



The benefits of a nurse plant, shade cloth, and nurse rock on *Carnegiea gigantea* (saguaro) growth and survival shift along a stress gradient

Helen I. Rowe^{a,b,*}, Mary Fastiggi^b, Debbie Langenfeld^c, Scott Milne^{d,e}, John Parente^c, Giavanna Raboin^d, Nikhil Sethi^d, Madelaine Stockman^a, Melanie Tluczek^b

^a Northern Arizona University, School of Earth and Sustainability, 86011, USA

^b McDowell Sonoran Conservancy, Parsons Field Institute, 15300 North 90th Street, Suite 400, Scottsdale, AZ, 85260, USA

^c McDowell Sonoran Conservancy, Citizen Science Program, 15300 North 90th Street, Suite 400, Scottsdale, AZ, 85260, USA

^d Scottsdale Unified School District, Saguaro High School, 6250 N 82nd St, Scottsdale, AZ, 85250, USA

^e Estrella Mountain Community College, 3000 N. Dysart Rd, Avondale, AZ, 85392, USA

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ABSTRACT

Facilitation tends to be prevalent in arid lands as exemplified by nurse plant relationships. *Carnegiea gigantea* (saguaro), a foundation species in the Sonoran Desert, faces threats of climate change and changing fire regimes. Since it is known to depend on nurse plants, restoring saguaros post-fire or plantings to support regeneration of the species will also require consideration of nurse plants. We sought to understand the specific tradeoffs and mechanisms of planting saguaros with nurse plants or structures mimicking nurse plants. We planted 40 saguaro plants in individual plots with a fully crossed combination of nurse plants, nurse rock, or shade cloth, and controls with five replicates in an outside planter in Scottsdale, Arizona, USA. We watered plots for ten months before turning off the irrigation. Saguaros grew best without nurse plants and nurse rocks in the first year, but only 15 survived the second summer without supplemental water, and of those, 14 were under nurse plants. Photosynthetically active radiation was associated with saguaro survival but not mycorrhizal inoculum potential or temperature. Nurse plants, but not treatments mimicking nurse plants, clearly facilitated saguaro survival under drought conditions, outweighing competition for light and slower growth.

1. Introduction

The balance of positive facilitation and negative competition feedback among plants has important ecological effects in structuring plant communities and helps explain community assembly (Callaway, 1995; Callaway and Walker, 1997). Researchers have shown many examples of facilitation in which one plant species has a positive effect on important life stages of another species (Callaway and Walker, 1997; Franco and Nobel, 1989; Nobel, 1980). The nurse plant relationship exemplifies one form of facilitation dynamics, which is most commonly reported in arid and semi-arid environments (Flores and Jurado, 2003) with higher levels of abiotic stress (Callaway and Walker, 1997; Maestre et al., 2009). In nurse plant relationships, an established plant facilitates the germination, establishment, and growth of seedlings (Callaway, 1995; Niering et al., 1963; Turner et al., 1966). In arid lands, many succulents associate with nurse plants that provide a variety of benefits for establishment and survival (Niering et al., 1963; Padilla and Pugnaire, 2006).

The benefits include shade (Valiente-Banuet and Ezcurra, 1991), a resource island effect of arbuscular mycorrhizal fungi (AMF) and nutrients (Bethlenfalvay et al., 2007; Camargo-Ricalde and Dhillion, 2003; Carrillo-Garcia et al., 1999, 2000), and protection from cold winter temperatures (Drezner, 2006a, 2007, 2010; Niering et al., 1963; Nobel, 1980). The resource island created by nurse trees and shrubs includes an enhanced soil microbial community and hyphal network, reduced erosion, and increased soil nutrients (Armbrust and Bilbro, 1997; Carrillo-Garcia et al., 1999; Halvorson et al., 1994).

Plant communities are complex, however, and facilitation and competition dynamics occur at the same time (Callaway and Walker, 1997), even with nurse plant relationships. The balance of the two dynamics likely depends on where the nurse plant and nursling lie on the stress gradient continuum (Bertness et al., 2024; Holmgren et al., 1997). That is, where growing conditions are optimal, negative effects such as competition may override any facilitative benefits of growing plants together (Padilla and Pugnaire, 2006). For example, in dry years, the

* Corresponding author. Northern Arizona University, School of Earth and Sustainability, 86011, USA

E-mail address: helen.rowe@nau.edu (H.I. Rowe).

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nurse plant may provide strong benefit to nurslings, whereas in wet years the nurse plant benefit may not be as strong or may even be negative (Chiquoine et al., 2022; Padilla and Pugnaire, 2006). The balance of positive facilitative and negative competitive interactions of nurse plants and nurslings may also change across the lifespan of the target species (McAuliffe, 1984; Padilla and Pugnaire, 2006).

Carnegie gigantea (saguaro) is a keystone species of the Sonoran Desert and strongly associated with nurse plants (Drezner, 2006b; Hutto et al., 1986; McAuliffe, 1984; Niering et al., 1963). In recent decades, the intensity and frequency of wildfires have increased in the Sonoran Desert, reducing the habitat of the saguaro (Albuquerque et al., 2024). Re-establishing saguaros into burned areas where associated nurse plants have also been killed by fire may pose a significant challenge. In the field, older trees and shrubs support more understory plants than younger plants (Bethlenfalvay et al., 2007; Carrillo-Garcia et al., 2000), indicating that it may take time to build up the resource island effect associated with nurse plants. Thus, planting nurse trees as seedlings together with saguaros likely will not provide the benefits expected from a mature nurse plant, such as climate regulation (shade and frost protection), nutrients (resource island), or an established AMF hyphal network right away. It would take many years to plant nurse trees first to allow the resource island to develop, then plant the saguaros. Further, nurse trees themselves may need nurse plants to facilitate their establishment (Gomez-Aparicio, 2009). Transplanting grown nurse trees into burned areas may be prohibitively expensive and logistically difficult across large areas. However, using abiotic treatments such as nurse rocks or shade to mimic the benefits of nurse plants without the need to establish a nurse plant may be a cost-effective restoration alternative to planting mature or seedling trees.

Rocks and shading can transfer some nurse structure benefits to cacti in the field, without competition for resources. Rocks can provide increased moisture capture and retention without casting shade (Peters et al., 2008), protection from rodents (Niering et al., 1963), and thermal regulation (Conver et al., 2020). When used in a restoration context, the nurse rocks offered a marked improvement in survival and growth for *Opuntia basilaris* in the disturbed areas during drought (Chiquoine et al., 2022). In another study, nurse rocks and nurse plants improved germination of columnar cactus *Pilosocereus leucocephalus* in comparison with open spaces (Munguía-Rosas and Sosa, 2008). Nurse rocks protected the seeds better than nurse plants, but seedling survival was better under a nurse plant than a nurse rock (Munguía-Rosas and Sosa, 2008). Turner et al. (1966) found that transplanted saguaros only survived with shade cloth. For the *Pachycereus pringlei* (cardon cactus), plants survived best with resource island soils and shading (Carrillo-Garcia et al., 1999).

We set out to compare the balance of competition and facilitation (as measured by growth and survival) among saguaros and nurse plants or abiotic nurse alternatives (rock and shade) along a stress gradient of water availability. We planted 40 saguaros under a fully crossed combination of shade, nurse rocks, and nurse plant treatments in a planter at Saguaro High School, Scottsdale, Arizona, USA. Saguaros and their nurse plants received regular water for the first ten months, before turning off the irrigation. Our objectives were to 1) identify which treatments most facilitated saguaro establishment as measured by growth and survival, 2) test whether the balance of facilitation and competition between the saguaro and nurse plant changed along a stress gradient, and 3) determine whether underlying differences in PAR, temperature, or mycorrhizal inoculum potential were drivers of treatment differences. We expected that the abiotic treatments would improve the growth and survival of the saguaros compared to biotic treatments due to the release from negative competition for resources. We also expected that facilitation would become more dominant as resources (water) became scarcer.

2. Methods

2.1. Study site

We installed this experiment in a 6m * 12m (72 m²) raised planter with cement walls at Saguaro High School (Scottsdale, Arizona, US; 33.52764216118918, -111.9065751329818) in April 2023. The planter had been fallow for at least seven years prior to the experiment. In August 2022, soil samples were taken to 30 cm deep from various locations across the planter, homogenized, and sent to Motzz lab (Phoenix, AZ) for soil testing. Soils had medium to high levels of N, P, and K and other micronutrients (Table S1). Soils were rototilled in fall 2022.

During the study period (April 2023–February 2025), the monthly mean temperatures ranged from 11.6 to 37.1 °C (PRISM Climate Group, 2022). Rainy seasons in the Sonoran Desert occur in the winter (October–March) and in the summer (monsoon, June–September). Annual rainfall during the study was significantly below average during the study period (Table 1).

2.2. Experimental design and treatments

We divided the planter into 40 - 1.2m × 1m plots (Fig. 1) and delineated five blocks from south to north within the planter to control for subtle environmental heterogeneity (Fig. 1). We tested two abiotic (shade/none, nurse rock/none) and one biotic (nurse plant/none) nurse plant factors on saguaro growth and survival (see photos, Fig. 2). These eight treatment combinations were randomly assigned to the eight plots within each block for a complete random block design (eight treatment combinations per block, five replicate blocks = 40 plots).

In each plot, we dug the center 60 cm diameter area to 15 cm deep and placed a 1.5m tall, 60 cm diameter cage made from hardware cloth (Acorn International 23-gauge silver galvanized steel, with 0.635 cm*0.635 cm mesh size) in the hole. A 1-gallon potted saguaro was planted in the center of the 60 cm diameter area of each plot on April 16, 2023. Saguaros came from seed from a single population that were originally planted in pots in late December 2019 and raised for three years in alternating greenhouse and plant nursery conditions to avoid frost damage. Shade treatments were created by cutting 50 % shade cloth (Agfabric 50 % Shade Cloth) and covering 25 % of the cage on the southwest aspect. We placed a cored concrete block (10.16 cm × 29.85 cm x 17.15 cm) to the northwest of saguaros as nurse rocks, following the nurse rock dimensions used in Chiquoine et al. (2022).

Saguaros establish preferentially beneath palo verde (*Parkinsonia microphylla*), mesquite (*Prosopis* sp.), and triangle-leaf bursage (*Ambrosia deltoidea*) compared to in the open or with creosote (*Larrea tridentata*) (Drezner, 2006b; Hutto et al., 1986). We chose the faster growing triangle-leaf bursage (hereby, bursage) to test as the nurse plant with the expectation that it will provide nurse plant benefits more quickly than slow growing trees. We planted 1-gallon potted triangle-leaf bursage to the northeast of the saguaro based on studies indicating that saguaros tend to occur to the southwest of their nurse plants (Drezner, 2010). Bursage and saguaro stems were planted approximately 16.5 cm from each other.

We hand-watered the plots for two weeks after planting, then an automatic irrigation system with a spigot to each plot watered the saguaros and nurse plants 1–4 times per week, depending on the season, for the first 10 months of the experiment (Table 2). Irrigation was turned off for the remainder of the experiment in mid-February 2024. The site received 51.97 mm of precipitation between the time the irrigation was turned off and the May 2024 sampling date (PRISM download March 12, 2025).

2.3. Sampling

We measured saguaro height and areoles (#) as proxies for growth

Table 1

Site precipitation and temperature normal and study period means. Data was downloaded from PRISM in April 2025 (PRISM Climate Group, 2022). Winter months include October–December of the previous year and January–March of the year labeled in the first column. Summer months include April–September. Climate data for 2025 goes through the study period (February 28, 2025).

Year	Annual ppt (mm)	Deviation from normal	Seasonal ppt (mm)		tmin (°C)	tmean (°C)	tmax (°C)	# days below 0 °C
			Winter	Summer				
1991–2020 Normals	218.95		193.19	62.48	15.78	22.89	30.00	
2023	146.81	−72.14	170.69	26.41	16.44	23.28	30.17	1
2024	146.30	−72.65	117.60	50.80	16.67	23.83	30.2	3
2025			4.06				31.00	0

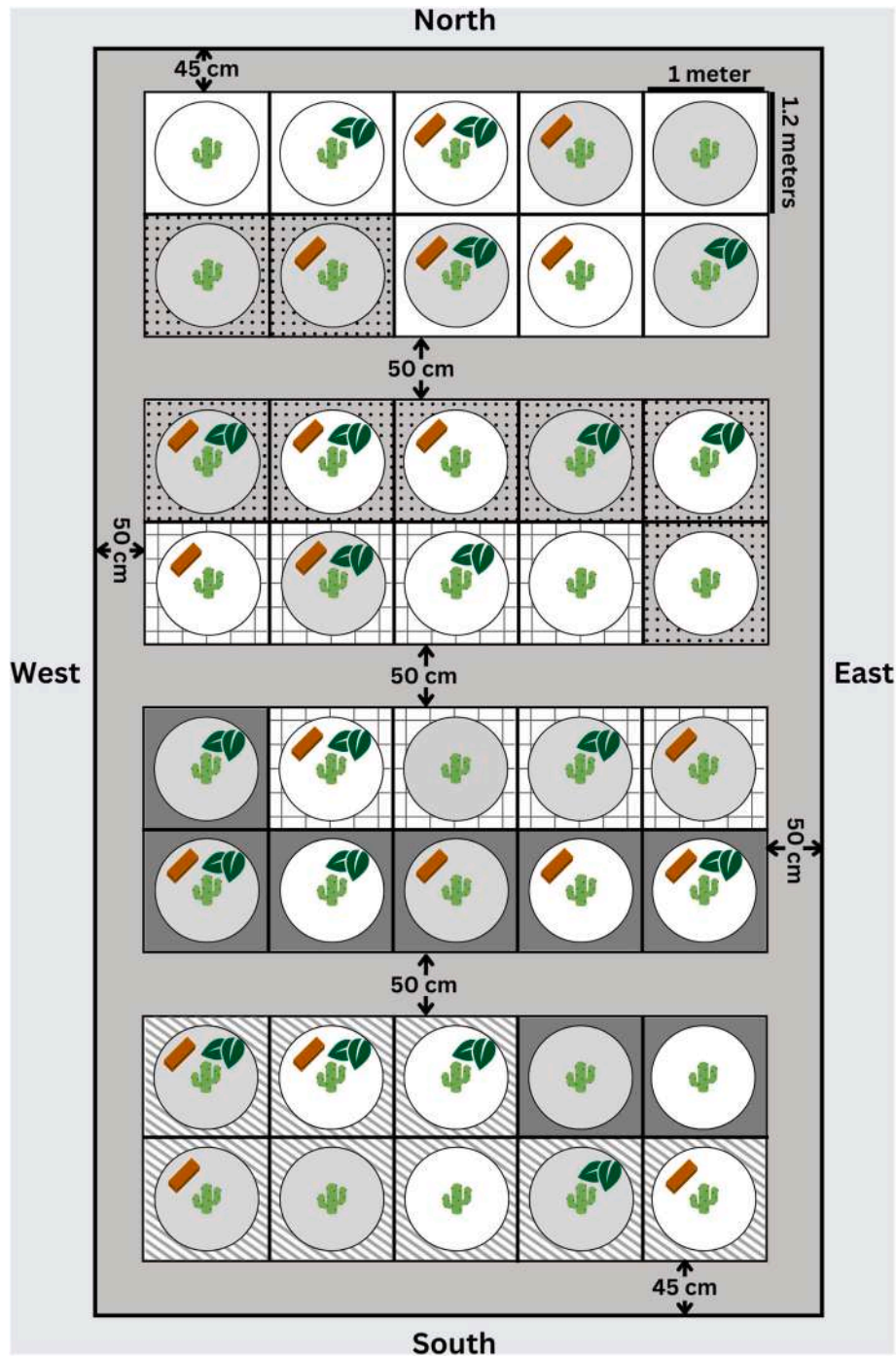


Fig. 1. A graphic representation of the experiment in a cement planter at Saguaro High School, Scottsdale, Arizona. Green saguaro icons represent saguaros planted in the center of each plot, brown blocks represent paving stones used as nurse rocks, and green leaves represent live nurse plants (triangle-leaf bursage). Plots with 50 % shade cloth on their southwest side are grey inside the circle. The five blocks are indicated by different shading in the square plots.

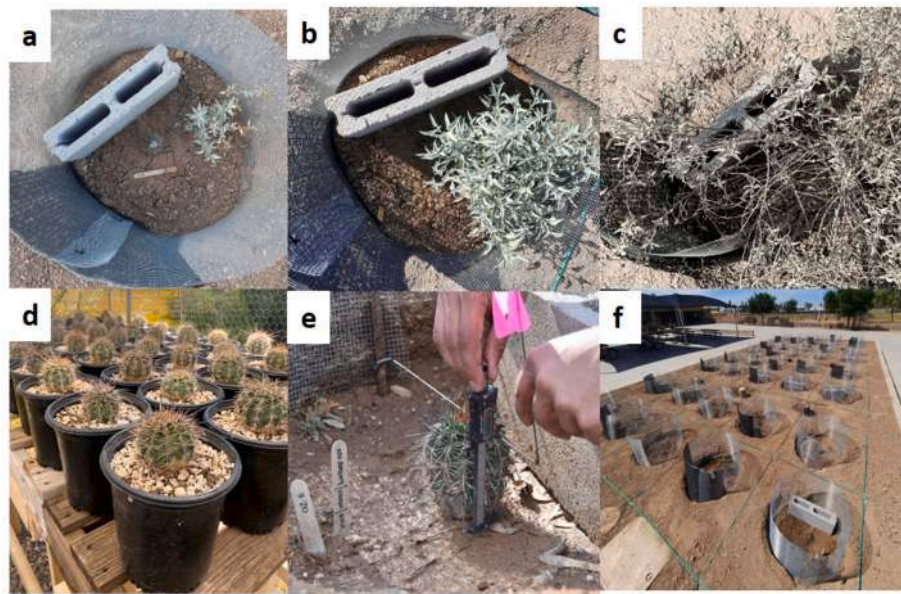


Fig. 2. Images of treatments and layout. Photos on the top row show saguaros with nurse rock and triangle leaf bursage nurse plant treatments on (a) April 25, 2023, shortly after installation, (b) June 14, 2023, and (c) September 11, 2024. On the bottom row, photos illustrate (d) saguaros in pots before planting, (e) saguardo measurements using the vertical height protocol, and (f) treatments just installed in the concrete planter at Saguardo High School. Photo credit: Debbie Langenfeld.

Table 2

Dates, frequency, and quantity of water delivered to each plot during the experiment.

Dates & frequency	Water (L) per plot
4/16/23 (planting date)	3.8
4/17/2023	1.9
4/20, 4/21, 4/24, 4/26, 4/28	1
4/29/23 - 5/22/23 every other day	1
5/22/23 - 12/6/23 M/W/F/Sat	1
12/6/23 - 1/16/24 Tues/Fri	1
1/16/24 - 2/13/24 Tuesdays	1
2/14/24 Irrigation turned off	0

within two weeks of planting (late April), December 2023, and May 2024. To measure saguardo height, we set a pin 2 cm from the soil surface on the base of the saguardo. For the first set of measurements, we used calipers to measure from the base pin mark to the center top of the saguardo, but this resulted in a slanted height measurement. To correct the slanting issue, we revised the approach in subsequent sampling (December 2023 and May 2024). For the vertical measurement method, we held a pin flag level and resting on the crest of the saguardo (beneath spines) and measured the distance between the base pin and the pin flag using calipers (Fig. 2e). In addition to sampling the vertical method in December 2023, we also measured 19 randomly selected saguaros using the baseline (slanted) method to ensure that the two height measurements were aligned. We counted areoles on the rib to the left of a mark we placed on the south side of each saguardo between ribs. We monitored survival in September 2023, May 2024, August 2024, November 2024, and February 2025. We estimated cover of nurse plants within 10 cover classes (Peet et al., 1998) in September and November 2023 and May and November 2024.

Air temperature and photosynthetically active radiation (PAR) were measured in mid-September 2024. On a single cloudless afternoon from 4 to 5pm, we measured PAR by resting a Gain Express Advanced Quantum PAR Meter APM092 (Measurement Range 0–5000 $\mu\text{mol}/\text{m}^2/\text{sec}$) on a pad atop the saguardo to ensure it was level. We rotated the PAR instrument in four cardinal directions and took readings at each placement to get a mean PAR reading for each saguardo. Air temperature was taken immediately above the saguardo without touching the plant using a

Kestrel 3000 Weather Meter.

2.4. Mycorrhizal inoculum potential (MIP)

To identify whether the soil microbial community may be a potential mechanism for differences between survival rates between plots with or without nurse plants, we conducted a mycorrhizal inoculum potential (MIP) experiment (Moorman and Reeves, 1979). A MIP experiment is a bioassay using corn to compare active arbuscular mycorrhizal fungi (AMF) inoculum in soils. We collected 200 mL of soils to 15 cm depth within 10 cm to the north of each saguardo stem in September 2024. Each soil sample was potted in a SC10 pot (164 mL), so that each plot was represented by one pot. We planted surface sterilized (10 % bleach solution for 5 min) organic corn seeds (Rike Co, Belleville, IL). After six weeks, we harvested the plants, rinsed the roots, and separated the roots from the shoots. We dried the aboveground biomass at 60°C for 72 h, then weighed each sample (Denver Instrument APX- 602). Roots were cleared by soaking in 2.5 % KOH solution for 72 h then stained in an ink (Shaeffer's) and vinegar solution at boiling temperature (Vierheilig et al., 1998). We scored percent colonization of AMF root structures using the gridline intersect approach (McGonigle et al., 1990) at 20 \times magnification.

2.5. Statistical analysis

To evaluate the effect of the treatments on saguardo shade, temperature, and MIP, we used a mixed model with treatments (shade: yes/no, nurse plant: yes/no, nurse rock: yes/no) and their interactions as the fixed effects, block as the random effect, and PAR, temperature, or % AMF colonization as the response variables. Three-way interactions were removed if not significant. We analyzed the effects of treatments on nurse plant cover using a similar model, but excluded plots with no nurse plant. We used a mixed model with treatments (shade: yes/no, nurse rock: yes/no), date (4 dates: September and November 2023 and May and November 2024) and their interactions as the fixed effects, plot nested in block as the random effect to control for repeated measures, and nurse plant cover as the response variable. Three-way interactions were removed if not significant. We checked model assumptions with residuals; no transformations were needed for temperature, PAR, % AMF

colonization, or nurse plant cover.

We used a mixed model to analyze growth of saguaros under the different treatments. We included the nurse treatments: bursage plant, nurse rock, and shade (presence/absence of each treatment) and their interactions as the fixed effects and the number of areoles or height taken in December 2023 and May 2024 as the response variable. We included block and sampling season as random effects to account for environmental gradients that may have occurred in the planter and for repeated measures, respectively. Three-way interactions were removed if not significant. The initial measurement (either height or areoles) taken at time of planting of each response variable was included in the model as a covariate to control for baseline differences. For the height model, we included baseline slanted height (April 2023) as a covariate fixed effect. Prior to including the baseline slanted height, we analyzed the two different sets of height data (slanted and linear) for the 19 saguaros that were measured using both methods in December 2023 using bivariate fit of mean (JMP Pro 18). The two height measurement approaches had a strong linear relationship ($F_{1,17} = 40.67$, $p < 0.0001$), indicating that it was appropriate to use the initial baseline height measurement as a covariate in the model. We checked model assumptions with residuals; height and areoles were log transformed to normalize the data.

To analyze the effects of treatments on saguaro survival, we ran a nominal logistic fit regression (chi-square) model using survival (yes/no) as the response variable and treatment factors (nurse plant, shade, and nurse rock) along with their interactions as predictors for May 2024, November 2024, and February 2025 data (survival was the same for August and November 2024). Three-way interactions were removed if not significant. We also tested whether PAR, MIP, or temperature predicted survival outcomes using a nominal logistic fit regression with survival as the response variable and PAR, MIP, and temperature as factors. We used JMP Pro 18 for all statistical analysis and graphs.

3. Results

3.1. Treatments: nurse plant growth, air temperature, PAR, and MIP

The canopy of the bursage nurse plants did not shade the saguaros at time of planting, but grew to cover half the plots (including the

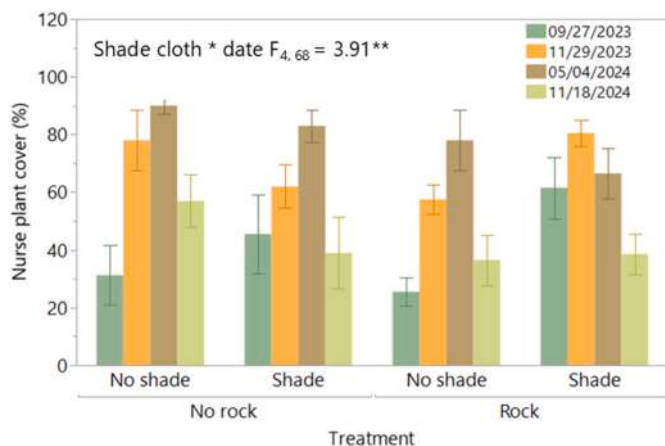


Fig. 3. Treatment (shade cloth and nurse rock) and time effects on nurse plants (*Ambrosia deltoidea*). Treatments were as follows. Shade: covering the southwest aspect of circular cages surrounding the saguaro and nurse plant with shade-cloth (Agfabric 50 % Shade Cloth) or no shade cloth (control). Rock: placing a cored concrete block (10.16 cm × 29.85 cm × 17.15 cm) to the northwest of the saguaro or no rock (control). Nurse plants were located to the northeast of the saguaros. Plots with no nurse plants are not included in this plot or analyses. Bars indicate one standard error of the mean. Shade cloth and date had a significant interaction, but there was no means separation between shade and no shade within date using Tukeys post hoc test. ** indicates $p < 0.01$.

saguaros) by fall 2023 (Fig. 3). Nurse plants grew in the first year, moderated by shade treatment (shade and date interaction, $F_{4,68} = 3.905$, $p = 0.006^*$, Fig. 3, Table SM2), such that after the first summer (September 2023), bursage plants were larger with shade, but were larger without shade by later that fall (November, Table SM3, Fig. 3). As expected, nurse plant cover did not differ by nurse rock treatment (Fig. SM2). None of the nurse plants died during the experiment, but by fall 2024 they had dropped many leaves, resulting in reduced cover, likely in response to the lack of irrigation and drought (Fig. 3). Mycorrhizal inoculum potential (MIP) as indicated by % root length colonization was marginally (at $\alpha = 0.1$) higher in plots with nurse plants (mean \pm s.e.: 52.6 ± 1.29 %) compared with no nurse plants (48.85 ± 1.81 %, Table 3). As expected, no differences in MIP root length colonization were detected for shade or nurse rocks (Table 3).

As expected, the shade and nurse plant treatments reduced PAR (Fig. 4). The shade and the nurse plant individually resulted in a similar level of PAR at the time measured, and the combination of shade and nurse plant resulted in the lowest PAR (Fig. 4a–Table 3 & SM4). The nurse rocks also provided some shade in the afternoon, due to their northwestern placement and resulted in lower PAR compared to no rock (Fig. 4b–Table 3). Only shade cloth resulted in a significant change in air temperature above the saguaros (no shade: 45.22 ± 0.26 ; shade 43.91 ± 0.30 ; Table 3, Fig. 4c).

3.2. Saguaro growth: height and areoles

In the first year, saguaros grew taller without the nurse plants (Fig. 5a, Table 3) and grew more areoles without a nurse plant and a nurse rock (nurse plant and rock interaction; Table 3 & SM5, Fig. 5b). In the height model the interaction between nurse plant and nurse rock was marginally significant (at the $\alpha = 0.10$ level, Table 3, Fig. 5a). There were no growth differences with the shade cloth treatment for either height or areoles (Table 3).

3.3. Saguaro survival

By May 2024, one year after transplant, only four saguaros had died (Fig. 6). By November 2024, following a hot and dry summer (Table 1), with no irrigation, 25 (62.5 %) of the saguaros died (Fig. 6a). Almost all of the surviving saguaros were under a nurse plant (14/15 or 93.33 % in November 2024 and 13/14 or 92.9 % by February 2025, Fig. 6). Chi square analyses (Likelihood Ratio) of saguaro survival in May 2024 detected no significant differences in survival among treatments (whole model test: $X^2 = 5.990$, $p = 0.424$, Table SM6). Chi square analyses (Likelihood Ratio) between saguaro survival in November 2024 and the treatments indicates that the probability for survival was significantly greater under the nurse plants ($X^2 = 22.82$, $p < 0.0001$), but not for nurse rocks, shade cloth, or any interactions (whole model test: $X^2 = 26.18$, $p = 0.0002$, Table SM6). Results were similar for February 2025 survival (whole model test: $X^2 = 23.32$, $p = 0.0007$; nurse plants: $X^2 = 20.60$, $p < 0.0001$, Table SM6). When testing whether surviving saguaros had different levels of PAR, MIP, or temperature than dead saguaros in September 2024 using the mixed model, PAR was significantly lower for alive saguaros compared with the dead saguaros, but temperature and MIP were not different (PAR $X^2 = 7.29$, $p = 0.007$; MIP $X^2 = 1.827$, $p = 0.176$; temperature $X^2 = 0.002$, $p = 0.966$, Fig. 6b).

4. Discussion

In this study, we set out to compare which nurse plant treatments (biotic bursage plant or abiotic shade cloth or rock) most facilitate growth and survival along a stress gradient of water availability. We found that when resources (water) were not limiting, saguaros grew taller without a nurse plant and grew more areoles without a nurse plant or rock. However, when resources were limited (hot summer conditions, no irrigation, and below-average monsoon rains), only saguaros with

Table 3

Mixed model results of treatment effects on photosynthetically active radiation (PAR), temperature, mycorrhizal inoculum potential (MIP), saguaro height, and saguaro areoles. The models included the three treatment combinations and their interactions as fixed effects. Block was included as a random effect in all models. Season was also included as a random effect for saguaro height and areole count models. Three-way interactions were removed because they were not significant. Baseline covariate was baseline height and areole count for the respective models and was left blank if not included in a model. Significance is indicated as follows: ^ < 0.10, * < 0.05, ** < 0.01, *** < 0.001, **** < 0.0001.

Response variable	Nurse plant (NP)		Shade (S)		NP*S		Nurse rock (NR)		NP*NR		S*NR		baseline covariate	
	df	F	df	F	df	F	df	F	df	F	df	F	df	F
PAR	1,29	46.328****	1,29	45.112****	1,29	5.613*	1,29	5.315*	1,29	1.169	1,29	2.849	-	-
Temperature (°C)	1,29	0.163	1,29	15.178***	1,29	0.665	1,29	0.402	1,29	0.49	1,29	1.026	-	-
MIP	1,29	2.955^	1,29	0.799	1,29	0.328	1,29	0.572	1,29	0.005	1,29	1.829	-	-
Saguaro height	1,63.7	5.118*	1,61.5	2.027	1,61.7	0.722	1,63.7	1.087	1,62.4	3.688^	1,61.2	0.075	1,27.6	15.386****
Saguaro areoles (#)	1,61.8	4.446*	1,60.5	0.768	1,60.5	2.161	1,63.9	0.127	1,61.6	7.717**	1,60.6	0.326	1,45.5	22.043****

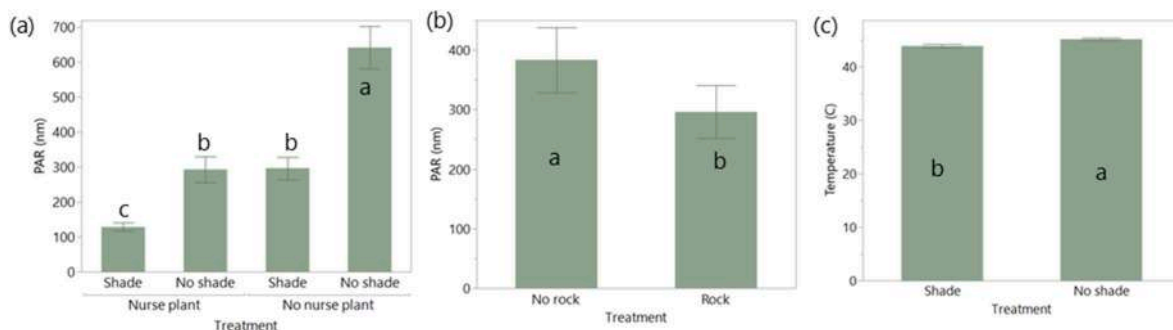


Fig. 4. Mean photosynthetically active radiation (PAR) with (a) shade cloth (shade) and nurse plant treatments and (b) nurse rock (rock) treatment and (c) temperature with shade cloth (shade) treatment. Treatments were as follows. Shade: covering the southwest aspect of circular cages surrounding the saguaro and nurse plant with shade cloth (Agfabric 50 % Shade Cloth) or no shade cloth (control). Rock: placing a cored concrete block (10.16 cm × 29.85 cm x 17.15 cm) to the northwest of the saguaro or no rock (control). Nurse plant: planting a triangle-leaf bursage plant to the northeast of the saguaros or no nurse plant (control). Bars indicate one standard error of the mean. Letters indicate differences between means using Tukey’s post hoc test or *t*-test (if only two levels).

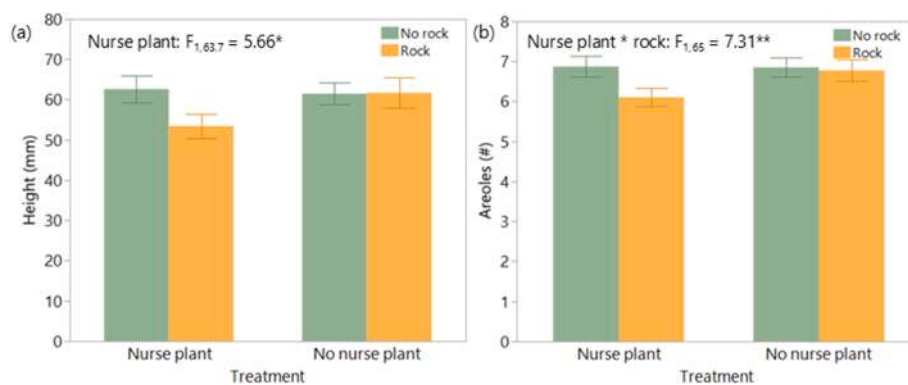


Fig. 5. Saguaro growth with nurse plant (nurse) and nurse rock (rock) treatments as measured by (a) vertical height (mm) and (b) areoles. Treatments were as follows. Shade: covering the southwest aspect of circular cages surrounding the saguaro and nurse plant with shade cloth (Agfabric 50 % Shade Cloth) or no shade cloth (control). Rock: placing a cored concrete block (10.16 cm × 29.85 cm x 17.15 cm) to the northwest of the saguaro or no rock (control). Nurse plant: planting a triangle-leaf bursage plant to the northeast of the saguaros or no nurse plant (control). Bars represent one standard error of the mean. Asterisks indicate significance at the following levels: **p* < 0.05, ***p* < 0.01.

nurse plants survived, except for one saguaro with shade and a nurse rock, indicating that the abiotic treatments mimicking nurse plants were not adequate to sustain young saguaros in drought conditions. Our findings provide potentially important insights into the regeneration niche for saguaros (Grubb, 1977). While we know that saguaros are widely associated with nurse plants (Drezner, 2006b) and that transplanted saguaro seedlings can’t survive without a nurse plant (Turner et al., 1966), many have recognized that the nurse plant relationship likely includes competition as well as facilitation (Badano et al., 2016; Holmgren et al., 1997; McAuliffe, 1984; Padilla and Pugnaire, 2006). In

this study, we saw that in ideal moisture conditions, nurse plants led to a small growth depression in saguaro height and areoles, indicative of competition with nurse plants compared to abiotic treatments. Similarly, other researchers studying the microhabitats and growth of saguaros concluded that shading and competition for water with the nurse plants reduced growth, but the magnitude of the reduction depended on seedling size and location under a nurse plant (Franco and Nobel, 1989). With respect to competition, McAuliffe (1984) found that older saguaros may outcompete their nurse plants. He found dieback and greater mortality for foothill palo verde trees (*Parkinsonia*

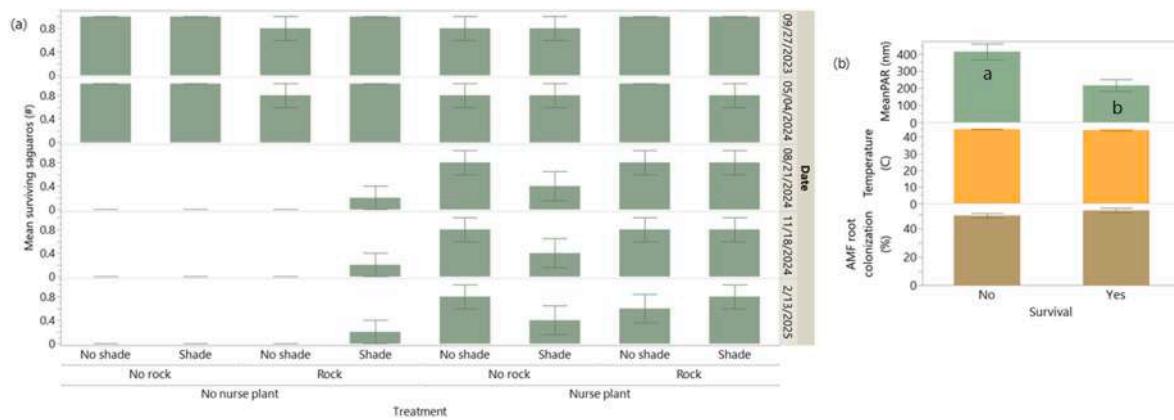


Fig. 6. Number of surviving saguaros by (a) treatment and sampling date and (b) afternoon photosynthetically active radiation (PAR), air temperature, and MIP (mycorrhizal inoculum potential quantified as percent AMF root colonization). Letters indicate differences between means using a Chi square analysis. Saguardo survival data used in 6b was observed and the same in August and November 2024; PAR and temperature measurements and soil samples were taken in September 2024. Treatments were as follows. Shade: covering the southwest aspect of circular cages surrounding the saguardo and nurse plant with shade cloth (Agfabric 50 % Shade Cloth) or no shade cloth (control). Rock: placing a cored concrete block (10.16 cm × 29.85 cm × 17.15 cm) to the northwest of the saguardo or no rock (control). Nurse plant: planting a triangle-leaf bursage plant to the northeast of the saguaros or no nurse plant (control). Bars indicate one standard error of the mean.

microphyllum) associated with close proximity of saguaros (McAuliffe, 1984). In this study, we found that in drought conditions common to the northern Sonoran Desert, nurse plants were essential for saguardo survival. Bursage plants were also reduced with these drought conditions, which may have resulted from the hot, dry conditions alone or in combination with competition for resources with the saguaros. Our results are supported by findings that the relationship with nurse plants is regulated by relative differences in climate stress; saguaros grow faster in cooler, wetter environments without a nurse plant, but faster in hotter, drier climates with a nurse plant (Drezner, 2015). Indeed, nurse plant relationships may be more important in arid and semi-arid environments (Flores and Jurado, 2003).

In a restoration context where physical conditions may limit establishment, it may be important to include nurse plants (Padilla and Pugnaire, 2006), but it requires time for the nurse plants to establish and provide the conditions necessary to protect the nursling. We chose to test a fast-growing, common shrub, bursage, shown to associate with saguaros more often than expected based on its cover (Drezner, 2006b). Saguaros also commonly associate with foothill palo verde (*Parkinsonia microphylla*) and mesquite (*Prosopis* spp.) trees (Drezner, 2006b; Franco and Nobel, 1989). The bursage plants grew quickly with irrigation, to provide canopy cover over the saguardo within the first six months. In a field setting, it remains to be tested how quickly bursage can provide canopy cover and other nurse plant benefits without added watering. However, researchers found that planting nurse tree seedlings (palo verde and mesquite) together with seedlings of the giant cardon cactus (*Pachycereus pringlei*) in the field increased survivorship of the cacti even after 11 years (Moreno et al., 2017).

We also tested whether abiotic treatments that mimic the effects of nurse plants (nurse rocks and shade cloth) could provide the same facilitation as nurse plants without competing for resources. In a test of 1200 saguardo seedling outplants, only those with shade survived, regardless of additional watering (Turner et al., 1966). Similarly, researchers found that both the common nurse plant and shade improved survival of the giant columnar cactus *Neobuxbaumia tetetzo* (Valiente-Banuet and Ezcurra, 1991). However, in our study the nurse rock nor shade cloth provided adequate protection during the drought period of the experiment. The surviving saguaros were strongly associated with lower PAR and the shade cloth provided similar levels of afternoon shade protection (PAR) as the nurse plant and slightly reduced temperature at the time of measurement (September 2024). However, in contrast to nurse plants that covered the saguaros and provided shade all day, the shade cloth was on the southwest side to protect during the

hottest time of the day, but did not provide morning shade or shade when the sun was at its highest. Similarly, the nurse rock provided shade in the afternoon. Therefore the abiotic treatments did not mimic nurse plants because they did not provide morning shade or shade overhead when the sun was at its highest. Unfortunately, we did not record PAR at different times or dates but researchers found that near equinox, a saguardo seedling receives 77 % less total daily PAR and reduces its predicted net CO₂ uptake by 90 % under *A. deltoidea* compared with an unshaded seedling (Franco and Nobel, 1989). It is possible that had we placed the shade cloth above the saguaros, survival may have been higher, however, it is also possible that the shade cloth alone cannot mimic other biotic factors. In the Chihuahuan Desert in New Mexico, USA, nurse plants provided greater concentrations of nutrients, lower soil temperature, and higher soil moisture compared with open spaces (Ferrenberg et al., 2023).

Below-ground mutualisms associated with the nurse plants may have also contributed to saguardo survival. Although differences in MIP did not explain the differential survival of saguaros with nurse plants, it is still possible that below-ground mechanisms played a role in protecting saguaros. The test for MIP indicates the availability of mycorrhizal inoculum in the soil (Moorman and Reeves, 1979), which in this case was similar with and without nurse plants. However, it does not characterize the AMF taxa, which can provide different benefits and mediate plant coexistence (Scheublin et al., 2007; Van Der Heijden et al., 2003, 2004). Saguaros with nurse plants may have accessed more resources through the shared mycorrhizal network between the saguardo and bursage than they were able to access alone (Egerton-Warburton et al., 2007; Van Der Heijden and Horton, 2009).

The intent of the nurse rock was to provide thermal insulation for the saguaros, because an important function of nurse structures is to protect saguaros from cold winter temperatures (Conver et al., 2020; Drezner, 2007), since they cannot survive freezing. However, we did not see a significant effect of rock on survival after the first full year or after the drought period. During the study period, there were four events in which the temperature fell below freezing, but perhaps the low temperatures did not persist long enough to cause epidermal damage. Also, the placement of the nurse rock to the NW of the saguardo provided a little shade, but only in the late afternoon. Overall, the nurse rocks did not improve survival, even though nurse rocks have been shown to reduce exposure to maximum high temperatures for saguaros (Conver et al., 2020). The nurse rocks may have had a stronger effect had we configured them differently, for example, Conver et al. (2020) studied rock cavities in which there were multiple rocks surrounding the saguardo. In

another study, *Opuntia basilaris* (beavertail prickly pear) individuals planted and surrounded by rocks had strong growth and flowering responses compared to those planted in the open (Chiquoine et al., 2022) and *Mammillaria* species tend to associate with rocks, which provide a moister environment without competition for light (Peters et al., 2008). Rock cavities have also been shown to provide protection against granivores for seeds better than nurse plants (Munguía-Rosas and Sosa, 2008).

The dramatic differences in saguaro survival with and without nurse plants in stressful conditions underscores the reliance on facilitation by nurse plants. Although much easier to apply in the field, unfortunately the abiotic treatments as applied in this study were insufficient protection. As the need grows for reestablishing saguaros after wildfire or for augmenting natural populations with low recruitment, planting saguaros with bursage holds promise. Practitioners may consider establishing bursage first, followed by saguaro plantings.

CRediT authorship contribution statement

Helen I. Rowe: Writing – original draft, Validation, Supervision, Methodology, Investigation, Formal analysis, Conceptualization. **Mary Fastiggi:** Writing – review & editing, Supervision, Resources, Project administration, Investigation. **Debbie Langenfeld:** Writing – review & editing, Project administration, Investigation. **Scott Milne:** Writing – review & editing, Supervision, Project administration, Investigation. **John Parente:** Writing – review & editing, Project administration, Investigation. **Giavanna Raboin:** Writing – review & editing, Investigation. **Nikhil Sethi:** Writing – review & editing, Visualization, Investigation. **Madelaine Stockman:** Writing – review & editing, Investigation, Formal analysis. **Melanie Tluczek:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization.

Ethics approval

Not applicable.

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Declaration of competing interest

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jaridenv.2025.105492>.

Data availability

Data and analysis will be made available on GitHub at <https://github.com/HelenIvy/HighSchoolSaguaros/tree/main> when published.

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