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Research Article

Do early-successional weeds facilitate or compete with seedlings in forest restoration? Disentangling abiotic versus biotic factors

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Abstract

1. Semi-arid forests need cost-effective restoration strategies to address their severe degradation. Tree shelters are often used to minimize abiotic and biotic stress during seedling establishment. We asked if early-successional weeds act as a natural shelter by facilitating native seedlings, contingent on abiotic and biotic stressors and seedling ecological strategy.

2. We conducted a manipulative weed exclusion experiment at a semi-arid site in South Texas targeted for large-scale forest restoration to discern the net effect of weeds on the growth and survival of target thornscrub tree and shrub seedlings. We assessed the roles of contrasting seedling ecological strategies (fast vs. slow growth habit), temporal variation in abiotic stress, microclimate and mammalian herbivory in modulating weed–seedling interactions.

3. Ungulate herbivory on seedlings was common, of similar frequency across most species, but not diminished by the presence of weed neighbours. On average, seedlings growing adjacent to weed neighbours experienced modest but non-significant increases in both height and mortality after 6 months, relative to weed-excluded areas. However, seedlings without significant herbivory and adjacent to weed neighbours grew more vigorously (increased height and branching) during hot and dry periods, particularly those species with a fast growth habit. Although seedling light-saturated photosynthetic capacity (A_{sat}) and air temperature were unaffected by weed presence during hot and dry periods, afternoon light levels were reduced by approximately 50%, possibly indicative of lower leaf temperatures and improved seedling water status.

4. Our results show that realizing the facilitative potential of weeds in semi-arid forest restoration requires minimizing mammalian herbivory and temporally separating competition for resources. Managing for intermediate but not excessive levels of forb canopy cover is likely required to reduce high radiation loads and reduce

transpiration without adverse competitive effects. Longer-term experiments manipulating cover crop identity, cover and mammalian herbivory will inform whether forbs can be effectively exploited to enhance restoration success at large scales.

1 | INTRODUCTION

Dryland ecosystems, characterized by water scarcity and encompassed by arid, semi-arid and dry-subhumid regions, occupy about 40% of the Earth's surface and support about a third of the global population (Millennium Ecosystem Assessment, 2005). As some form of severe degradation is present in 10%–20% of these ecosystems, it is also estimated that the extent of drylands will increase to 56% of the global land area by 2100 (Huang et al., 2016; Prăvălie, 2016; Reynolds et al., 2007). While both the fraction of drylands with tree cover and the area which can be reforested have been debated as of late (Bastin et al., 2017; Veldman et al., 2019), there is no question that a significant fraction of forests has been lost (Lindquist et al., 2010), and thus in need of restoration. Limited rainfall, combined with high temperatures and low nutrient levels and water holding capacity, present increasing challenges for the restoration of these highly degraded ecosystems under global climate change and increased land use for farming or urbanization (Cherlet et al., 2018). Despite the efforts to restore these ecosystems through native plant seeding or transplanting, managed grazing, prescribed fire treatments and weed management, the success of these efforts remains low, indicating a need for different approaches to restoring these systems (James et al., 2013). Often tree shelters, such as tree tubes, are promoted as they minimize the negative effects of herbivory and excessive light loads (Dick et al., 2016), but these are not without cost and must be removed before they degrade or are lost.

Herbaceous vegetation (hereafter, weeds) often dominates early-successional stages (0–5 years) of restoration sites, particularly those which were previously agricultural (Falkowski et al., 2020; Guariguata & Ostertag, 2001). Weeds may have either positive, negative or neutral effects on target restoration plants (Elgar et al., 2014; Fagundes et al., 2017). Negative consequences may arise due to the sharing of already limited resources such as nutrients, water and light (Cuesta et al., 2010; Standish et al., 2001), whereas positive effects generally occur through some form of habitat amelioration, or the minimization of otherwise harsh conditions (Bertness & Callaway, 1994; Padilla & Pugnaire, 2006; Smit et al., 2007). The potential exists, therefore, for weeds to act as nurse plants in restoration contexts by improving microclimatic conditions, retaining nutrients and water in the soil, protecting seedlings from herbivores and attracting beneficial pollinators to target plants (Niering et al., 1963; Padilla & Pugnaire, 2006; Padilla & Pugnaire, 2009). It is therefore imperative to explore the facilitative potential of weeds as an alternative to costly management strategies (Castro et al., 2002; Chirino et al., 2009).

Though promising, facilitation is likely contingent on multiple factors (Callaway & Walker, 1997; Padilla & Pugnaire, 2006). The stress-gradient hypothesis posits that facilitation is more likely under harsh environmental conditions (Bertness & Callaway, 1994; Callaway et al., 2002). In harsh conditions, because growth rates are less than optimal, competition is reduced, while the likelihood increases that one aspect of plant microclimate is favourably altered (shade, heat, moisture, nutrients). In addition, herbaceous weeds may further contribute to shielding target species from mammalian herbivory (Smit et al., 2007). Browsing by mammalian herbivores during restoration activities can be substantial and thus act as a significant constraint on forest restoration (Opperman & Merenlender, 2000). Third, species identity and growth rate, both of nurse weeds and target plants, are likely to play a role (Fagundes et al., 2017; Numata, 1982). Some nurse species may outlive and eventually harm target species, and vice versa, emphasizing the notion that facilitation and competition act simultaneously and their net effect ought to be considered when encouraging nurse–plant interactions (Callaway, 1995). Target seedling ecological strategy is an important consideration because of its dual role in succession and weed–seedling interactions. Different growth habits (e.g. the fast–slow continuum of Reich, 2014) or ecological strategies (e.g. Grime's adaptive strategy theory; Grime, 1977) likely underpin varying degrees of species survival in restoration settings (Martínez-Garza et al., 2013), but also imply different responses to shading and other aspects of the microclimate that are modified by adjacent weeds.

In the lower Rio Grande Valley of Texas, approximately 95% of the original extent of Tamaulipan thornscrub has been lost due to conversion to agriculture and subsequent urbanization (Leslie, 2016). Reforestation, primarily through seedling transplantation, has been ongoing in the region for more than 30 years, but assessment of such efforts has been limited until recently. Previous work has experimented with restoration interventions such as tube shelters (Dick et al., 2016), slow-release moisture and mycorrhizal inoculation (Mohsin et al., 2021). Collectively, this work has shown that seedling shelters significantly reduce mammalian browsing, and, together with management of invasive grasses, can improve first-year seedling survival, yet large species differences in survival remain. The interaction of other non-invasive forbs, species identity and mammalian herbivory has not yet been studied.
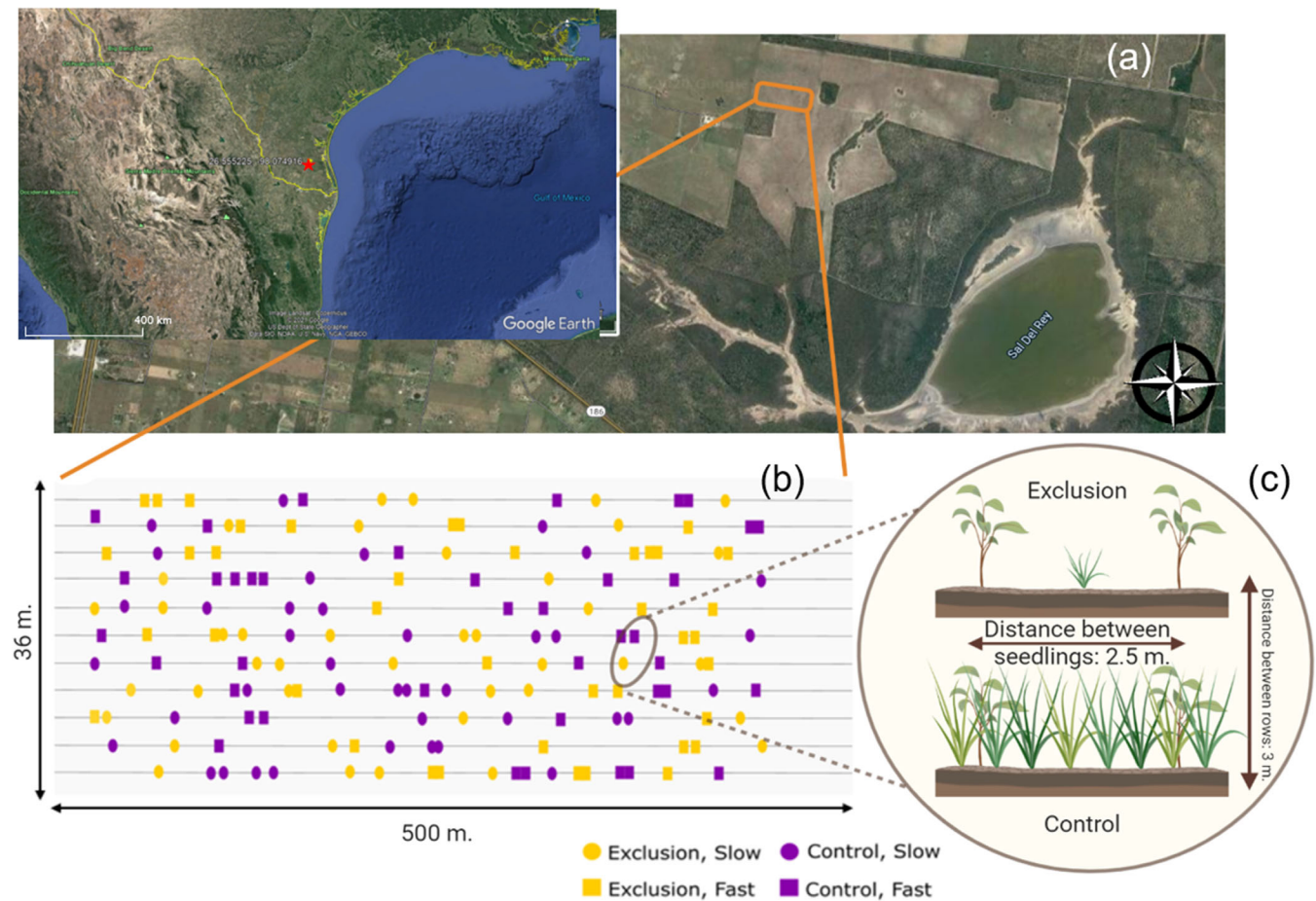
FIGURE 1 Study site and experimental design. (a) Study location map; red star denotes study site (credit: Google Earth). (b) Layout of study plot showing study seedling individuals by treatment (control, weed exclusion) and species growth habit (fast, slow). (c) Close-up showing average distance between planted seedlings and inter-row distance. Actual distance between study individuals was often greater than 2.5 m because not all seedlings were part of study (see Section 2). A total of 160 target seedlings (8 species × 2 treatments × 10 replicate individuals) were studied. Panels (b) and (c) created with Inkscape 1.0 (https://inkscape.org/) and BioRender.com, respectively

We addressed these knowledge gaps by conducting a manipulative weed exclusion experiment at a semi-arid site recently targeted for large-scale forest restoration (>100,000 woody seedlings planted annually over several years) and subsequently dominated by early-successional weeds. The objectives of this study are to (1) discern the net effect (positive, negative, neutral) of naturally occurring weeds on native thornscrub tree and shrub seedlings of contrasting growth rates, (2) disentangle the abiotic versus biotic mechanisms associated with any effects or the lack thereof and (3) understand how temporal variation in abiotic stress modulates weed–seedling interactions. Overall, we hypothesize that the net effects of interactions between weed cover and target seedlings will be facilitative given the overall harsh arid conditions, and that facilitative effects will be most pronounced during the hottest and driest periods. We also hypothesize that fast-growing species of target seedlings will disproportionately benefit from weeds over their slow-growing counterparts, given that species stress tolerance tends to trade off with growth rate (Chapin et al., 1986).

2 | MATERIALS AND METHODS

2.1 | Study site

The study took place within the La Sal del Rey Tract (26.555225° N, −98.074916° W) of the Lower Rio Grande Wildlife Refuge, near Linn, TX (Figure 1), at the northern margin of Tamaulipan thorn forest (Jahrsdoerfer & Leslie, 1988; NRCS, n.d.; Richardson & King, 2011). The closest site of undisturbed thorn forest, about 15 km to the south, consists of continuous closed canopy of trees 3–4 m in height and a variety of understory shrubs (Flores, 2019). Between 1939 and 1959, most of the La Sal del Rey tract was cleared for agricultural dryland crop production (e.g. *Sorghum bicolor*) with no irrigation. The U.S. Fish and Wildlife Service (USFWS) purchased the land in 1992, and since 1993, has reforested sub-tracts through direct seeding and tree seedling transplanting. Air temperatures in the summer can reach upwards of 40°C, with mild winters and occasional freezes. The site receives 682 mm annually on average, with peak precipitation in the months of

TABLE 1 Species traits, growth habit classification, RGRh and survival from Mohsin et al. (2021) for the eight focal species in the present study. Initial height (cm) and total height growth (cm) are for the duration of the present study

Species	Family	Growth Habit	RGRh (weeks^{-1})	Survival	Initial height (cm)	Total Growth (cm)
Forestiera angustifolia	Oleaceae	Slow	0.27 ± 0.11	0.66	28 ± 2	10 ± 4
Celtis ehrenbergiana	Ulmaceae	Slow	0.51 ± 0.17	0.74	30 ± 2	11 ± 3
Senegalia wrightii	Fabaceae	Slow	0.47 ± 0.06	0.86	49 ± 5	14 ± 2
Amyris texana	Rutaceae	Slow	0.73 ± 0.15	0.82	13 ± 2	12 ± 2
Zanthoxylum fagara	Rutaceae	Slow	0.78 ± 0.13	0.94	17 ± 2	20 ± 4
Havardia pallens	Fabaceae	Fast	1.18 ± 0.09	0.76	24 ± 3	38 ± 4
Chromolaena odorata	Asteraceae	Fast	1.28 ± 0.18	0.7	41 ± 4	54 ± 11
Vachellia rigidula	Fabaceae	Fast	1.54 ± 0.07	0.9	23 ± 2	44 ± 3

September and October. Several browsing mammalian species are present on site, such as white-tailed deer (*Odocoileus virginianus* Zimmerman) and feral hogs (*Sus scrofa* Linnaeus), as well as exotic species such as the nilgai antelope (*Boselaphus tragocamelus* Pallas) (Leslie, 2016). In October–November 2018, over 100,00 native tree and shrub seedlings of 24 species were planted as part of a joint effort between Land Life Company (www.landlifecompany.com) and the USFWS. Linear rows were approximately 3 m apart and seedlings were spaced 2–3 m within each row, resulting in a planting density of approximately 988 seedlings/ha. The rows were ripped to a depth of 30 cm and seedlings were planted at 20 cm depth.

2.2 | Species selection and experimental design

A subset of 3600 individuals (150 individuals per each of 24 species) were assessed in intensive seedling demography plots for growth and mortality over 1 year (Mohsin et al., 2021). In May 2019, we opportunistically designed the present experiment using pre-existing planted seedlings and preliminary data from the intensive seedling demography plots. We selected a subset of eight focal species that were planted at sufficiently high densities within relatively close proximity to each other in an adjacent 500 × 36 m plot (Figure 1b), and which spanned a wide range of growth rates and survival. After initiating the experiment, we later classified our selected species into fast- and slow-growing based on a full year of growth and survival from the intensive seedling demography plots (Table 1 and Figure S1).

We identified three fast-growing focal species: tenaza (Fabaceae: *Havardia pallens* [Benth.] Britton & Rose, tree), crucita (Asteraceae: *Chromolaena odorata* [L.] R.M. King & H. Rob, shrub) and blackbrush (Fabaceae: *Vachellia rigidula* [Benth.] Seigler & Ebinger, shrub), and five slow-growing species: elbowbush (Oleaceae: *Forestiera angustifolia* [Torr.], shrub), granjeno (Ulmaceae: *Celtis ehrenbergiana* [Klotzsch] Liebm., shrub), Wright's acacia (Fabaceae: *Senegalia wrightii* [Benth.] Britton & Rose, tree), chapotillo (Rutaceae: *Amyris texana* [Buckley] P. Wilson, shrub) and colima (Rutaceae: *Zanthoxylum fagara* [L.] Sarg., shrub). We verified growth habit classifications with two independent sources, that of Flores and Jurado (1998) and an unpublished classification based on anecdotal observations (K. Wahl, unpublished

dataset). Notably, all three species classified by our field data as fast-growing were also classified as such by one or the other of the two sources, and our five slow-growing species had classifications other than 'fast-growing' by the unpublished dataset. These five species likely represent a range of growth habits from slow to moderate, and thus should be thought of as slow-growing relative to the three fast-growing species (Figure S1), not in an absolute sense. We used an iterative approach for selecting 10 pairs of experimental individuals per species (160 individuals total) in order to distribute species, growth habits and treatments in a homogenous way throughout the study plot (see Methods S1 for full details). We accomplished weed exclusion by mowing a 6-foot radius around weed exclusion seedlings using a FS 560 C-EM model brush cutter (STHIL Incorporated; Virginia Beach, VA) to guarantee close cutting of grasses and defined areas, and as needed to prevent the incidence of grasses in exclusion areas. Mowing was completed in July 2019 and September 2019, as needed to guarantee full exposure of exclusion seedlings to sunlight. Weed cover assessments (see site photo; Figure S2) were conducted by three independent observers in June 2019 (baseline), a month post-treatment in August 2019 and 3 months post-treatment in October 2019 (see Methods S1 for full details).

2.3 | Response variables – Seedling vital rates and physiology

We conducted monthly to bi-monthly seedling demographic surveys and recorded plant vigour on a 0–3 scale (0 = dead, 1 = 25%–50%, 2 = 50%–75%, 3 ≥ 75% green leaves), plant height, numbers of main branches and animal damage on a 0–3 scale (0 = no damage, 1 = minimal damage, 2 = moderate damage, 3 = severe damage), following a similar approach used by others (Muiruri et al., 2018). In addition, in July, August and October 2019, we measured net photosynthetic rate on seedlings using a Licor 6400 XT infrared gas analyser (LI-COR Biosciences; Lincoln, NE) with a 6400–22 opaque conifer chamber attachment in lieu of the standard 2 × 3 cm chamber, because the majority of our species had a very limited leaf area, which was often compound leaves with short petioles and petiolules. The short stature and limited branching of many seedlings precluded

illuminating branches from above. We instead illuminated seedlings from the side, placing the seedling stem base at one side and we recorded the length of stem inside the chamber. Photosynthetic measurements were conducted with reference CO_2 of 400 ppm and a light intensity of 2000 μmol m^{-2} s^{-1} PAR in 5–15 min intervals to allow for stabilization. We did not harvest leaf area inside the chamber to avoid damaging the seedlings. While this prevented us from determining photosynthesis on a per unit leaf area basis, we controlled for differences in plant size by normalizing photosynthesis by dividing by stem length present inside the chamber.

2.4 | Response variables – Seedling microclimate

We measured soil temperature and moisture in September 2019 using a TEROS 12 sensor (METER Group Inc.; Pullman, WA) and ProCheck C device (Edaphic Scientific; AU), under 16 replicate control and exclusion seedlings. For a more complete picture of how weeds alter seedling microclimate during hot, dry conditions, in May 2020, we made additional microclimate measurements. We measured incoming afternoon photosynthetically active radiation (PAR μmol m^{-2} s^{-1}), relative humidity (%) and air temperature (°C) over a period of 7 min at a constant height of 35 cm under each of four weed canopies and adjacent to seedlings in five exclusion areas using a Licor 6400 XT (LI-COR Biosciences) held level to ground level and with its chamber left open. Because the weed composition in May 2020 was no longer the same, weed canopy estimates were replicated under the shade of the most prominent weed, *Prosopis glandulosa* (Torr.).

2.5 | Data analyses

All data analyses were performed in R v3.6.0 (R Core Team, 2019). Because a small number of tagged experimental individuals died ($n = 6$ total) prior to initiation of the first mowing treatment in July 2019 ($t0$), we estimated mortality (fraction of individuals) at a given time t for each experimental unit i as the number of newly dead individuals since the first mowing ($n_{\text{dead},i,t} - n_{\text{dead},i,t0}$) divided by the number of live individuals at the time of the first mowing ($n_{\text{live},i,t0}$):

$$\text{mortality}_{i,t} = \frac{n_{\text{dead},i,t} - n_{\text{dead},i,t0}}{n_{\text{live},i,t0}}$$

We calculated relative height growth rate for each experimental unit i at any given time t (RGRh$_{i,t}$: cm cm^{-1} month^{-1}) as

$$\text{RGRh}_{i,t} = \frac{\ln \frac{H_{i,t2}}{H_{i,t1}}}{t2 - t1},$$

where $H_{i,t2}$ and $H_{i,t1}$ are seedling height at the current and previous census, respectively, and $t2$ and $t1$ indicate time (months) of the current and previous census, respectively.

For analyses of RGRh, we used a repeated measures linear mixed effects model (lme4; Bates et al., 2015) with treatment (control vs.

weed exclusion), growth habit, presence/absence of herbivory and their two- and three-way interactions as factors. We used the same factors for height, first taking the square root transform and using a three-way ANOVA on the final heights attained at the end of the experiment. We tested species as a random factor because they have different growth habits, but these models failed to converge. We instead ran a separate three-way model (for height only, where we had sufficient degrees of freedom) where we substituted species identity for growth habit to assess whether effects of weed presence were conditional on species identity. For analyses of mortality, it was not possible to include species identity or to use repeated measures, as these analyses were done at the population level and the small sample size within a population ($n = 10$) precluded estimates of per capita mortality through time due to non-negligible changes in population size with each mortality event. We therefore assessed the cumulative treatment effects on mortality (proportion dead) at the end of the experiment (6 months) using a generalized linear model with treatment and species growth habit (fast vs. slow) and their interaction as factors, using a binomial logit link function. We present analyses for specific time points of interest corresponding to the end of the experiment (January 2020), and relatively high (August–September 2019) and low (October–December 2019) periods of abiotic stress as indicated by water deficit. For all statistical models, factors were sequentially removed until only significant factors at the $\alpha = 0.05$ level remained (Crawley, 2013).

Abiotic stress was inferred according to the ecosystem water deficit, estimated as the difference between potential evapotranspiration (PET; mm) and incoming precipitation (mm). PET was estimated at the daily timescale using the R package 'Evapotranspiration' (Guo et al., 2019), which estimates PET according to the Penman–Monteith equation using daily minimum and maximum air temperature (°C) and relative humidity (%), wind speed (m s^{-1}) and solar radiation (W m^{-2}) as inputs. Meteorological data were sourced from a nearby met station (approximately 1 mile from study plot) within the refuge, accessed from the MesoWest network API (https://mesowest.utah.edu/) using the R package 'mesowest' (Fick, 2019). Figure 2 highlights periods of high and low abiotic stress according to the ecosystem water deficit, which averaged −5.9 and −3.2 mm/day during August–September and October–December, respectively (a 59% difference).

Finally, we used a post hoc test to assess if individuals with and without herbivory differed in their RGRh separately during periods of high and low abiotic stress. We defined plants with substantial herbivory according to three criteria: those with a mean animal damage score of ≥0.2 or substantial reductions in height over the entire study period (16 and 74 plants, respectively, described below) or those with an animal damage score >1 and a 2.5 cm or greater reduction in plant height during a single analysis period. This left us with 58 and 33 individuals without substantial herbivory during high and low abiotic stress periods, respectively. We defined a substantial reduction in height over the entire study period as the 50th percentile of the total height reduction (THR; cm), which for each individual is the sum of only those height changes from one census to the next that are negative (Figure S4). Thus, the THR accounts both for animal damage evidenced
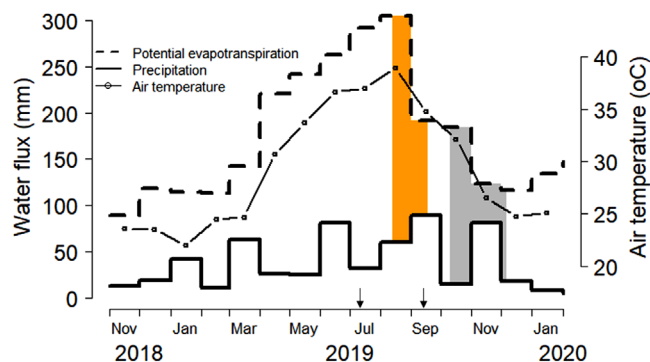
FIGURE 2 Experimental design and climate data during the study period approximately 1 mi from study site (MesoWest station ID 'LSRT2'). Blue and red step lines indicate monthly precipitation (mm) and potential evapotranspiration (PET) following the Penman–Monteith equation (mm), respectively. Difference between PET and monthly precipitation indicates climatic water deficit (mm). The black dashed line indicates monthly mean air temperature. Arrows indicate when mowing occurred. Red and blue shaded regions denote 'stressful' (high water deficit) and 'non-stressful' (low water deficit) periods, corresponding to Figure 5

as a large one-time reduction in height, or as a persistent low level of browsing, evidenced by frequent, small reductions in height. Despite the application of these criteria, we note that it was not possible to fully separate out the covarying effects of herbivory, weed cover and abiotic stress. The progression from high (August–September) to low (October–December) abiotic stress periods also coincided with a trend of reducing weed cover (Figures S2 and S3).

3 | RESULTS

3.1 | Pre-treatment assessment and weed composition and cover

At the start of the experiment, no pre-existing significant effects on mean plant height or total mortality among treatments were present (Table S1; Figure S5). Weed composition assessments indicated a dominant cover of cowpen daisy during non-stressful months, which gradually decreased and turned into a mixed dominant cover of doveweed and Texas signalgrass during periods of water deficit. Bare ground fluctuated from a 30% to 55% from June to October and no invasive grass species were recorded (Figure S3).

3.2 | Weed presence and species identity effects on herbivory

Herbivory was prevalent, and for the most part, similar across all species: with the exception of one species (*C. odorata*), the proportion of each species' population experiencing mild to moderate animal damage was between 20% and 40%, and most species' pairwise comparisons of animal damage were indistinguishable (Figure 3; Wilcoxon
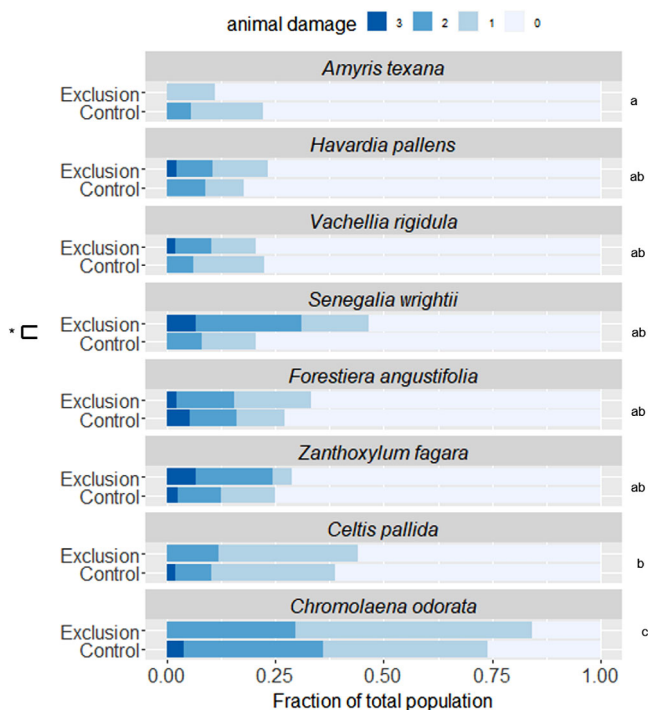

FIGURE 3 Frequency of four different classes of animal damage (see methods) by species and treatment. On right, letters indicate pairwise species differences based on multiple Mann–Whitney U tests using the Benjamini–Hoch correction for multiple tests. On left, significant effects of weed treatment effect within each species are shown, else blank, based on Dunn post hoc tests using Benjamini–Hoch correction for multiple tests

rank sum test with continuity correction: $0.13 \leq p \leq 1.0$ for all pairwise comparisons excluding *C. pallida* and *C. odorata*). Overall, the presence of weed neighbours did not significantly reduce herbivory relative to weed-excluded areas (Mann–Whitney unpaired U test; $U = 60{,}517$; $p = 0.13$), nor on a species-specific basis except for *S. wrightii* (Figure 3; $Z = -3.1$, $p_{adj} = 0.009$). We note that herbivory was mostly due to large ungulates as we observed minimal chewing or sucking damage from arthropods.

3.3 | Weed presence effects on growth and mortality conditional on climate and herbivory

Overall, the presence of weed neighbours had no significant effect on seedling height and mortality at the end of the experiment (Figure 4; two-way ANOVA, height: $F = 1.464$, $p = 0.228$; two-way binomial GLM, mortality: dev $= 13.130$, $p = 0.297$; Table 2). There was a significant interaction between the presence of weed neighbours and growth habit for mortality (Table 2); however, a Tukey post hoc test did not indicate that this difference was significant ($p = 0.166$). Replacing growth habit with species identity into an alternate model of plant height with presence/absence of animal damage as an additional factor only demonstrated expected species-specific differences in plant height and did not indicate any species-specific effects of weed
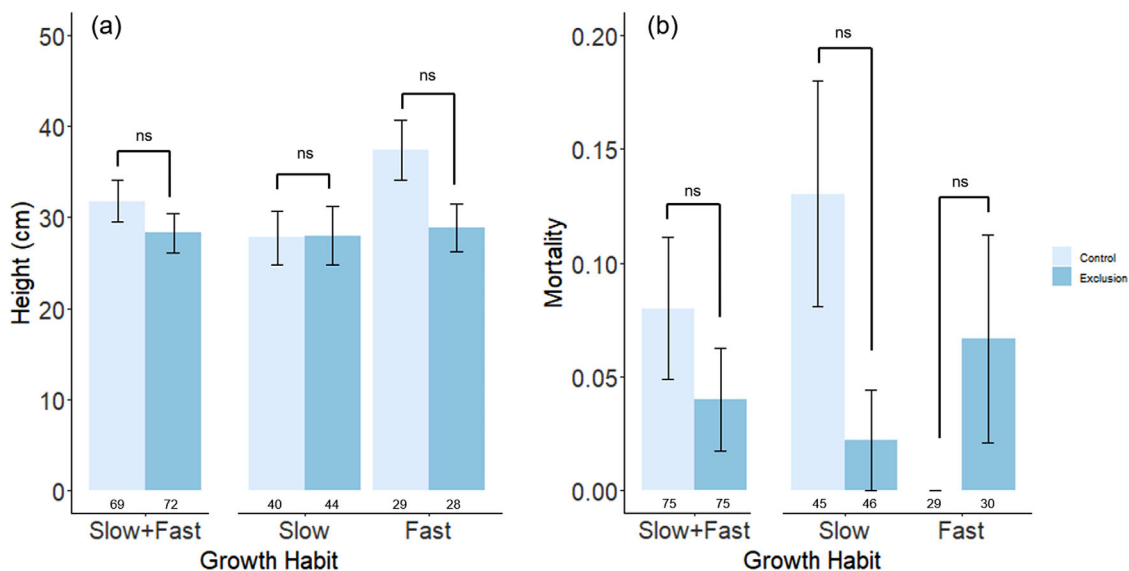
FIGURE 4 Mean seedling height (a) and total mortality (b) ± SE (error bars) in January 2020, 6 months post-treatment. Numbers beneath each bar correspond to the number of individuals in panel (a), and the total number of live individuals in July 2019 for panel (b); mortality represents the fraction of new deaths relative to live individuals in July 2019. ***$p < 0.001$; **$p < 0.01$; *$p < 0.05$; ns = $p > 0.05$

TABLE 2 Two-way ANOVA on the square root-transformed plant height and analysis of deviance for mortality using a two-way binomial GLM in January 2020, for eight species of thornscrub seedlings growing for 6 months in control and weed-excluded plots

	Response variable								
	Square root-transformed plant height				**Mortality**				
Effect	**Df**	**Sum Sq**	**Mean Sq**	**F-value**	**Pr(> F)**	**Df**	**Deviance**	**Resid. Df**	**Resid. Dev**	**Pr(> Chi)**
Treatment	1	3.4	3.40	1.46	0.229	1	1.08	14	13.13	0.298
Growth rate	1	10.83	10.83	4.66	0.033	1	1.24	13	11.89	0.265
Treatment × Growth rate	1	4.76	4.76	2.05	0.155	1	5.85	12	6.03	0.016

neighbour presence (Table S2). On average, slow-growing plants grew 13 cm in height as opposed to 45 cm in the case of fast-growing plants over the 6-month period.

The repeated measures linear model with herbivory presence or absence best explained RGRh over the course of the entire experiment ($F = 9.73$; $p = 0.002$; Table 3). Considering all individuals, the presence of weed neighbours had no net effect on RGRh, regardless of moisture stress level (Figure 5a,b). However, an analysis restricted to only those individuals without substantial herbivory during the period of high water deficit (August–September) showed that the presence of weed neighbours significantly increased relative height growth rate (Figure 5c), which was driven primarily by fast-growing species adjacent to weed neighbours (Tukey HSD post hoc test; $t = 3.619$, $p = 0.001$). Seedling branching of these same individuals was unaffected by weed neighbours (unpaired Mann–Whitney U test; $U = 610$, $p = 0.25$; Figure S6c). In contrast, during periods of low moisture stress, the beneficial effect of weeds was lost (two-way ANOVA; $F = 0.669$, $p = 0.42$; Figure 5d). However, this period also corresponded to a period when most canopy-forming weeds had fully senesced (Figure S2).

3.4 | Weed presence effects on seedling microclimate and photosynthetic capacity

Weed exclusion did not significantly affect light-saturated photosynthetic rate per unit stem length of slow- or fast-growing seedlings (Figure 6a; two-way ANOVA; $F = 0.547, p = 0.473$). In contrast, weeds had a significant effect on the microclimatic conditions of adjacent seedlings, with relative humidity (%) and photosynthetically active radiation (PAR μmol m^{-2} s^{-1}) significantly higher in exclusion areas relative to control (Figure 6a,b; Wilcoxon rank sum test; $W = 0$; $p = 0.016$). Midday air temperature (°C), however, is not altered by the presence of weeds near fast- or slow-growing seedlings (Wilcoxon rank sum test; $W = 15$; $p = 0.286$).

4 | DISCUSSION

We show that naturally recruiting weeds do not significantly diminish the negative effects of browsing by ungulates in the early stages

TABLE 3 Repeated measures linear mixed effects model (Type III ANOVA Table with Satterthwaite's method) on RGRh for eight species of thornscrub seedlings growing for 6 months in control and weed-excluded plots

| Effect	Sum Sq	Mean Sq	Num DF	Den DF	F value	Pr(> F)
Treatment	0.15458	0.15458	1	684	2.2653	0.133
Species	0.42438	0.06063	7	684	0.8884	0.515
Herbivory	0.66394	0.66394	1	684	9.7294	0.002
Treatment × Species	0.14594	0.02085	7	684	0.3055	0.952
Treatment × Herbivory	0.02586	0.02586	1	684	0.379	0.538
Species × Herbivory	0.57237	0.08177	7	684	1.1982	0.301
Treatment × Species × Herbivory	0.43436	0.06205	7	684	0.9093	0.499
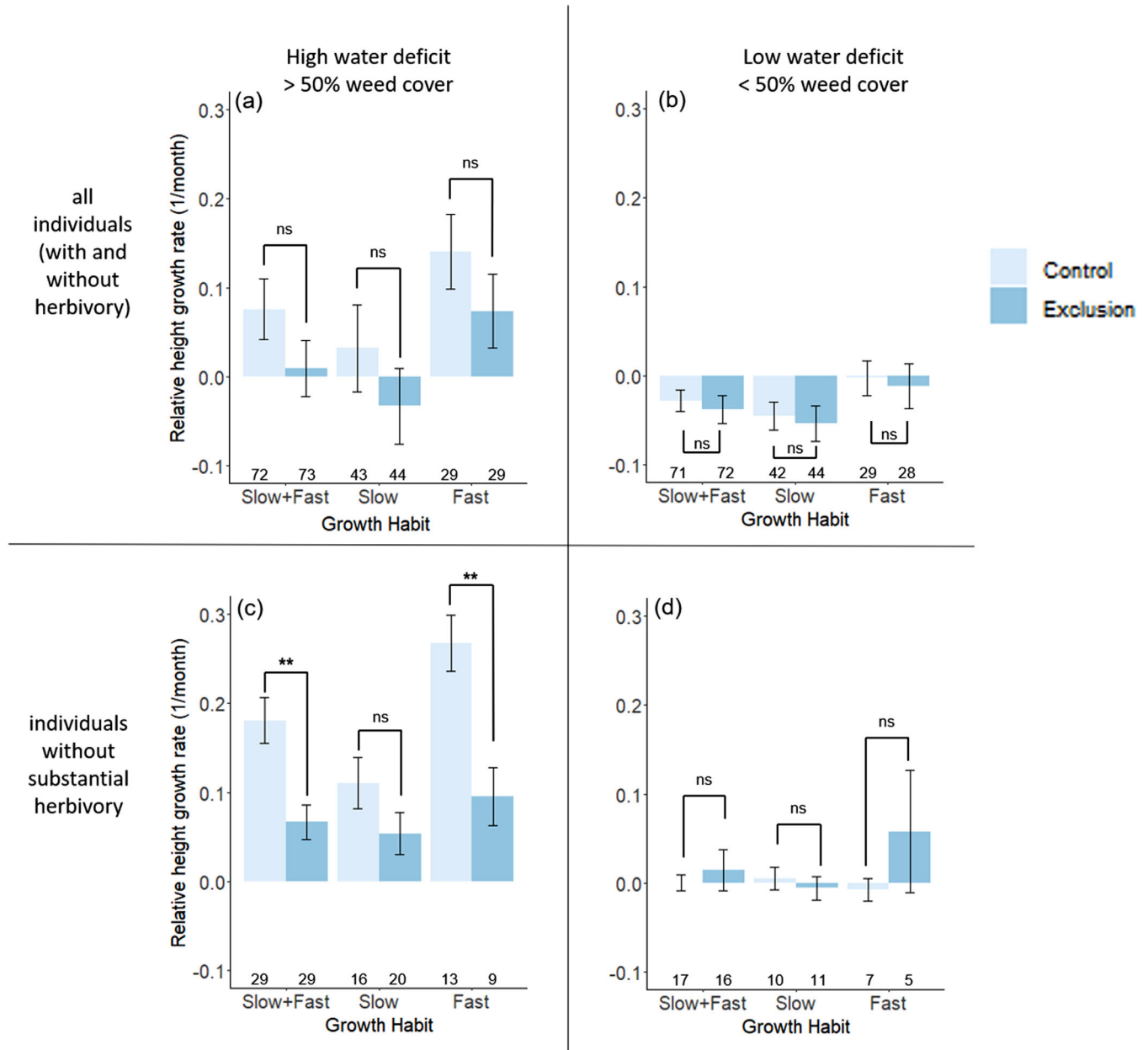
FIGURE 5 Relative seedling height growth rate (RGRh) ± SE (error bars) in relation to animal damage and contrasting abiotic stress. Panels (a) and (b) are all individuals regardless of degree of animal damage, and panels (c) and (d) are only individuals unaffected by substantial animal damage (see Section 2.5). Panels (a) and (c) correspond to large water deficit (August–September 2019), and panels (b) and (d) correspond to small water deficit (October–December 2019; Figure 1). Number of individuals given beneath each bar. ***$p < 0.001$; **$p < 0.01$; *$p < 0.05$; ns = $p > 0.05$
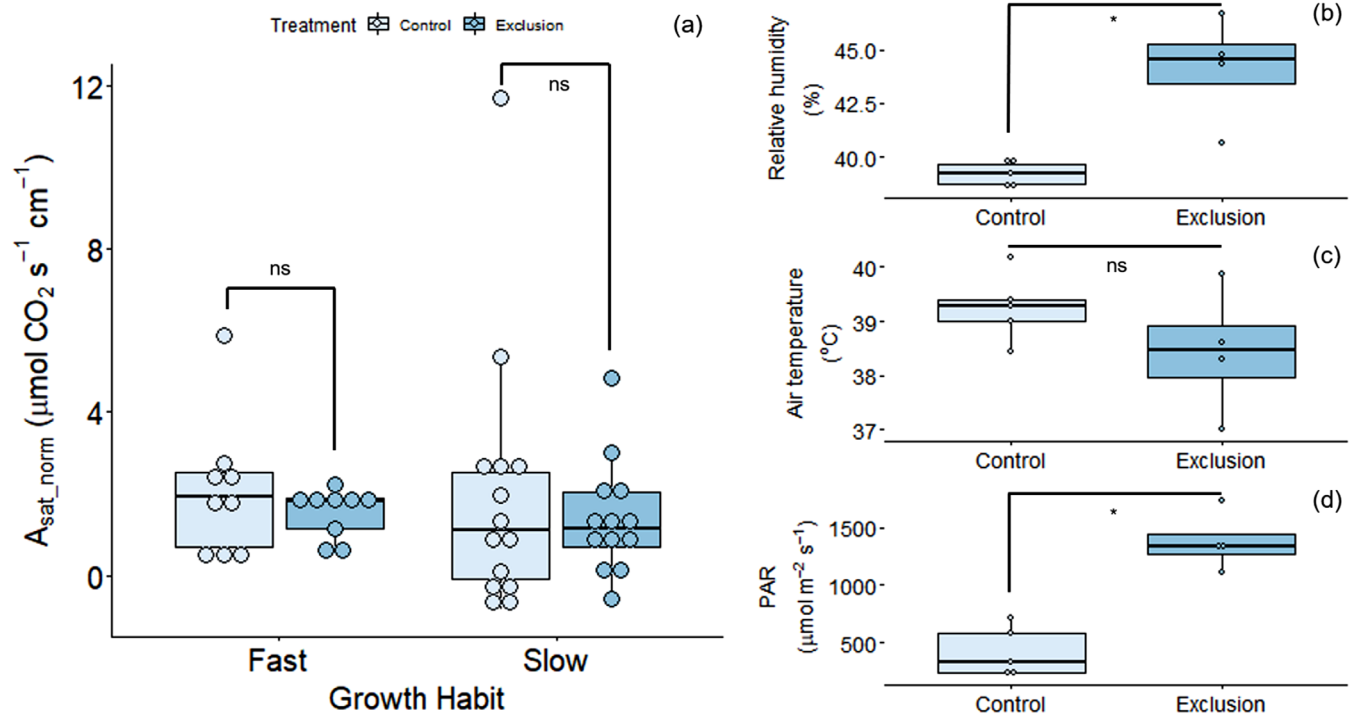
FIGURE 6 Seedling photosynthetic capacity and comparable microclimate conditions adjacent to saplings (see Section 2.3 and 2.4). (a) Light-saturated photosynthetic rate per unit stem length (A_{sat_norm}; μmol CO_2 s^{-1} cm^{-1}) for fast- and slow-growing species in August 2019 when water deficit is high (Figure 1). (b) Relative humidity (%). (c) Air temperature (°C). (d) Photosynthetically active radiation (PAR) (μmol m^{-2} s^{-1}). In panel (a), measurements were conducted with reference CO_2 of 400 ppm and a light intensity of 2000 μmol m^{-2} s^{-1} PAR. In panels (b–d), results of unpaired two-sample Wilcoxon rank sum tests are shown above. *$p < 0.05$; ns = not significant. In all boxplots, horizontal line, lower and upper hinge and whiskers indicate median, 25th and 75th percentile and data points closest to (but not exceeding) 1.5 times the inter-quartile range (IQR), respectively

(6 months) of semi-arid forest restoration (Figure 3), and have no detectable effect on mortality or plant height (Figure 4). However, separating out individuals with substantial herbivory revealed that weed neighbours intermittently significantly enhance height growth (Figure 5c) without impacting seedling branching (Figure S6c). They also do not negatively impact seedling light-saturated inherent photosynthetic capacity while reducing incident solar radiation (Figure 6). These results collectively suggest that animal damage supersedes weed–seedling interactions, which are likely intermittently competitive as well as facilitative. Facilitative effects (enhanced height growth) may be associated with improved microclimatic conditions that improve plant water status under hot and dry conditions, which supports predictions of the stress-gradient hypothesis. This implies that management decisions that provide weed canopy cover during hot and dry conditions while controlling for mammalian herbivory may be a mechanism to exploit facilitative aspects of weeds in semi-arid forest restoration. While the short nature of our experiment precludes us from disentangling the effect of species identity, palatability and early-successional weeds on the long-term successional trajectory of planted forests, it informs future experimental work, which, if replicated across space or time while manipulating herbivory, will help to disentangle these factors.

4.1 | Minimizing mammalian herbivory is critical for realizing the nurse potential of early-successional weeds

We found an important role for mammalian herbivory modulating plant–plant facilitation in our study (Figure 5a,c). Therefore, while weeds do facilitate certain species during stressful conditions in accordance with expectations, they may not necessarily shield them from herbivores as initially assumed (Opperman & Merenlender, 2000; Smit et al., 2007). Interestingly, previous work has shown that grazing-mediated facilitation occurs under high abiotic stress rather than in non-stressful periods (Callaway, 2007; Gómez-Aparicio et al., 2004; Soliveres et al., 2012).

4.2 | Co-occurrence of competition and facilitation

We found no definitive evidence for an overall net negative or positive interaction between weed neighbours and woody seedlings in the early stages (Figure 4); this may indicate that competition is negligible, or that it is present and balanced by the co-occurrence of facilitation. Competition could be above or belowground, though synthesis

work suggests that under moisture stress (the conditions which prevailed in this study), belowground competition would be more likely (Foxx & Fort, 2019). Our analysis shows that weeds may have facilitated growth of seedlings without substantial animal damage during hot, dry periods with large water deficits (August–September; Figure 5c), but conferred no net benefit during cooler periods with smaller water deficits (October–December; Figure 5d), supporting our hypothesis that the facilitative effects of weeds would predominate during periods of intense abiotic stress (Fagundes et al., 2017). However, the lack of a treatment effect during this latter period may be due more to the lack of weed cover than a treatment effect per se, as a significant fraction of forb weed canopy leaf area was lost during this time, leaving greater than 50% bare ground (Figure S2). Regardless, the senescing forb weeds and grasses present during non-stressful periods did not significantly impact seedling growth.

We speculate that height growth alone could be indicative of aboveground competition via shade avoidance response and such responses also tend to be accompanied by increases in internode and petiole length, reductions in leaf area and branching, among others (Casal, 2012; Green-Tracewicz et al., 2011). While we did not collect data on most of these variables, we did find that branching was not diminished adjacent to weed neighbours (Figure S6c), which suggests that the observed responses are indicative of enhanced overall growth rather than shade avoidance response. Second, we note that in semi-arid environments, shade not only reduces light levels but can also have positive effects on water status during hot and dry conditions because of reduced transpiration even if soil moisture is moderately decreased from the presence of neighbours (Holmgren et al., 1997 and refs therein). Because plant growth is highly sensitive to changes in plant water status via drought effects on cell turgor (Muller et al., 2011), it follows that enhanced growth is possible under even the slightest ameliorating effects of plant water status from shade. We were unable to measure plant water status in this study since it would require destructive harvests of seedling branches; therefore, such reasoning remains speculative, but we still deem likely that shade ameliorated abiotic stress to some degree. Our results therefore tentatively support a growing body of evidence in support of the stress-gradient hypothesis of plant facilitation (Bertness & Callaway, 1994; Dohn et al., 2013; Klanderud et al., 2021; Maestre et al., 2009; but see O'Brien et al., 2017), and in particular, underscore the importance of temporal variation in the balance of competition and facilitation, which could inform restoration management practices, such as termination of nurse cover crops (Liu et al., 2013).

The improvement in abiotic conditions associated with weed cover was mixed: under weed canopies relative to exclusion areas, air temperature was not significantly cooler (Figure 5c) and relative humidity was even slightly lower (Figure 5b). Only light conditions were significantly more shaded under weed canopies, by about 50% (Figure 5d). A lower radiation load, however, almost certainly implies a lower leaf temperature, even if overall air temperature is unaffected (Blonder & Michaletz, 2018, but see Cavieres et al., 2005). Therefore, because seedling light-saturated photosynthetic rates ($A_{sat,norm}$) were not significantly different between treatments (Figure 6a), we conclude that the positive effect of weed exclusion on fast-growing plants is due to improved microclimatic conditions rather than developmental changes in inherent photosynthetic capacity per se. Possible effects of improved microclimatic conditions are to bring leaf temperature closer to the temperature optimum of photosynthesis (Sage & Kubien, 2007), a reduced leaf-to-air vapor pressure deficit (due to lower leaf temperature) and hence less stomatal closure (Grossiord et al., 2020), or a combination of the two.

4.3 | Fast-growing species disproportionately benefit from weeds

The facilitative effect of weeds during periods of intense abiotic stress was driven primarily by a positive effect on fast-growing species (Figure 4c). While fast-growing species are desired from a restoration perspective, they may be more prone to succumbing to drought- or heat-induced stress. In contrast, slow-growing species may be better poised to maintain physiological integrity during periods which severely restrict growth, such as in nutrient- and light-deficit conditions (Chapin et al., 1986; Reich, 2014). In this manner, fast-growing species may experience higher mortality rates if under stress, as fast above-ground growth may come at the expense of below-ground resource allocation (Tilman, 1985). Therefore, cover cropping strategies in restoration (Flores & Jurado, 2003) may require incorporating early-successional weed forbs that develop substantial canopies early in the growing season and persist sufficiently long to offer shade during periods of high temperature and vapor pressure deficit (VPD) if they are to benefit fast-growing target species. Alternatively, fast-growing restoration species may themselves act as nurse protégés, providing shade to other seedlings during stressful periods, which could be accomplished in restoration pockets (Ren et al., 2008).

4.4 | Future directions

In particular, future work should screen native weeds in terms of their ability to repel herbivores, either through visual shielding or other means, in order to offset mammalian herbivory. Invasive herbivores remain a significant force in structuring novel ecosystems in semi-arid areas, and the Rio Grande Valley of Texas in particular (e.g., feral hogs, nilgai antelopes and other small mammals; Leslie, 2016). Previous work has shown that native shrub and forb vegetation can play an important role in shielding target restoration species from herbivory; however, more work is needed to determine if facilitative effects from nurses are enough to mitigate the effects of herbivory, or if more drastic shielding measures are necessary (Cushman et al., 2011). Applying cluster reforestation of simple or complex plantings (Saha et al., 2012) could provide a seed source for further expansion of target species. Such aggregated plantings could, simultaneously, place fast-growing individuals and native weeds as a barrier against mammals while shielding

slow-growing species from herbivory (Stanturf et al., 2014). In addition, such clustered plantings could attract various beneficial or negative herbivores, and the effects of those and weed cover should be investigated with respect to the arthropod community (Losapio et al., 2019). While mammalian herbivory had significant impacts here, arthropod community dynamics can also play a significant role, and should be examined in detail (Bangert et al., 2013; Cole et al., 2016).

4.5 | Recommendations for practice

Exploiting native weeds (forbs or grasses) as early stage facilitators of forest seedlings in ecological restoration practice will thus depend on some degree of management of weed cover. Management strategies must minimize the effects of herbivory in successional restoration projects if nurse–protégé interactions are to be fully realized. Moreover, a holistic assessment of all species interactions and target plant–environment relationships is needed to maximize the benefits of plant–plant facilitation in restoration settings.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS
BC, RK and MA designed the study. MA, SM and JC collected data. MA and BC analysed data. MA wrote a first draft with input from BC. BC and RK revised the manuscript. All authors reviewed the manuscript prior to submission.

DATA AVAILABILITY STATEMENT
Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.c59zw3r7j (Arias et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.