was measured with a high distance spot infrared thermometer (ST670, Sentry) and soil moisture (at 1 cm depth) with a hygrometer (Hydrosense, Campbell Scientific Australia). PFD was recorded by the sensor in the leaf clip of the portable pulse amplitude modulation fluorometer (Mini-PAM; H. Walz, Effeltrich, Germany).

Physiological variables.—Non-destructive measurements of ecophysiological variables were done (i.e., variables related to chlorophyll fluorescence): Quantum yield of photosystem II photochemistry (Φ_{PSII}) and electron transport rate (ETR), using the portable pulse amplitude modulation fluorometer. The rounds of chlorophyll fluorescence measurements were conducted at noon (between 12:00 and 14:00 h), when plants faced the maximum daily temperature, at days 7, 21, 35, 49, 77 and 105 after planting. We estimated the effective quantum yield of photosystem II (Φ_{PSII}). This variable was computed as $\Phi_{PSII} = (F'_m - F_t)/F'_m$, where F_t is the chlorophyll fluorescence emitted by plants under steady-state illumination (i.e., light conditions in the field) and F'_m is the maximum fluorescence emitted by chlorophyll when a saturating pulse of actinic light is superimposed to environmental levels of light (Genty et al. 1989).

We also calculated the electron transport rate (ETR) across the electron chain of chloroplasts. This variable was then estimated as $ETR = \Phi_{PSII} \times PFD \times 0.84 \times 0.5$, where PFD is the photosynthetic photon flux density recorded by the sensor in the leaf clip of the fluorometer; 0.84 is the estimated mean proportion of incident light absorbed by the photosystems (Ehleringer 1981) and 0.5 is the required reflection factor for photosystems I and II to absorb photons (Roberts et al. 1996). ETR represents a measure of the capacity for photosynthetic activity and can be used to compare plant species or treatments in an experimental setting (Stemke and Santiago 2011).

Morphology variables.—Seedling growth was analyzed, determining relative growth rate (RGR) and its components "leaf area ratio" (LAR) and "net assimilation rate" (NAR). LAR = total leaf or photosynthetic area/total biomass, TLA/TB, cm^2/g); NAR represents an increase in plant total weight per leaf or photosynthetic area unit and time unit ($NAR = (TB_2 - TB_1)/(T_2 - T_1) \times 2/(TLA_1 + TLA_2)$; $mg/day/cm^2$). Although NAR is a physiological component, we included it as a morphological variable because it is estimated using weight and area. Relative growth rate (RGR) can be expressed as: $RGR = (TB_2 - TB_1)/(T_2 - T_1) \times 2/(TB_1 + TB_2)$, expressed in mg/day/g. T_1 and T_2 are the initial and final time of two extractions. RGR is also equivalent to the product: $LAR \times NAR$ (Cardillo and Bernal 2006).

We also evaluated resource allocation (root to shoot ratio; R/S) and relative water content (RWC). RWC is expressed as fresh mass − dry mass/saturation mass − dry mass) × 100 (Reigosa-Roger 2001). All these variables were measured in the Ecology Lab of the Instituto Potosino de Investigación Científica y Tecnológica (IPICyT). Seedlings were harvested to coincide with photosynthesis efficiency measurements. Harvested samples were dried at 70°C for 3 days prior to weighing.

Seedlings were transplanted at the end of summer and most harvests (7, 21, 35, 49 and 77 d) were done in autumn, except for the last one at 105 d that was done in winter. Harvest samples were weighed immediately after collection and then placed in water for 24 h to be weighed again in order to obtain turgent weight. Dry weight was determined after 3 d in a stove at 70°C. Shoot and root of each seedling were dissected and weighed separately.

Statistical analyses

Two-way ANOVAs were carried out for environmental variables (soil temperature, soil moisture, and photosynthetic photon flux), with microenvironment (under nurse plant an under direct sunlight) and time as factors. Factorial ANOVAs were carried out for root/shoot ratio (R/S), relative growth rate (RGR), leaf area ratio (LAR), net assimilation rate (NAR) and relative water content (RWC) having microenvironment and time as factors. There were two microenvironment levels (under nurse plant an under direct sunlight) and six levels for time since planting (7, 21, 35, 49, 77 and 10 d). For physiological variables, quantum yield of photosystem II photochemistry (Φ_{PSII}) and electron transport rate (ETR), time to harvest and microenvironment were also factors, but the ANOVAS used were for repeated measurements. Species were analyzed separately. Tukey tests were used to detect different means. Analyses were carried out using STATISTICA (8) with $\alpha = 0.05$. Data were transformed, if required to comply with the assumption of normal distribution (Sokal and Rohlf 1995).

Results

Environmental variables

Soil temperature was affected by the time factor ($F = 65$, $P < 0.001$), with lower soil temperature at days 77 (26.55° ± 0.98°C), and

105 (24.84° ± 0.68°C), while the highest soil temperature was recorded at day 21 (37.19° ± 2.21°C). Soil temperature was also affected by microenvironment ($F = 1023$, $P < 0.001$), having higher values under direct sunlight (37.42° ± 1.07°C) than under mesquite trees (24.62° ± 0.56°C). The interaction of microenvironment × time was also significant ($F = 48$, $P < 0.001$), showing higher soil temperatures in open sites during the warmer days, and relatively constant lower temperatures under nurse plants (Fig. 1A).

Soil moisture was affected by the time factor ($F = 47.43$, $P < 0.001$), with the highest humidity at day 105, and the lowest at day 1, the rest of the days presented an intermediate moisture (Fig. 1B). The microenvironment factor and the interaction of microenvironment * time were not significant.

Photon flux density (PFD) was affected by the time factor ($F = 40$, $P < 0.001$), being of greater intensity at days 1, 7, 21 and 35 (735.47 ± 55.43, 735.47 ± 55.43, 694.34 ± 51.98 and 751.49 ± 57.25 μmol m^{-2} s^{-1}, respectively), not coinciding with the highest PFD recorded at day 105 (381.59 ± 17.04 μmol m^{-2} s^{-1}). The PFD was also affected by the microenvironment factor ($F = 1238$, $P < 0.001$), showing higher light intensity in areas under direct sunlight (926.75 ± 21.21 μmol m^{-2} s^{-1}) than under nurse plants (306.34 ± 11.45 μmol m^{-2} s^{-1}). The microenvironment × time interaction was significant ($F = 32$, $P < 0.001$), showing higher PFD in open sites during the warmer days, and constantly low PFD values under nurse plants (Fig. 1C).

These results are in agreement with seasonal variation, since the beginning of the experiment (26 September 2012) started in the late summer and early autumn, when rainfall was low and light intensity was high, the experiments ended in winter (9 January 2013) when some light rains occurred and light intensity was lower.

Physiology variables

Quantum yield of photosystem II photochemistry (Φ_{PSII}).—In general, Φ_{PSII} of seedlings from all species was greater under nurse plants (Appendix: Table A1). Time factor had an effect on Φ_{PSII} of *Agave lechuguilla*, *Yucca filifera*, *Ferocactus histrix* and *Stenocactus coptonogonus* (Appendix: Table A1). The microenvironment × time interaction was significant for seedlings of *Y. filifera* ($F = 5.09$, $P = 0.001$) in that Φ_{PSII} values were lower under direct sunlight for days 21, 35, 49 and 77 (Fig. 2A). This interaction was also significant for *M. geometrizans* ($F = 3.36$, $P = 0.013$) in that Φ_{PSII} values were lower under direct sunlight but statistical differences were only found for day 21 (Fig. 2B).

Electron transport rate (ETR).—ETR differed between microenvironments across species (Appendix: Table A2), and was always greater for seedlings grown under direct sunlight. Time factor had an effect on all species (Appendix: Table A2), while the time × microenvironment interaction was significant only for *Y. filifera* ($F = 21.24$, $P < 0.001$) and *M. geometrizans* ($F = 3.53$, $P = 0.01$); *Yucca filifera* seedlings showed a lower ETR under the shade of nurse trees at day 7 (Fig. 3A); while *M. geometrizans* seedlings had a lower ETR under the shade of nurse trees at days 7, 35 and 49; at the other days it was a tendency to same pattern (Fig. 3B).

Morphology variables

Relative growth rate (RGR).—Microenvironment affected RGR of three species: *Yucca filifera* ($F = 6.298$, $P = 0.016$), *Agave salmiana* ($F = 7.142$, $P = 0.01$) and *Mirtyllocactus geometrizans* ($F = 4.894$, $P = 0.03$). Seedlings of *Y. filifera* and *M. geometrizans* had higher RGR under nurse plants contrary to seedlings of *Agave salmiana* that had higher RGR values under direct sunlight. RGR for *Agave lechuguilla* seedlings differed in time ($F = 5.614$, $P < 0.001$; Appendix: Tables A3 and A4).

The microenvironment × time interaction was significant for *Agave salmiana* ($F = 3.421$, $P = 0.01$) and *Yucca filifera* ($F = 2.868$, $P = 0.02$; Appendix: Tables A3 and A4). At day 7, shaded seedlings of *Y. filifera* showed higher RGR than those grown under direct sunlight (Fig. 4A). *A. salmiana* seedlings grown under the sun showed higher RGR at day 7 than those grown under nurse trees at 7, 21, 77 and 105 d (Fig. 4B).

Net assimilation rate (NAR).—For seedlings of *Yucca filifera*, *Echinocactus platyacanthus*, *Ferocactus histrix*, *Myrtillocactus geometrizans* and *Stenocactus coptonogonus*, NAR was not affected by time, microenvironment or their interaction (Appendix: Table A5). For seedlings of *A. lechuguilla* ($F = 3.524$, $P = 0.009$) and *A. salmiana* ($F = 40.93$, $P < 0.001$) NAR differed in time.

Leaf area rate (LAR).—Under nurse plants LAR

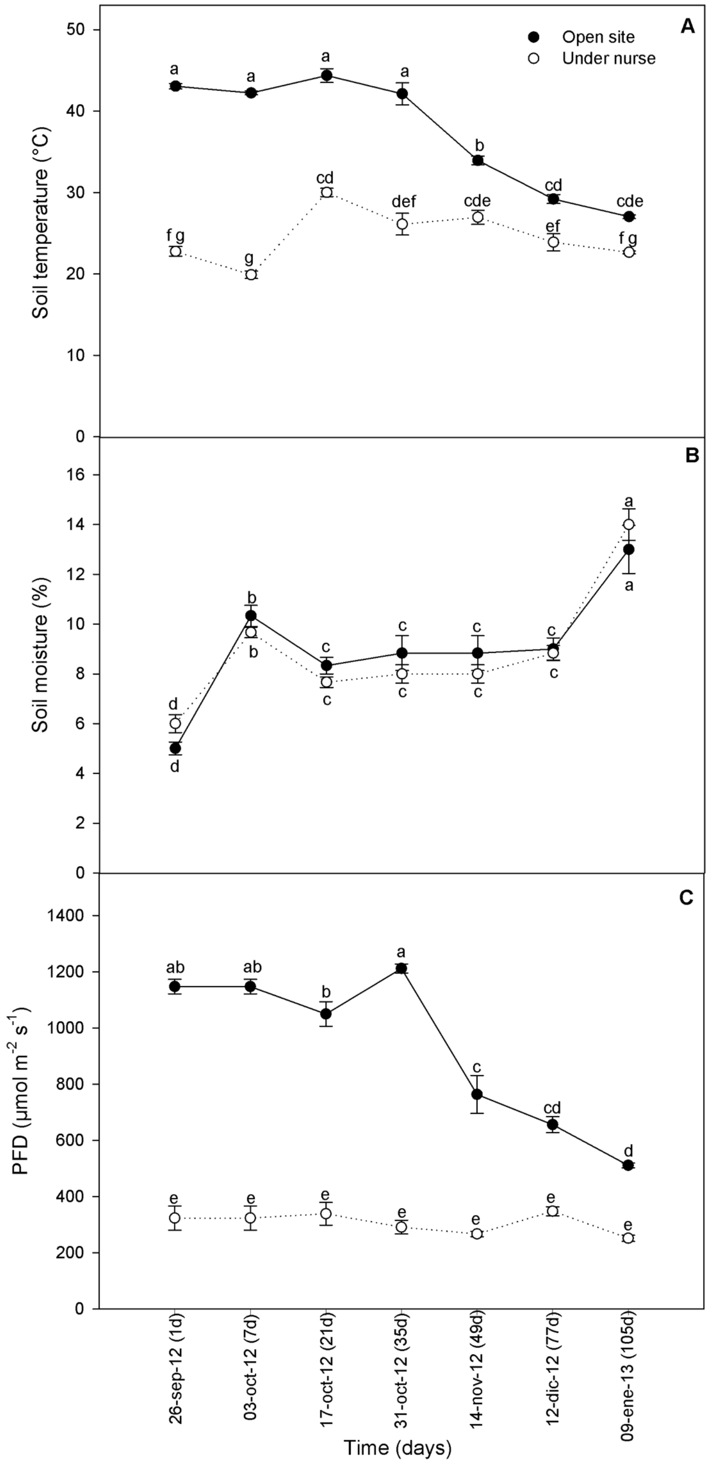

Fig. 1. Environmental variables (mean ± SE) at different harvest times: (A) soil temperature, (B) soil moisture, and (C) light (PFD, photosynthetic flux density). Data collected from 12:00 to 14:00 h.

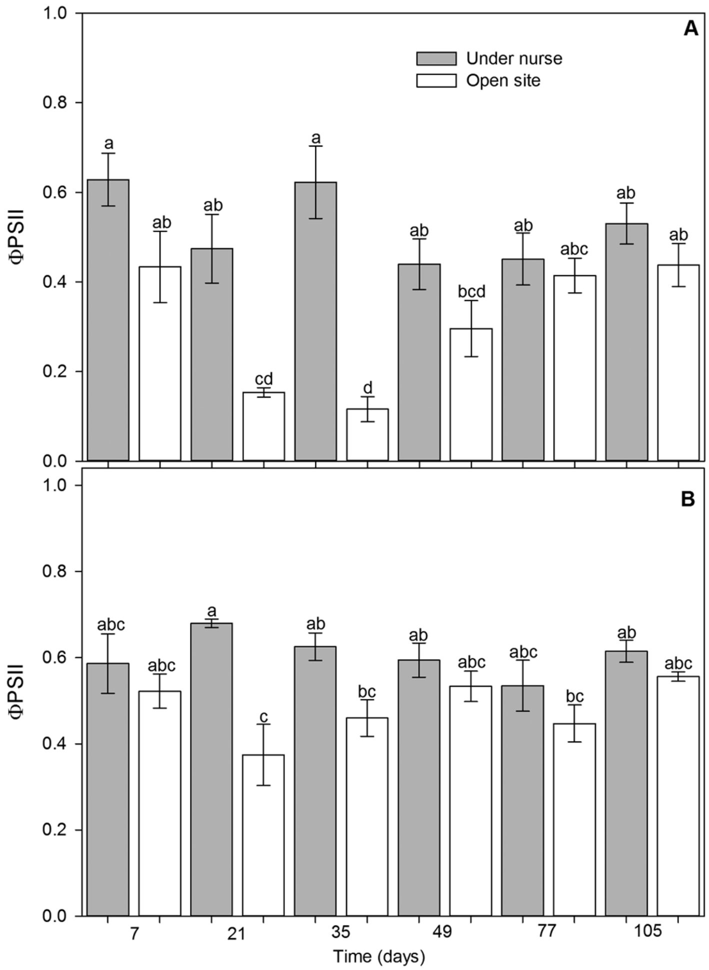

Fig. 2. Effect of microenvironment × time interaction on quantum yield of photosystem II photochemistry (Φ_{PSII}) (mean ± SE) for (A) *Yucca filifera* and (B) *Myrtillocactus geometrizans*. Different letters indicate statistical differences ($P < 0.05$).

of seedlings of two species differed, *Echinocactus platyacanthus* ($F = 4.295$, $P = 0.044$) and *Stenocactus coptonogonus* ($F = 15.51$, $P < 0.001$), with lower LAR under nurse trees (0.147 ± 0.009 for *E. platyacanthus*; and 0.114 ± 0.004 for *S. coptonogonus*) than under direct sunlight (0.173 ± 0.012 for *E. platyacanthus* and 0.149 ± 0.009 for *S. coptonogonus*). LAR differed in time across species but was not affected by the time × light interaction (Appendix: Table A6).

Root/shoot ratio (R/S).—In general time to harvest and microenvironment showed no effect on R/S for any of the studied species (Appendix: Table A7). R/S of *Myrtillocactus geometrizans* seedlings was affected by time ($F = 7.386$, $P <$ 0.001) and by the microenvironment × time interaction ($F = 2.64$, $P < 0.035$; Appendix: Table A7), in that R/S was higher at 35 d under the shade and lower at 77 d under the shade. However, seedlings of *M. geometrizans* always had heavier shoots than roots.

Relative water content (RWC).—RWC of *Stenocactus coptonogonus* seedlings differed according to microenvironment ($F = 20.13$, $P < 0.001$; Appendix: Table A8). RWC was higher for seedlings grown under direct sunlight (62.68 ± 1.35) than for those grown in the shade of nurse trees (55.55 ± 1.56). Time had a significant effect on RWC of seedlings across species (Appendix: Table A8). The time × microenvironment inter-

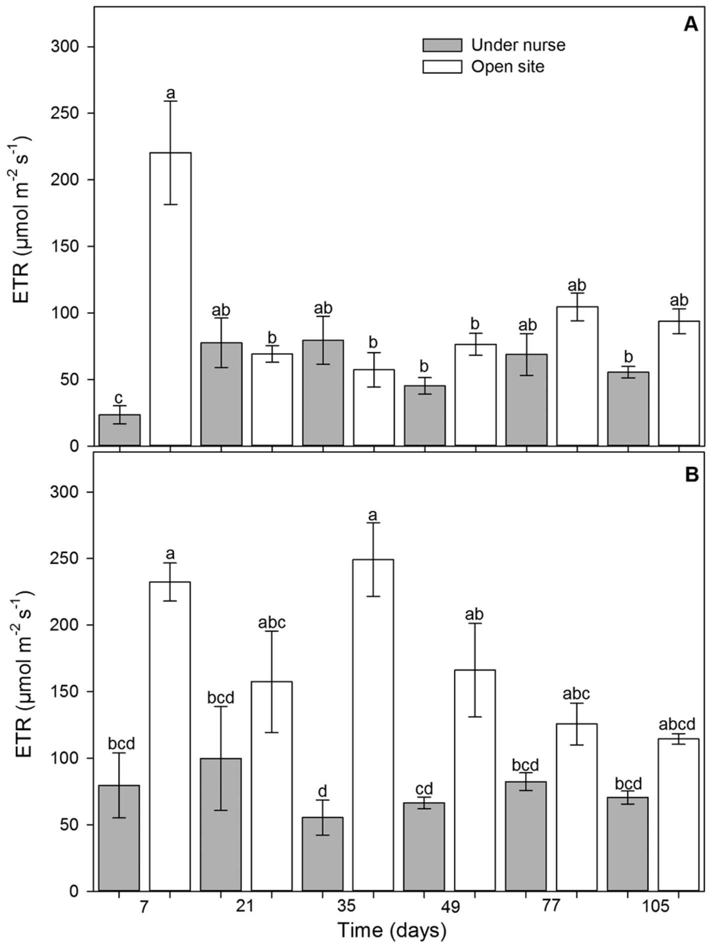

Fig. 3. Effect of microenvironment × time interaction on electronic transport rate (ETR) (mean ± SE) for (A) *Yucca filifera* and (B) *Myrtillocactus geometrizans*. Different letters indicate statistical differences ($P < 0.05$).

action was significant for the RWC of *Agave salmiana* seedlings ($F = 3.0$, $P = 0.020$), in that RWC was higher for nursed seedlings on days 7 and 105 (85.33 ± 1.38 and 88.59 ± 0.81) than for seedlings grown under direct sunlight on day 7 (85.57 ± 0.92).

Discussion

Lower Φ_{PSII}, ETR, LAR, R/S ratio, and RWC, but higher RGR and NAR, were expected for seedlings grown under direct sunlight than for those grown under nurse plants. This hypothesis was partially fulfilled, in that Φ_{PSII} of seedlings from all species was greater under nurse plants than in open spaces, which means that seedlings in open spaces had higher stress. The Φ_{PSII} has become an important tool for determining the level of stress on plant photosynthetic processes (Maxwell and Johnson 2000).

This is the first field experiment evaluating variables of chlorophyll fluorescence for succulent species as mechanisms of nurse effect, so there are no other field results to compare, however our expectations were generally met. Yang et al. (2010) evaluated chlorophyll fluorescence parameters for seedlings of the non-succulents *Schima superba*, *Michelia macclurei*, and *Castanopsis fissa* from South China, under a nurse plant (*Rhodomyrtus tomentosa*) and in open sites. Authors found that *M. macclurei* had higher maximum photochemical efficiency of Φ_{PSII} (F_v/F_m) for seedlings under *R. tomentosa*, whereas F_v/F_m was lower at open spaces, which indicates

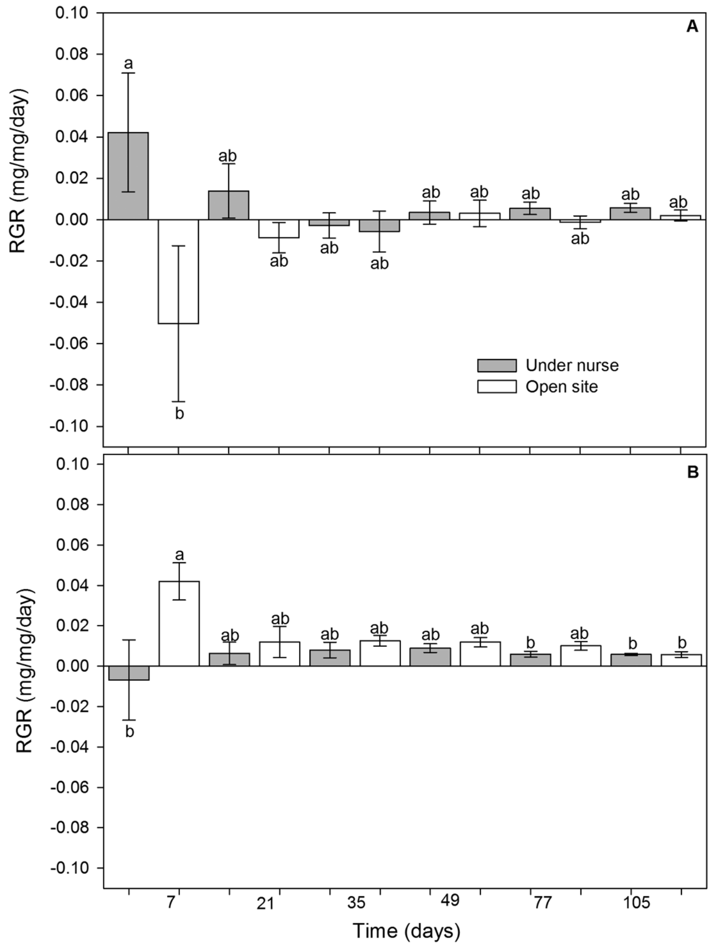

Fig. 4. Effect of microenvironment × time interaction on relative growth rate (RGR) (mean ± SE) for (A) *Yucca filifera* and (B) *Agave salmiana*. Different letters indicate statistical differences ($P < 0.05$).

that nurse plant efficiently helps the photosynthetic complex to adequately function. Similar results were found by Rodríguez-Calcerrada et al. (2008) for *Quercus petraea* and *Q. pirenaica*, also non-succulent plants. Liu et al. (2014) also studied the beneficial effects of a native shrub (*Rhodomyrtus tomentosa*) on seedling establishment of two tree species in Tropical China. They found that photoinhibition was reduced for *Castanopsis fissa* seedlings under medium canopies and for *Syzygium hancei* seedlings under large canopies. The different response between species is in agreement with our results in that our species did not respond equally to treatments.

Contrary to our hypothesis, the other response variable of chlorophyll fluorescence, ETR, was greater across species for seedlings grown under direct sunlight. Highly succulent tissues have greatly enlarged vacuoles that occupy more than 90% of the cell volume, helping to improve their water storage capacity (Ogburn and Edwards 2010). This capacity could explain why we did not find differences in RWC between treatments (under nurse plants and under direct sunlight) for most species. The size of the vacuole determines the capacity to store malic acid (De Mattos and Lüttge 2001), which is also required as a source of CO_2 to maintain a high level of electron transport (Barker and Adams 1997). Thus, high ETR at excess radiation indicates down regulation of $_{PSII}$, rather than photoinhibition or photodamage (Cheeseman et al. 1997, Rossa and von Willert 1999).

Higher RGR and lower R/S was expected for seedlings grown under direct sunlight than for those grown under nurse plants as a result of a lower photosynthesis rate for shaded seedlings. We did not find an effect of time to harvest and shade on R/S for any of the studied species, but R/S values were low in general, similar to findings by Miquelajauregui and Valverde (2010) for seedlings of two cactus species, *Neobuxbaumia macrocephala* and *N. mezcalaensis*, under shade and well lit conditions, indicating that more biomass was allocated to the shoot development than to the root.

Higher RGR was expected for seedlings grown under direct sunlight. However this was the case for only *Agave salmiana*. These results are similar to findings by Ruedas et al. (2000), that found higher RGR for seedlings of *Mammillaria magnimamma* (Cactaceae) at full solar radiation than under 40% light; and to Miquelajauregui and Valverde (2010), that found higher RGR for two columnar cacti (*Neobuxbaumia macrocephala* and *N. mezcalaensis*) at high solar radiation (189 ± 38 μmol $m^{-2}s^{-1}$) than under the shade (76 ± 4.7 μmol $m^{-2}s^{-1}$). In contrast, seedlings of two species, *Y. filifera* and *M. geometrizans*, had higher RGR under nurse plants, which implies that for these species the microenvironment under nurse plants is a safer site to establish than under direct sunlight. These results are in agreement with findings by Cardillo and Bernal (2006) for seedlings of the non-succulent *Quercus suber*. Delgado-Sánchez et al. (2013) found higher RGR for watered seedlings of *Opuntia streptacantha* (Cactaceae) under shade than under high solar radiation.

Higher NAR was expected for seedlings grown under direct sunlight than for those grown under nurse plants as a result of a lower photosynthesis rate for shaded seedlings. However, NAR was not affected by time, light or their interaction. Our findings are in contrast to results by Cardillo and Bernal (2006) for seedlings of the non-succulent *Quercus suber*. These differences may be by the type of species evaluated, having lower growth and photosynthetic area the succulent species than *Quercus* spp. seedlings.

Higher LAR, the morphological component of the RGR, was expected for seedlings grown under nurse plants than for those grown under direct sunlight, because seedlings in the shade might require a higher leaf area to capture light for photosynthesis (Kitajima 1994). However, two species (*Echinocactus platyacanthus* and *Stenocactus coptonogonus*), had lower LAR under nurse trees than under direct sunlight and the other species were no affected by the treatment.

In conclusion, succulent seedlings grown under nurse plants had higher Φ_{PSII} and lower ETR than those grown under direct sunlight. RWC, R/S ratio, and RGR and its components varied in response to microenvironments for some species but not consistently. In this study we transplanted seedlings under nurse plants and in open spaces. The physiological and morphological response of seedlings from seeds sown in the field remains to be evaluated, but higher survival has been found under nurse plants for seedlings grown from seeds than for those in open spaces (Flores et al. 2004). This is the first study evaluating growth responses at both physiological and morphological levels for seedlings of succulent species under nurse plants and under high solar radiation. These results give us a better comprehension of the mechanisms of succulent seedlings to survive under environmental stresses, and they could have important implications for planning reforestation practices and rural land uses, as well as for predicting the impact of climate change on natural desert regeneration. In here we have shown that succulent seedlings may be responding to elevated radiation not necessarily with morphology, but also with physiological changes to compensate growth.

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Supplemental Material

Appendix A

Table A1. Effect of microenvironment, time, and their interaction on quantum yield of photosystem II photochemistry (Φ_{PSII}) for the seven species studied. An asterisk indicates significant effect ($P < 0.05$).

Category and statistic	Al	As	Ep	Fh	Mg	Sc	Yf
Microenvironment							
F	0.058	0.399	0.075	1.014	3.783	0.356	0.384
P	0.101	0.530	0.785	0.319	0.058	0.553	0.538
Under nurse plants							

Table A1. Continued.

Category and statistic	Al	As	Ep	Fh	Mg	Sc	Yf
Mean	0.254	0.286	0.152	0.214	0.253	0.610	0.848
SE	(0.021)	(0.012)	(0.009)	(0.024)	(0.033)	(0.047)	(0.046)
Open site							
Mean	0.246	0.274	0.149	0.179	0.195	0.636	0.897
SE	(0.022)	(0.016)	(0.009)	(0.012)	(0.018)	(0.038)	(0.066)
Time (days)							
F	1.450	0.996	2.275	1.793	7.386	0.759	2.381
P	0.224	0.430	0.062	0.132	<0.001*	0.584	0.052
7							
Mean	0.315	0.255	0.151	0.192	0.156	0.577	0.640
SE	(0.048)	(0.029)	(0.016)	(0.016)	(0.016)[b]	(0.065)	(0.060)
21							
Mean	0.204	0.284	0.142	0.223	0.191	0.731	0.806
SE	(0.027)	(0.031)	(0.012)	(0.067)	(0.023)[ab]	(0.111)	(0.094)
35							
Mean	0.290	0.325	0.175	0.232	0.381	0.543	0.815
SE	(0.041)	(0.014)	(0.008)	(0.021)	(0.080)[a]	(0.073)	(0.046)
49							
Mean	0.239	0.270	0.126	0.158	0.171	0.575	0.951
SE	(0.042)	(0.022)	(0.015)	(0.015)	(0.022)[b]	(0.059)	(0.122)
77							
Mean	0.209	0.270	0.135	0.145	0.140	0.676	0.963
SE	(0.023)	(0.025)	(0.018)	(0.014)	(0.011)[b]	(0.075)	(0.076)
105							
Mean	0.243	0.275	0.177	0.229	0.305	0.635	1.059
SE	(0.025)	(0.018)	(0.015)	(0.031)	(0.029)[a]	(0.043)	(0.127)
Microenvironment × Time (days)							
F	0.62	0.94	1.77	0.80	2.64	0.56	0.25
P	0.69	0.46	0.14	0.55	0.036*	0.73	0.94
Under nurse plants/7 d							
Mean	0.365	0.255	0.184	0.197	0.173	0.614	0.695
SE	(0.055)	(0.038)	(0.020)	(0.024)	(0.009)[bc]	(0.094)	(0.097)
Under nurse plants/21 d							
Mean	0.200	0.309	0.135	0.307	0.237	0.796	0.718
SE	(0.040)	(0.036)	(0.017)	(0.127)	(0.031)[abc]	(0.205)	(0.087)
Under nurse plants/35 d							
Mean	0.310	0.296	0.175	0.246	0.529	0.572	0.782
SE	(0.075)	(0.016)	(0.017)	(0.034)	(0.123)[a]	(0.144)	(0.085)
Under nurse plants/49 d							
Mean	0.217	0.264	0.138	0.16	0.158	0.483	0.950
SE	(0.027)	(0.037)	(0.029)	(0.02)	(0.033)[bc]	(0.015)	(0.144)
Under nurse plants/77 d							
Mean	0.215	0.306	0.126	0.130	0.131	0.614	0.917
SE	(0.029)	(0.016)	(0.022)	(0.019)	(0.022)[c]	(0.095)	(0.105)
Under nurse plants/105 d							
Mean	0.215	0.287	0.157	0.246	0.289	0.582	1.027
SE	(0.033)	(0.027)	(0.023)	(0.046)	(0.040)[abc]	(0.039)	(0.121)
Open site/7 d							
Mean	0.264	0.254	0.118	0.188	0.140	0.540	0.585
SE	(0.077)	(0.048)	(0.013)	(0.025)	(0.031)[bc]	(0.097)	(0.071)
Open site/21 d							
Mean	0.209	0.258	0.149	0.139	0.145	0.667	0.894
SE	(0.041)	(0.053)	(0.018)	(0.015)	(0.022)[bc]	(0.105)	(0.168)
Open site/35 d							
Mean	0.271	0.354	0.175	0.219	0.233	0.514	0.849
SE	(0.044)	(0.013)	(0.004)	(0.029)	(0.056)[abc]	(0.055)	(0.043)
Open site/49 d							
Mean	0.260	0.277	0.114	0.157	0.184	0.667	0.953
SE	(0.084)	(0.029)	(0.008)	(0.026)	(0.032)[bc]	(0.106)	(0.215)
Open site/77 d							
Mean	0.203	0.234	0.143	0.160	0.148	0.739	1.009
SE	(0.039)	(0.044)	(0.032)	(0.019)	(0.007)[bc]	(0.119)	(0.118)
Open site/105 d							
Mean	0.271	0.264	0.197	0.211	0.321	0.688	1.090
SE	(0.036)	(0.024)	(0.019)	(0.046)	(0.044)[ab]	(0.075)	(0.241)

Note: Species abbreviations are: Al, *A. lechuguilla*; As, *A. salmiana*; Ep, *E. platyacanthus*; Fh, *F. histrix*; Mg, *M. geometrizans*; Sc, *S. coptonogonus*; Yf, *Y. filifera*.

Table A2. Effect of microenvironment, time, and their interaction on electronic transport rate (ETR) (μmol m^{-2} s^{-1}) for the seven species studied. An asterisk indicates significant effect ($P < 0.05$).

Category and statistic	Al	As	Ep	Fh	Mg	Sc	Yf
Microenvironment							
F	3.66	1.68	2.15	1.89	0.05	20.13	0.10
P	0.06	0.20	0.15	0.18	0.83	<0.001*	0.75
Under nurse plants							
Mean	81.98	80.58	61.01	53.60	62.80	55.55	82.27
SE	(1.18)	(1.02)	(2.11)	(2.21)	(1.77)	(1.56)^{b}	(0.94)
Open site							
Mean	80.04	79.39	63.96	55.94	63.31	62.68	82.00
SE	(0.84)	(0.89)	(1.85)	(2.03)	(2.08)	(1.35)^{a}	(0.93)
Time (days)							
F	12.02	12.47	12.05	25.38	14.69	9.11	17.81
P	<0.001*	<0.001*	<0.001*	<0.001	<0.001*	<0.001*	<0.001*
7							
Mean	87.21	85.45	76.74	72.20	72.18	68.07	88.79
SE	(1.00)^{a}	(0.78)^{a}	(1.10)^{a}	(2.74)^{a}	(1.61)^{a}	(1.30)^{a}	(0.70)^{a}
21							
Mean	80.26	77.72	61.67	48.03	56.97	55.90	79.24
SE	(0.75)^{bc}	(1.20)^{b}	(2.20)^{bc}	(1.73)^{cd}	(2.07)^{bc}	(2.03)^{c}	(1.28)^{b}
35							
Mean	79.13	79.08	55.55	46.79	65.51	57.38	81.36
SE	(0.998)^{c}	(1.27)^{b}	(2.65)^{c}	(1.81)^{cd}	(4.17)^{ab}	(1.73)^{bc}	(0.51)^{b}
49							
Mean	79.04	75.25	61.80	54.39	55.81	56.51	77.92
SE	(1.237)^{c}	(1.42)^{b}	(1.81)^{bc}	(2.35)^{bc}	(1.49)^{bc}	(3.02)^{bc}	(1.32)^{b}
77							
Mean	75.47	78.23	52.71	45.48	53.98	52.45	79.26
SE	(1.915)^{c}	(0.82)^{b}	(2.91)^{c}	(2.34)^{d}	(1.51)^{c}	(2.31)^{c}	(1.14)^{b}
105							
Mean	84.95	84.15	66.46	61.75	73.87	64.39	86.29
SE	(1.68)^{ab}	(1.64)^{a}	(3.52)^{ab}	(1.57)^{b}	(1.17)^{a}	(2.68)^{ab}	(0.86)^{a}
Microenvironment × Time (days)							
F	2.04	3.0	1.06	1.37	0.45	0.84	0.57
P	0.09	0.02*	0.39	0.25	0.81	0.53	0.72
Under nurse plants/7 d							
Mean	87.86	85.33	75.24	72.56	73.06	66.37	88.515
SE	(1.83)	(1.38)^{ab}	(1.47)	(1.43)	(1.39)	(2.21)	(0.27)
Under nurse plants/21 d							
Mean	81.19	77.06	65.00	46.23	59.09	53.06	78.316
SE	(0.82)	(0.94)^{c}	(2.92)	(1.65)	(2.73)	(1.05)	(1.66)
Under nurse plants/35 d							
Mean	80.30	79.30	53.50	46.14	64.10	55.59	81.450
SE	(1.24)	(1.42)^{bc}	(1.45)	(3.22)	(4.48)	(2.63)	(0.94)
Under nurse plants/49 d							
Mean	78.44	75.73	57.70	50.38	55.59	50.44	77.770
SE	(2.06)	(2.12)^{c}	(2.16)	(2.67)	(2.32)	(4.51)	(2.15)
Under nurse plants/77 d							
Mean	74.89	77.44	50.91	42.07	52.29	48.61	79.997
SE	(3.54)	(1.15)^{c}	(5.80)	(2.62)	(1.69)	(2.77)	(1.54)
Under nurse plants/105 d							
Mean	89.19	88.59	63.73	64.25	72.65	59.25	87.578
SE	(0.53)	(0.81)^{a}	(6.62)	(1.61)	(1.92)	(3.47)	(0.73)
Open site/7 d							
Mean	86.56	85.57	78.23	71.84	71.30	69.77	89.063
SE	(0.96)	(0.92)^{ab}	(1.48)	(5.63)	(3.07)	(1.11)	(1.44)
Open site/21 d							
Mean	79.34	78.37	58.34	49.83	54.85	58.74	80.170
SE	(1.20)	(2.33)^{bc}	(2.77)	(3.03)	(3.10)	(3.65)	(2.05)
Open site/35 d							
Mean	77.96	78.87	57.59	47.44	66.92	59.18	81.277
SE	(1.50)	(2.29)^{bc}	(5.23)	(2.04)	(7.56)	(2.21)	(0.56)
Open site/49 d							
Mean	79.64	74.77	65.90	58.40	56.03	62.57	78.062
SE	(1.57)	(2.12)^{c}	(1.33)	(3.10)	(2.17)	(1.52)	(1.78)
Open site/77 d							
Mean	76.05	79.02	54.50	48.89	55.67	56.29	78.434
SE	(1.96)	(1.2)^{bc}	(1.66)	(3.46)	(2.45)	(3.00)	(1.77)

Table A2. Continued.

Category and statistic	Al	As	Ep	Fh	Mg	Sc	Yf
Open site/105 d							
Mean	80.70	79.71	69.18	59.25	75.10	69.54	85.004
SE	(1.86)	(1.27)[bc]	(2.85)	(2.30)	(1.30)	(2.67)	(1.40)

Note: Species abbreviations are: Al, *A. lechuguilla*; As, *A. salmiana*; Ep, *E. platyacanthus*; Fh, *F. histrix*; Mg, *M. geometrizans*; Sc, *S. coptonogonus*; Yf, *Y. filifera*.

Table A3. Effect of microenvironment, time, and their interaction on relative growth rate (RGR; mg day^{-1} mg^{-1}) for *A. lechuguilla* (Al), *A. salmiana* (As), *E. platyacanthus* (Ep) and *F. histrix* (Fh). An asterisk indicates significant effect ($P < 0.05$).

Category and statistic	Al	As	Ep	Fh
Microenvironment				
F	19.05	7.92	7.52	31.10
P	0.002*	0.023*	0.025*	0.001*
Under nurse plants				
Mean	0.61	0.61	0.66	0.67
SE	(0.04)[a]	(0.02)[a]	(0.02)[a]	(0.03)[a]
Open site				
Mean	0.36	0.53	0.58	0.43
SE	(0.04)[b]	(0.02)[b]	(0.02)[b]	(0.03)[b]
Time (days)				
F	3.47	1.54	2.38	2.71
P	0.011*	0.201	0.056	0.034*
7				
Mean	0.52	0.59	0.60	0.61
SE	(0.05)[a]	(0.05)	(0.03)	(0.04)[a]
21				
Mean	0.54	0.57	0.64	0.57
SE	(0.03)[a]	(0.04)	(0.03)	(0.03)[ab]
35				
Mean	0.51	0.53	0.61	0.48
SE	(0.05)[ab]	(0.04)	(0.03)	(0.02)[b]
49				
Mean	0.45	0.59	0.63	0.51
SE	(0.04)[ab]	(0.04)	(0.04)	(0.04)[b]
77				
Mean	0.38	0.49	0.57	0.53
SE	(0.04)[b]	(0.04)	(0.04)	(0.04)[ab]
105				
Mean	0.53	0.63	0.68	0.59
SE	(0.04)[a]	(0.03)	(0.01)	(0.03)[a]
Microenvironment × Time (days)				
F	1.42	1.05	1.476	2.04
P	0.237	0.404	0.219	0.094
Under nurse plants/7 d				
Mean	0.64	0.66	0.66	0.68
SE	(0.06)	(0.07)	(0.04)	(0.06)
Under nurse plants/21 d				
Mean	0.71	0.62	0.72	0.68
SE	(0.04)	(0.05)	(0.04)	(0.04)
Under nurse plants/35 d				
Mean	0.68	0.63	0.67	0.68
SE	(0.07)	(0.06)	(0.04)	(0.02)
Under nurse plants/49 d				
Mean	0.59	0.63	0.62	0.65
SE	(0.06)	(0.06)	(0.05)	(0.06)
Under nurse plants/77 d				
Mean	0.46	0.50	0.61	0.61
SE	(0.06)	(0.06)	(0.05)	(0.06)
Under nurse plants/105 d				
Mean	0.60	0.62	0.71	0.71
SE	(0.06)	(0.04)	(0.01)	(0.05)
Open site/7 d				

Table A3. Continued.

Category and statistic	Al	As	Ep	Fh
Mean	0.41	0.52	0.55	0.53
SE	(0.06)	(0.07)	(0.04)	(0.06)
Open site/21 d				
Mean	0.38	0.52	0.55	0.45
SE	(0.04)	(0.05)	(0.04)	(0.04)
Open site/35 d				
Mean	0.34	0.43	0.54	0.29
SE	(0.07)	(0.06)	(0.04)	(0.02)
Open site/49 d				
Mean	0.31	0.56	0.63	0.36
SE	(0.06)	(0.06)	(0.05)	(0.05)
Open site/77 d				
Mean	0.30	0.49	0.53	0.44
SE	(0.06)	(0.06)	(0.05)	(0.06)
Open site/105 d				
Mean	0.45	0.65	0.66	0.47
SE	(0.06)	(0.04)	(0.01)	(0.05)

Table A4. Effect of microenvironment, time, and their interaction on relative growth rate (RGR; mg day^{-1} mg^{-1}) for *Myrtillocactus geometrizans* (Mg), *S. coptonogonus* (Sc), and *Y. filifera* (Yf). An asterisk indicates significant effect ($P < 0.05$).

Category and statistic	Mg	Sc	Yf
Microenvironment			
F	10.19	35.32	26.94
P	0.013*	<0.001*	0.001*
Under nurse plants			
Mean	0.61	0.69	0.53
SE	(0.03)^{a}	(0.03)^{a}	(0.03)^{a}
Open site			
Mean	0.48	0.50	0.31
SE	(0.03)^{b}	(0.03)^{b}	(0.03)^{b}
Time (days)			
F	1.49	3.94	4.54
P	0.215	0.005*	0.002*
7			
Mean	0.55	0.55	0.531
SE	(0.04)	(0.03)	(0.05)^{a}
21			
Mean	0.53	0.53	0.314
SE	(0.04)	(0.05)	(0.04)^{c}
35			
Mean	0.54	0.56	0.369
SE	(0.03)	(0.03)	(0.04)^{bc}
49			
Mean	0.56	0.65	0.368
SE	(0.03)	(0.02)	(0.04)^{bc}
77			
Mean	0.49	0.61	0.433
SE	(0.04)	(0.02)	(0.04)^{abc}
105			
Mean	0.59	0.67	0.484
SE	(0.01)	(0.03)	(0.03)^{ab}
Microenvironment × Time (days)			
F	3.36	0.30	5.09
P	0.013*	0.908	0.001*
Under nurse plants/7 d			
Mean	0.59	0.65	0.63
SE	(0.06)^{abc}	(0.04)	(0.07)^{a}
Under nurse plants/21 d			
Mean	0.68	0.65	0.47

Table A4. Continued.

Category and statistic	Mg	Sc	Yf
SE	(0.05)^{a}	(0.08)	(0.06)^{ab}
Under nurse plants/35 d			
Mean	0.63	0.68	0.62
SE	(0.04)^{ab}	(0.04)	(0.06)^{a}
Under nurse plants/49 d			
Mean	0.59	0.73	0.44
SE	(0.04)^{ab}	(0.03)	(0.06)^{ab}
Under nurse plants/77 d			
Mean	0.54	0.70	0.45
SE	(0.05)^{abc}	(0.03)	(0.05)^{ab}
Under nurse plants/105 d			
Mean	0.62	0.74	0.53
SE	(0.02)^{ab}	(0.04)	(0.05)^{ab}
Open site/7 d			
Mean	0.52	0.46	0.43
SE	(0.06)^{abc}	(0.04)	(0.07)^{ab}
Open site/21 d			
Mean	0.37	0.41	0.15
SE	(0.05)^{c}	(0.08)	(0.06)^{cd}
Open site/35 d			
Mean	0.46	0.45	0.12
SE	(0.04)^{bc}	(0.04)	(0.06)^{d}
Open site/49 d			
Mean	0.53	0.57	0.30
SE	(0.04)^{abc}	(0.03)	(0.06)^{bcd}
Open site/77 d			
Mean	0.45	0.51	0.41
SE	(0.05)^{bc}	(0.03)	(0.05)^{abc}
Open site/105 d			
Mean	0.56	0.60	0.44
SE	(0.02)^{abc}	(0.04)	(0.05)^{ab}

Table A5. Effect of microenvironment, time, and their interaction on net assimilation rate (NAR; mg day^{-1} cm^{-2}) for the seven species studied. An asterisk indicates significant effect ($P < 0.05$).

Category and statistic	Al	As	Ep	Fh	Mg	Sc	Yf
Microenvironment							
F	11.67	51.04	133.40	34.91	93.34	40.31	11.09
P	0.009*	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*	0.010*
Under nurse plants							
Mean	78.50	82.38	77.16	81.70	75.68	93.85	58.41
SE	(12.94)[b]	(8.51)[b]	(8.21)	(8.92)[b]	(9.54)[b]	(9.01)[b]	(8.08)[b]
Open site							
Mean	136.48	183.49	211.19	150.38	174.18	174.78	103.64
SE	(12.94)[a]	(8.51)[a]	(8.21)	(8.92)[a]	(9.54)[a]	(9.01)[a]	(8.08)[a]
Time (days)							
F	4.34	0.93	6.50	3.79	0.83	2.51	3.73
P	0.003*	0.48	<0.001*	0.01*	0.538	0.045*	0.007*
7							
Mean	118.93	160.63	195.53	202.17	155.92	172.1	121.96
SE	(16.71)[abc]	(14.84)	(29)[a]	(27.7)[a]	(14.1)	(24.7)[a]	(19.67)[b]
21							
Mean	153.34	154.24	168.19	109.37	128.59	133.41	73.44
SE	(25.98)[a]	(23.46)	(23.70)[ab]	(11.8)[b]	(27.33)	(18.16)[ab]	(9.78)[ab]
35							
Mean	134.29	143.74	193.39	106.01	152.28	151.21	68.44
SE	(23.30)[ab]	(18.97)	(14.23)[a]	(8.68)[b]	(15.33)	(14.58)[ab]	(11.07)[ab]
49							
Mean	93.19	125.11	102.24	98.7	116.27	113.32	60.90
SE	(19.5)[abc]	(25.55)	(14.35)[b]	(12)[b]	(17.75)	(7.84)[ab]	(5.16)[ab]
77							
Mean	67.12	102.54	104.71	96.49	104.05	129.36	86.75
SE	(7.51)[c]	(7.59)	(6.42)[b]	(9.54)[b]	(8.51)	(11.82)[ab]	(9.39)[a]
105							
Mean	78.07	111.36	100.99	83.49	92.45	106.49	74.67
SE	(7.99)[bc]	(8.97)	(4.29)[b]	(7.45)[b]	(3.13)	(8.11)[b]	(5.10)[a]
Microenvironment × Time (days)							
F	2.20	1.5	2.20	2.1	3.53	1.82	21.24
P	0.073	0.192	0.0.78	0.082	0.010*	0.130	<0.001*
Under nurse plants/7 d							
Mean	54.86	73.7 6	113.4	131.12	79.54	133.5	23.54
SE	(23.64)	(20.99)	(41.01)	(39.13)	(19.94)[bcd]	(34.93)	(27.82)[c]
Under nurse plants/21 d							
Mean	127.46	125.52	75.04	58.62	99.82	62.8	77.6
SE	(36.75)	(33.17)	(33.52)	(16.77)	(38.65)[bcd]	(25.69)	(13.8)[ab]
Under nurse plants/35 d							
Mean	100.3	66.18	96.06	66.58	55.36	90.74	79.54
SE	(32.96)	(26.8)	(20.13)	(12.27)	(21.68)[d]	(20.61)	(15.7)[ab]
Under nurse plants/49 d							
Mean	57.6	80.42	52.33	79.38	66.44	91.63	45.28
SE	(27.6)	(36.13)	(20.29)	(17.05)	(25.10)[cd]	(11.09)	(7.3)[b]
Under nurse plants/77 d							
Mean	65.98	73.54	64.36	85.14	82.42	108.24	68.92
SE	(10.63)	(10.74)	(9.09)	(13.50)	(12.04)[bcd]	(16.72)	(13.3)[ab]
Under nurse plants/105 d							
Mean	64.82	74.88	61.78	69.36	70.48	76.22	55.58
SE	(11.3)	(12.68)	(6.06)	(10.54)	(4.43)[bcd]	(11.47)	(7.21)[b]
Open site/7 d							
Mean	183	247.5	277.66	273.22	232.3	210.7	220.38
SE	(23.64)	(20.99)	(41.01)	(39.13)	(19.94)[a]	(34.93)	(27.82)[a]
Open site/21 d							
Mean	179.22	182.96	261.34	160.12	157.36	204.02	69.28
SE	(36.75)	(33.17)	(33.52)	(16.77)	(38.65)[abc]	(25.69)	(13.83)[b]
Open site/35 d							
Mean	168.28	221.30	290.72	145.44	249.2	211.68	57.34
SE	(32.96)	(26.80)	(20.13)	(12.27)	(21.68)[a]	(20.61)	(15.7)[b]
Open site/49 d							
Mean	128.78	169.80	152.16	118.02	166.1	135.02	76.52
SE	(27.60)	(36.13)	(20.29)	(17.05)	(25.1)[ab]	(11.09)	(7.30)[b]
Open site/77 d							
Mean	68.26	131.54	145.06	107.84	125.68	150.48	104.58
SE	(10.63)	(10.74)	(9.09)	(13.50)	(12.04)[abc]	(16.72)	(13.3)[ab]

Table A5. Continued.

Category and statistic	Al	As	Ep	Fh	Mg	Sc	Yf
Open site/105 d							
Mean	91.32	147.84	140.20	97.62	114.42	136.76	93.76
SE	(11.3)	(12.68)	(6.06)	(10.54)	(4.43)^{abcd}	(11.47)	(7.21)^{ab}

Note: Species abbreviations are: Al, *A. lechuguilla*; As, *A. salmiana*; Ep, *E. platyacanthus*; Fh, *F. histrix*; Mg, *M. geometrizans*; Sc, *S. coptonogonus*; Yf, *Y. filifera*.

Table A6. Effect of microenvironment, time, and their interaction on leaf area rate (LAR; cm^2/mg) for the seven species studied. An asterisk indicates significant effect ($P < 0.05$).

Category and statistic	Al	As	Ep	Fh	Mg	Sc	Yf
Microenvironment							
F	2.79	7.14	0.03	2.07	4.89	0.96	6.30
P	0.101	0.010*	0.860	0.156	0.032*	0.333	0.016*
Under nurse plants							
Mean	0.006	0.005	0.012	−0.011	−0.002	0.000	0.011
SE	(0.004)	(0.003)^{b}	(0.004)	(0.006)	(0.007)^{b}	(0.005)	(0.006)^{a}
Open site							
Mean	0.013	0.016	0.011	0.001	0.006	0.006	−0.010
SE	(0.004)	(0.003)^{a}	(0.003)	(0.006)	(0.006)^{a}	(0.004)	(0.007)^{b}
Time (days)							
F	5.61	0.63	1.54	0.75	0.37	1.96	0.10
P	<0.001*	0.677	0.195	0.587	0.870	0.103	0.992
7							
Mean	0.036	0.018	0.026	−0.021	−0.004	0.025	−0.004
SE	(0.010)^{a}	(0.013)	(0.012)	(0.024)	(0.023)	(0.016)	(0.027)
21							
Mean	−0.003	0.009	0.006	−0.009	−0.002	−0.004	0.003
SE	(0.006)^{b}	(0.005)	(0.008)	(0.007)	(0.011)	(0.006)	(0.008)
35							
Mean	0.006	0.010	0.014	0.003	−0.002	−0.004	−0.004
SE	(0.004)^{b}	(0.002)	(0.014)	(0.006)	(0.007)	(0.003)	(0.005)
49							
Mean	0.009	0.010	0.008	−0.010	0.005	0.003	0.003
SE	(0.003)^{b}	(0.002)	(0.008)	(0.002)	(0.003)	(0.004)	(0.004)
77							
Mean	0.005	0.008	0.006	−0.010	0.007	−0.001	0.002
SE	(0.002)^{b}	(0.001)	(0.006)	(0.002)	(0.002)	(0.002)	(0.002)
105							
Mean	0.004	0.006	0.006	0.010	0.009	0.002	0.004
SE	(0.002)^{b}	(0.001)	(0.005)	(0.002)	(0.002)	(0.002)	(0.002)
Microenvironment × Time (days)							
F	3.42	7.14	0.12	1.23	1.65	0.12	2.87
P	0.010*	0.010*	0.987	0.310	0.165	0.989	0.024*
Under nurse plants/7 d							
Mean	0.03	−0.007	0.030	−0.05	−0.030	0.022	0.042
SE	(0.018)	(0.02)^{b}	(0.017)	(0.033)	(0.037)	(0.028)	(0.029)^{a}
Under nurse plants/21 d							
Mean	−0.009	0.006	0.003	−0.007	0.011	−0.011	0.014
SE	(0.007)	(0.006)^{b}	(0.015)	(0.01)	(0.005)	(0.008)	(0.013)^{ab}
Under nurse plants/35 d							
Mean	0.001	0.008	0.015	−0.006	−0.012	−0.006	−0.003
SE	(0.006)	(0.004)^{ab}	(0.008)	(0.010)	(0.007)	(0.004)	(0.006)^{ab}
Under nurse plants/49 d							
Mean	0.009	0.009	0.008	−0.007	0.003	0.003	0.003
SE	(0.004)	(0.002)^{ab}	(0.003)	(0.004)	(0.003)	(0.005)	(0.006)^{ab}
Under nurse plants/77 d							
Mean	0.001	0.006	0.007	0.008	0.008	−0.005	0.006
SE	(0.002)	(0.001)^{b}	(0.003)	(0.002)	(0.005)	(0.003)	(0.003)^{ab}
Under nurse plants/105 d							
Mean	0.002	0.006	0.006	0.002	0.010	0.000	0.006
SE	(0.002)	(0.001)^{b}	(0.001)	(0.003)	(0.004)	(0.002)	(0.002)^{ab}
Open site/7 d							
Mean	0.042	0.042	0.023	0.007	0.021	0.028	−0.050
SE	(0.013)	(0.009)^{a}	(0.017)	(0.035)	(0.027)	(0.019)	(0.038)^{b}

Table A6. Continued.

Category and statistic	Al	As	Ep	Fh	Mg	Sc	Yf
Open site/21 d							
Mean	0.003	0.012	0.010	0.004	−0.014	0.002	−0.009
SE	(0.009)	(0.008)[ab]	(0.009)	(0.008)	(0.021)	(0.009)	(0.007)[ab]
Open site/35 d							
Mean	0.011	0.013	0.012	0.011	0.009	−0.003	−0.006
SE	(0.005)	(0.003)[ab]	(0.005)	(0.007)	(0.011)	(0.004)	(0.010)[ab]
Open site/49 d							
Mean	0.008	0.012	0.008	−0.013	0.007	0.002	0.003
SE	(0.005)	(0.002)[ab]	(0.004)	(0.003)	(0.005)	(0.008)	(0.006)[ab]
Open site/77 d							
Mean	0.010	0.010	0.006	−0.001	0.005	0.004	−0.001
SE	(0.003)	(0.002)[ab]	(0.001)	(0.003)	(0.002)	(0.003)	(0.003)[ab]
Open site/105 d							
Mean	0.006	0.006	0.005	−0.001	0.008	0.004	0.002
SE	(0.002)	(0.001)[b]	(0.001)	(0.002)	(0.002)	(0.002)	(0.003)[ab]

Note: Species abbreviations are: Al, *A. lechuguilla*; As, *A. salmiana*; Ep, *E. platyacanthus*; Fh, *F. histrix*; Mg, *M. geometrizans*; Sc, *S. coptonogonus*; Yf, *Y. filifera*.

Table A7. Effect of microenvironment, time, and their interaction on root to shoot (R/S) ratio for the seven species studied. An asterisk indicates significant effect ($P < 0.05$).

Category and statistic	Al	As	Ep	Fh	Mg	Sc	Yf
Microenvironment							
F	1.89	0.001	0.24	2.06	1.16	1.61	2.74
P	0.18	0.93	0.624	0.16	0.286	0.211	0.1
Under nurse plants							
Mean	0.158	0.145	0.068	−0.032	−0.007	−0.012	0.421
SE	(0.100)	(0.072)	(0.019)	(0.03)	(0.037)	(0.031)	(0.18)
Open site							
Mean	0.250	0.405	0.055	0.017	0.047	0.037	−0.344
SE	(0.062)	(0.069)	(0.015)	(0.02)	(0.031)	(0.022)	(0.28)
Time (days)							
F	3.52	40.93	0.997	0.4	0.18	1.36	0.5
P	0.009*	<0.001*	0.43	0.85	0.97	0.26	0.78
7							
Mean	0.719	0.392	0.109	−0.043	−0.029	0.115	−0.089
SE	(0.239)	(0.285)[a]	(0.048)	(0.09)	(0.129)	(0.094)	(0.97)
21							
Mean	−0.074	0.221	0.047	0.000	0.002	−0.038	0.035
SE	(0.126)	(0.114)[b]	(0.042)	(0.03)	(0.056)	(0.043)	(0.29)
35							
Mean	0.130	0.279	0.091	0.023	0.008	−0.029	−0.203
SE	(0.102)	(0.062)[bc]	(0.029)	(0.029)	(0.043)	(0.020)	(0.25)
49							
Mean	0.238	0.311	0.047	−0.037	0.028	0.018	0.225
SE	(0.080)	(0.05)[cd]	(0.015)	(0.01)	(0.020)	(0.030)	(0.16)
77							
Mean	0.118	0.272	0.042	0.002	0.048	−0.010	0.096
SE	(0.053)	(0.056)[d]	(0.013)	(0.006)	(0.018)	(0.020)	(0.11)
105							
Mean	0.094	0.175	0.032	0.01	0.065	0.017	0.167
SE	(0.038)	(0.02)[cd]	(0.007)	(0.01)	(0.016)	(0.014)	(0.08)
Microenvironment × Time (days)							
F	0.36	1.86	0.29	1.19	1.48	0.13	0.73
P	0.87	0.12	0.918	0.33	0.21	0.99	0.61
Under nurse plants/7 d							
Mean	0.736	−0.164	0.14	−0.151	−0.177	0.086	1.52
SE	(0.449)	(0.397)	(0.073)	(0.13)	(0.208)	(0.172)	(0.82)
Under nurse plants/21 d							
Mean	−0.218	0.176	0.026	−0.017	0.057	−0.086	0.507
SE	(0.207)	(0.131)	(0.07)	(0.06)	(0.026)	(0.06)	(0.39)
Under nurse plants/35 d							
Mean	0.052	0.211	0.103	−0.018	−0.072	−0.045	−0.156

Table A7. Continued.

Category and statistic	Al	As	Ep	Fh	Mg	Sc	Yf
SE	(0.182)	(0.103)	(0.051)	(0.04)	(0.048)	(0.032)	(0.23)
Under nurse plants/49 d							
Mean	0.295	0.271	0.051	−0.024	0.012	0.017	0.141
SE	(0.124)	(0.071)	(0.023)	(0.01)	(0.020)	(0.037)	(0.23)
Under nurse plants/77 d							
Mean	0.025	0.195	0.047	0.01	0.061	−0.048	0.266
SE	(0.064)	(0.051)	(0.026)	(0.01)	(0.034)	(0.025)	(0.13)
Under nurse plants/105 d							
Mean	0.061	0.184	0.040	0.014	0.079	0.002	0.246
SE	(0.050)	(0.020)	(0.012)	(0.01)	(0.029)	(0.019)	(0.09)
Open site/7 d							
Mean	0.701	0.949	0.079	0.065	0.119	0.144	−1.7
SE	(0.234)	(0.231)	(0.067)	(0.13)	(0.143)	(0.099)	(1.51)
Open site/21 d							
Mean	0.070	0.266	0.068	0.017	−0.054	0.01	−0.438
SE	(0.137)	(0.200)	(0.054)	(0.03)	(0.11)	(0.060)	(0.34)
Open site/35 d							
Mean	0.209	0.347	0.079	0.065	0.087	−0.013	−0.251
SE	(0.103)	(0.066)	(0.032)	(0.04)	(0.054)	(0.026)	(0.48)
Open site/49 d							
Mean	0.183	0.350	0.043	−0.050	0.044	0.019	0.308
SE	(0.108)	(0.060)	(0.022)	(0.01)	(0.035)	(0.050)	(0.25)
Open site/77 d							
Mean	0.212	0.349	0.037	0.000	0.036	0.029	−0.074
SE	(0.066)	(0.092)	(0.007)	(0.01)	(0.016)	(0.022)	(0.17)
Open site/105 d							
Mean	0.127	0.167	0.024	0.003	0.052	0.032	0.089
SE	(0.058)	(0.044)	(0.007)	(0.01)	(0.013)	(0.020)	(0.13)

Note: Species abbreviations are: Al, *A. lechuguilla*; As, *A. salmiana*; Ep, *E. platyacanthus*; Fh, *F. histrix*; Mg, *M. geometrizans*; Sc, *S. coptonogonus*; Yf, *Y. filifera*.

Table A8. Effect of microenvironment, time, and their interaction on relative water content (RWC) (%) for the seven species studied. An asterisk indicates significant effect ($P < 0.05$).

Category and statistic	Al	As	Ep	Fh	Mg	Sc	Yf
Microenvironment							
F	2.48	0.16	4.30	1.98	0.79	15.51	0.002
P	0.12	0.69	0.04*	0.17	0.38	<0.001*	0.97
Under nurse plants							
Mean	0.038	0.032	0.147	0.185	0.146	0.114	0.023
SE	(0.002)	(0.002)	(0.009)^{b}	(0.010)	(0.010)	(0.005)^{b}	(0.001)
Open site							
Mean	0.041	0.032	0.173	0.206	0.155	0.149	0.024
SE	(0.002)	(0.002)	(0.012)^{a}	(0.012)	(0.012)	(0.009)^{a}	(0.002)
Time (days)							
F	7.12	38.67	8.37	4.49	8.16	5.22	9.48
P	<0.001*	<0.001*	<0.001*	0.002*	<0.001*	0.001*	<0.001*
7							
Mean	0.046	0.050	0.236	0.267	0.216	0.159	0.037
SE	(0.003)^{ab}	(0.003)^{a}	(0.014)^{a}	(0.020)^{a}	(0.014)^{a}	(0.013)^{a}	(0.004)^{a}
21							
Mean	0.049	0.037	0.175	0.179	0.167	0.117	0.024
SE	(0.002)^{a}	(0.002)^{b}	(0.018)^{ab}	(0.01)^{b}	(0.013)^{ab}	(0.007)^{ab}	(0.001)^{b}
35							
Mean	0.040	0.031	0.133	0.163	0.155	0.154	0.024
SE	(0.002)^{abc}	(0.001)^{bc}	(0.019)^{bc}	(0.011)^{b}	(0.031)^{bc}	(0.016)^{a}	(0.002)^{b}
49							
Mean	0.033	0.027	0.152	0.210	0.131	0.135	0.019
SE	(0.002)^{c}	(0.001)^{c}	(0.013)^{bc}	(0.021)^{ab}	(0.006)^{bc}	(0.014)^{ab}	(0.002)^{b}
77							
Mean	0.032	0.022	0.115	0.176	0.119	0.100	0.017
SE	(0.002)^{c}	(0.001)^{d}	(0.010)^{c}	(0.013)^{b}	(0.009)^{bc}	(0.009)^{b}	(0.001)^{b}
105							
Mean	0.037	0.026	0.151	0.179	0.116	0.125	0.019

Table A8. Continued.

Category and statistic	Al	As	Ep	Fh	Mg	Sc	Yf
SE	(0.003)[bc]	(0.002)[cd]	(0.013)[bc]	(0.020)[b]	(0.008)[c]	(0.010)[ab]	(0.001)[b]
Microenvironment × Time (days)							
F	0.61	1.71	1.49	0.78	1.09	0.25	0.26
P	0.69	0.15	0.21	0.57	0.38	0.94	0.94
Under nurse plants/7 d							
Mean	0.041	0.054	0.198	0.266	0.244	0.137	0.033
SE	(0.003)	(0.004)	(0.009)	(0.026)	(0.016)	(0.010)	(0.005)
Under nurse plants/21 d							
Mean	0.050	0.036	0.194	0.177	0.152	0.109	0.025
SE	(0.005)	(0.002)	(0.025)	(0.018)	(0.012)	(0.011)	(0.002)
Under nurse plants/35 d							
Mean	0.039	0.032	0.118	0.171	0.137	0.134	0.024
SE	(0.004)	(0.002)	(0.012)	(0.015)	(0.014)	(0.010)	(0.002)
Under nurse plants/49 d							
Mean	0.030	0.027	0.145	0.187	0.129	0.110	0.019
SE	(0.002)	(0.002)	(0.019)	(0.022)	(0.006)	(0.010)	(0.002)
Under nurse plants/77 d							
Mean	0.032	0.021	0.102	0.161	0.107	0.090	0.018
SE	(0.002)	(0.001)	(0.009)	(0.019)	(0.013)	(0.004)	(0.002)
Under nurse plants/105 d							
Mean	0.035	0.023	0.128	0.150	0.105	0.107	0.019
SE	(0.002)	(0.002)	(0.017)	(0.017)	(0.011)	(0.008)	(0.002)
Open site/7 d							
Mean	0.050	0.046	0.273	0.267	0.188	0.180	0.040
SE	(0.005)	(0.003)	(0.007)	(0.035)	(0.015)	(0.022)	(0.008)
Open site/21 d							
Mean	0.048	0.038	0.156	0.181	0.182	0.126	0.024
SE	(0.003)	(0.003)	(0.025)	(0.007)	(0.023)	(0.009)	(0.002)
Open site/35 d							
Mean	0.040	0.030	0.147	0.154	0.174	0.173	0.024
SE	(0.003)	(0.001)	(0.036)	(0.017)	(0.063)	(0.029)	(0.003)
Open site/49 d							
Mean	0.037	0.026	0.157	0.233	0.132	0.159	0.019
SE	(0.004)	(0.002)	(0.019)	(0.036)	(0.011)	(0.022)	(0.004)
Open site/77 d							
Mean	0.032	0.022	0.128	0.191	0.130	0.111	0.017
SE	(0.003)	(0.002)	(0.017)	(0.016)	(0.013)	(0.017)	(0.002)
Open site/105 d							
Mean	0.040	0.029	0.175	0.209	0.126	0.144	0.019
SE	(0.006)	(0.002)	(0.014)	(0.034)	(0.009)	(0.014)	(0.002)

Note: Species abbreviations are: Al, *A. lechuguilla*; As, *A. salmiana*; Ep, *E. platyacanthus*; Fh, *F. histrix*; Mg, *M. geometrizans*; Sc, *S. coptonogonus*; Yf, *Y. filifera*.