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Native tree and shrub canopy facilitates oak seedling regeneration in semiarid woodland

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Abstract. Oaks (*Quercus* spp.) are currently declining worldwide due to a multitude of threats. Woodland management is often heavily focused on thinning and burning nontarget species to reduce competition and promote oak dominance in the overstory. These techniques have typically been developed in temperate regions, such as eastern U.S. forests, but whether they are the most effective strategy for promoting oak regeneration in semiarid woodlands has not been sufficiently examined. We conducted our study on the eastern Edwards Plateau in central Texas, where several oak species are codominant with Ashe juniper (*Juniperus ashei*) over karst limestone terrane. These juniper-oak woodlands provide habitat for many endemic species and play an essential role in the maintenance of key aquifers. A history of canopy clearing and a severe drought in 2011 generated patches of living and dead juniper-oak canopy interspersed with canopy gaps in our study area. In November 2013, we planted 200 shin oak (*Quercus sinuata* var. *breviloba*) acorns in each of three habitat treatments, replicated six times: (1) live canopy, (2) dead canopy, and (3) open invasive grassland. We monitored emergence and survival each year, harvesting five seedlings from each replicate in October 2017 to assess shoot height, rooting depth, biomass, ectomycorrhizal colonization, and foliar nutrients. Canopy trees, living or dead, significantly enhanced seedling emergence and survival. Survival was positively associated with increasing Ashe juniper and oak basal area, shrub cover, and soil organic matter, and negatively associated with increasing canopy gap size (complete mortality in gaps >220 m^2). Seedling biomass increased significantly in dead and open treatments along with foliar nutrients N, P, and S (dead treatments) or S and Fe (open treatments), whereas ectomycorrhizal colonization and foliar nutrients Ca, Mg, and Mn increased under living canopy. Our findings suggest that oak regeneration in these juniper-oak woodlands closely resembles that of Mediterranean regions, where canopy facilitates seedling survival. Both living and dead trees and shrubs enhanced oak regeneration, with seedling survival depending on proximity to larger trees, living roots, shrubs, and juniper-oak canopy. Planting acorns under canopy is an inexpensive, sustainable, and effective restoration practice in drought-prone ecosystems.

Key words: ectomycorrhizal fungi; Edwards Plateau; facilitation; forest; juniper-oak woodland; Juniperus; nurse plant; oak regeneration; *Quercus*; restoration.

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Introduction

With over 500 species distributed worldwide (McShea and Healy 2002), *Quercus* is a diverse genus occupying a wide variety of habitat conditions, ranging from lowland to mountainous, mesic to xeric, and closed-canopy forests to scrublands (Johnson et al. 2005). Given their ecological, aesthetic, and economic importance, sustaining healthy stands is a priority for many land managers; yet, loss of oak trees is widespread and has been attributed to herbivory, fungal disease, insect damage, succession, and climatic changes (McShea and Healy 2002, Johnson et al. 2005, Juzwik et al. 2008, McEwan et al. 2011, Ramírez-Valiente et al. 2015). Understanding the factors that facilitate oak regeneration in different ecosystems is fundamental to countering these loss-inducing processes and implementing successful forest management and restoration practices.

Although oak species richness is exceptionally high in North America (200–240 species), particularly in mountainous regions of Mexico and the southeastern United States (Valencia-A 2004, Nixon 2006), much of the available research on oak management strategies is derived from forests in the eastern United States. In these temperate forests, management-intensive xerifying disturbance regimes of prescribed burns and canopy thinning are aimed at promoting oak dominance in the overstory by reducing mid-canopy structure and allowing light to reach regenerating seedlings (McShea and Healy 2002, Johnson et al. 2005, Brose et al. 2013). In mesic environments where hardwood species proliferate, removing overstory trees (e.g., *Acer* sp.) can be effective in promoting oak seedling recruitment (Nowaki and Abrams 2008, Brose et al. 2013). However, a growing body of literature in Mediterranean ecosystems suggests that canopy thinning to reduce competition may be ineffective or counterproductive. In these hotter, more xeric, environments, oak seedlings often experience severe abiotic stresses such as summer drought (Gómez-Aparicio et al. 2004, 2008, Valladares et al. 2005, Sánchez-Gómez et al. 2006). While as a group, oaks are generally considered to be drought-tolerant, there is considerable interspecific variation in response to drought stress and adaptations to avoid desiccation (Abrams 1990, Johnson et al. 2005, Marshall et al. 2009, Ramírez-Valiente et al. 2015, Kotlarz et al. 2018), with seedlings representing the most vulnerable stage (Cavender-Bares and Bazzaz 2000, Johnson et al. 2005). Hence, successful strategies for managing oak regeneration in temperate regions may not be the most appropriate for more xeric ecosystems.

In drought-prone areas, facilitation through spatial proximity often becomes more important than competition in organizing plant communities (Gómez-Aparicio et al. 2004, He et al. 2013, Andivia et al. 2017). For example, nurse-plant canopies facilitate seedling growth and development through multiple processes (Brooker et al. 2008), including amelioration of environmental stresses (Ren et al. 2008, Caldeira et al. 2014), improved moisture retention (Nagra et al. 2016), protection from browsing (Russell and Fowler 2004), provision of nutrients (Filazzola and Lortie 2014), and access to ectomycorrhizal fungi (Pickles and Simard 2017). Ectomycorrhizal fungi can provide a host plant with a range of benefits that enhance their survival, including improved plant health and protection from pathogens (Fitter and Garbaye 1994, Laliberté et al. 2015), enhanced nutrient uptake (Read and Perez-Moreno 2003), and resistance to drought (Pickles and Simard 2017). Increased seedling survival under nurse plants has been demonstrated in semiarid Californian woodlands (Callaway 1992*a*, *b*), Mediterranean open woodlands and forests (Castro et al. 2004, Christian et al. 2008, Andivia et al. 2017), and moist subtropical forest (Ren et al. 2008). These studies suggest that facilitation by nurse plants may offer a novel, inexpensive, and low-impact reforestation technique.

Few studies have examined strategies for promoting oak regeneration in central Texas, which has a subtropical subhumid climate (Larkin and Bomar 1983) that is intermediate between more mesic eastern forests and arid western environments. Here, Ashe juniper (*Juniperus ashei*) is codominant with several oak species (Diamond and True 2008). Whereas oak resprouting has been documented following wildfire and prescribed burns, regeneration of new individuals from seed has not (Reemts and Hansen 2008, Andruk et al. 2014, Reidy et al. 2016). However, Ashe juniper saplings have been observed to protect oak seedlings from browsing by white-tailed deer (*Odocoileus virginianus*), and acting as nurse plants may thereby outweigh interspecific competition (Russell and Fowler 2004). Hence, facilitation could be a viable regeneration strategy in these semiarid ecosystems.

We conducted a four-year field experiment to investigate the role of facilitation in oak regeneration within a juniper-oak woodland, where an extreme drought event from May to December 2011 resulted in significant tree mortality (Crouchet et al. 2019). Historical canopy clearing followed by drought-induced mortality generated a mosaic of three structurally distinct types of habitat: live canopy, dead canopy, and open invasive grassland. We planted white shin oak (other common names include scaly bark oak, bigelow oak, and limestone Durand oak, hereafter "shin oak"; *Quercus sinuata* var. *breviloba*) acorns into each of these habitat treatments. We then examined biotic and abiotic differences between treatments and investigated how seedling performance was affected by measuring emergence and survival rates, growth, ectomycorrhizal colonization, soil fertility, and foliar nutrients. We hypothesized that seedling regeneration success in these semiarid woodlands would be greatest under living canopy as is often observed in Mediterranean woodlands.

METHODS

Study area

We conducted this study from 2013 to 2017 on the Sam Hamilton Memorial Reserve tract (30°40′ N, 97°84′ W; 300 m elevation) within the Balcones Canyonlands Preserve, on the eastern Edwards Plateau west of Austin, Texas. This region is characterized by steep limestone karst terrane with a deep, cavernous aquifer (Edwards Aquifer) and has been identified as a biodiversity hot spot with many endemic and imperiled species, including cave and spring invertebrates, *Eurycea* salamanders, and the Golden-cheeked Warbler (*Setophaga chrysoparia*). The Edwards Aquifer is "one of the largest and most productive aquifer systems in the United States" (Schindel and Gary 2017). This and other karst terranes make up an estimated 25% of the United States' land surface and 25% of the land surface of Texas (Weary and Doctor 2014). Forests play a key role in the maintenance of karst aquifers by reducing evaporation during drought (Chandler 2006, Hauwert and Sharp 2014, Nagra et al. 2016), increasing infiltration (Slaughter 1997, Lindley 2005, Dasgupta et al. 2006), and reducing erosion (Bray 1904, Urich 2002). Threats to oak regeneration and recruitment in central Texas include widespread mortality due to oak wilt fungus (*Ceratocystis fagacearum*; Juzwik et al. 2008), land clearing and development (Duarte et al. 2013), herbivory (Russell and Fowler 2004), and severe drought (Schwantes et al. 2017).

According to a decadal series of aerial photographs from 1940 to 2012, our study area originally supported a mature, closed-canopy juniper-oak forest that was cleared of most trees prior to 1980 and thinned intermittently thereafter (Fig. 1). The present woodlands, which include stands dominated by young (≤40 years old) Ashe juniper trees mixed with young and mature plateau live oak (*Quercus fusiformis*), Texas red oak (*Quercus buckleyi*), and cedar elm (*Ulmus crassifolia*), experienced expanding tree mortality following the extreme drought of 2011 (500 mm total annual precipitation). By 2013, the study area contained a mosaic of three distinct habitat types: (1) live juniper-oak woodland patches (live), (2) post-drought dead juniper-oak woodland patches (dead), and (3) open grassland patches (open) dominated by invasive King Ranch bluestem (*Bothriochloa ischaemum* var. *songarica*). A 2.4-m game fence around the preserve perimeter limited, but did not preclude, herbivory by white-tailed deer and feral hogs (*Sus scrofa*) within our study area. Weather data for the years of our study are provided in Appendix S1: Table S1.

Study species

Shin oak is one of the three oak species that occur commonly in the vicinity of our study area. The other two species, plateau live oak and Texas red oak, are codominant with Ashe juniper. We chose shin oak as our study species because it is common in the surrounding woodlands but absent from the study site; hence, we were reasonably certain that emerging shin oak seedlings were experimentally planted. Shin oak grows as a shrub or tree on limestone hills in central and north Texas, southern Oklahoma, and northern Mexico. It is often clonal with multiple trunks

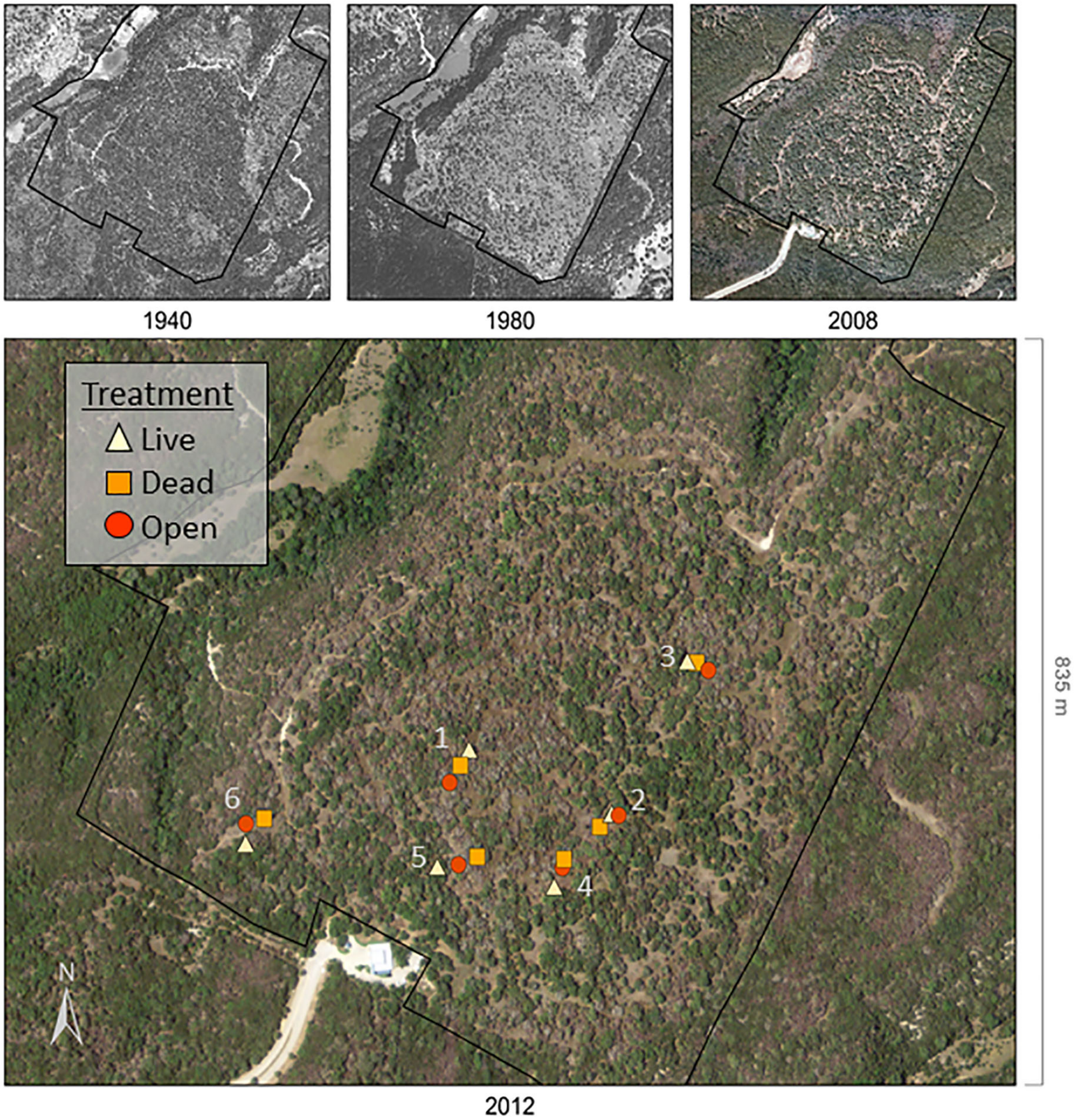


Fig. 1. Aerial photographs of land cover change on the study area, Balcones Canyonlands Preserve, Austin, Texas (30°40′ N, 97°84′ W), illustrating vegetation structure from 1940 to 2012. 1940: closed-canopy juniper-oak forest, 1980: cleared juniper-oak canopy, 2008: recovering juniper-oak canopy of young trees interspersed with patches of mature trees, and 2012: post-drought juniper-oak canopy featuring patches of tree mortality.

forming thickets or shinneries following disturbance; however, single trees ranging from 4.3 to 16.6 m are found in mature forests (City of Austin, *unpublished data*). As a white oak, it is more drought-tolerant (Nokes 2001) and resistant to infection by oak wilt than either Texas red oak or plateau live oak (Juzwik et al. 2008), making it a species of interest for habitat restoration.

Experimental design

For each habitat treatment (live, dead, and open), we established six circular plots with a radius of 3 m for a total of 18 plots (Fig. 1). To select plot locations, we generated a map of six random-systematic points across the study area using the Fishnet tool in ArcMap 10.0 (Environmental Systems Research Institute, Redlands, California, USA). We located each point in the field and set up one plot for each treatment in the appropriate habitat patch nearest that point after confirming there were no mature shin oaks in the vicinity. For the live and dead plots, plot centers were placed >3 m from the woodland edge to ensure the entire plot was under canopy. We marked the plot center using a live or dead Ashe juniper tree within a predominantly living or dead woodland patch (live and dead plots, respectively) or a 1.5-m rebar (open plots) and recorded their locations using handheld Garmin global positioning system (GPS) units (Garmin International, Olathe, USA). We measured soil depth (depth to the first limestone layer) at twelve points per plot (three per quadrant) by scraping off the litter layer with a trowel and inserting a pointed metal rod into the soil until we hit an impermeable or restrictive layer.

Shin oak acorns were collected on 23 October 2013 from a shinnery 2.6 km southwest of the study site and stored at 9°C until planting. Between 1 and 14 November 2013, we sowed 200 acorns per plot on their sides at 2.5–5 cm depth and spaced them as uniformly as possible in a grid fashion (~15–20 cm apart), for a total of 1200 acorns per treatment (3600 acorns across the 18 plots). Immediately before planting, acorns were randomly selected from the collection and assessed for viability using the float test (Morina et al. 2017): Floating, cracked, or soft acorns were discarded. We further tested acorn viability under controlled conditions by randomly selecting 60 acorns, planting them in separate pots in our greenhouse on 6 November 2013, and recording emergence (40%) in May 2014. We tracked seedling emergence and survival within the treatment plots on five occasions post-planting (May 2014, October 2014, September 2015, September 2016, and October 2017). We used a HOBO Micro Station data logger (Onset Computer, Bourne, Massachusetts, USA) to measure organic horizon soil temperature and moisture in each plot quadrant on each visit for 5–10 min (10-s logging interval).

In October 2017, we randomly selected five seedlings per plot, measured their height, and destructively harvested them, carefully excavating to extract entire root systems including all ectomycorrhizal fine roots. To assess soil conditions, we sampled ~100 g of soil associated with each seedling for routine (pH, NO_3-N, conductivity, P, K, Ca, Mg, Na, S), textural, and organic matter analyses (Texas A&M AgriLife Extension, College Station, Texas, USA). We placed seedlings and soil samples into labeled ziplock bags and stored them on ice in coolers. We assessed seedling colonization by counting all live ectomycorrhizal fine root tips. To evaluate foliar nutrients, we oven-dried seedlings at 60°C for 72 h to obtain dry weight measurements of root and shoot biomass (± 0.01 g), then removed the oven-dried leaves, and sent them for analyses of major elements (Al, B, Ca, Cu, Fe, Mg, Mn, P, K, S, Zn) and total C and N (Analytical Chemistry Services Laboratory, Victoria, British Columbia, Canada).

Within each plot quadrant, we followed a modified BBIRD protocol (Martin et al. 1997) to measure vegetation structure in October 2017. We recorded the diameter at breast height (dbh) of all live and dead Ashe juniper and oak trees >2.5 cm dbh in an 11.3 m radius from the plot center using a Biltmore stick, converting dbh to basal area (m^2/ha), and measured canopy cover with a concave spherical densitometer, averaging four readings taken from the plot center facing the four cardinal directions. We visually estimated percent cover of shrubs, grasses, litter, and bare ground in a 5-m radius around the plot center. We calculated the area of canopy gaps around each open plot from 2017 aerial imagery in ArcMap 10.6.1 (range: 152–938 m^2; Appendix S1: Table S2).

Statistical analyses

We conducted all statistical analyses in R v3.4.3 (R Core Team 2018). We assessed differences between the treatments in measured abiotic, biotic, and seedling growth variables using linear mixed models with a normal distribution and the maximum-likelihood approach in R package lme4 (Bates et al. 2015). We included plot, and for repeat measures also time, as a random effect. To evaluate model fit, we calculated marginal R^2 ($R^2_{(m)}$; variance explained by fixed factors) and conditional R^2 (($R^2_{(c)}$; variance explained by fixed and random factors) using the methods of Nakagawa and Schielzeth (2013). We used Satterthwaite approximations to obtain degrees of freedom and *F*-values for models using lmerTest (Kuznetsova et al. 2017).

We modeled seedling emergence, survival, and ectomycorrhizal colonization independently as a function of biotic and abiotic variables, using an information-theoretic approach to compare the fit among alternative models derived from a priori hypotheses about the relationships between seedling characteristics and environmental variables (Burnham and Anderson 2002). To assess multicollinearity, we examined the variance inflation factor for all model covariates, all of which were <3. Our alternative models were (1) biotic: living Ashe juniper basal area, living plateau live oak basal area, dead Ashe juniper basal area, and shrub cover; (2) abiotic: soil P and organic matter; (3) global: all previous variables; and (4) null: intercept only. For seedling emergence and 4-year survival, we fit generalized linear mixed models (GLMMs) with a binomial distribution in lme4 (Bates et al. 2015) including plot as a random effect. For ectomycorrhizal colonization, we fit a general linear model (GLM) with a normal distribution and evaluated goodness of fit using adjusted R^2. We ranked the models in each competing set using Akaike's information criteria adjusted for small sample sizes (AICc) and then compared them using ΔAICc in relation to the most supported model (lowest AICc; Burnham and Anderson 2002); models with $\Delta AICc < 2$ have strong support, 2–10 have low empirical support, and >10 have no empirical support. Fixed effect coefficients with 95% confidence intervals that excluded zero were considered statistically significant.

We used R packages FactoMineR (Le et al. 2008) and factoextra (Kassambara and Mundt 2017) for principal component analysis (PCA) of foliar macro- and micronutrient data. We examined correlations between the PCA axes and the measured abiotic and biotic factors, adjusting for multiple testing using the Bonferroni correction.

RESULTS

Treatment differences

All treatments in this study were located on clay-dominated soils with soil depth ranging from 16 to 18 cm. Soil and biotic factors varied significantly among treatments in several key properties (Appendix S1: Table S3; Appendix S2: Fig. S1). Live treatment plots had a closed canopy of trees with the highest leaf litter levels and lowest grass cover, and exhibited lower soil pH and temperature, and higher soil P and Mg than dead and open treatment plots. Living Ashe juniper and oak trees in the live treatment had approximately twice the basal area as in dead, and their basal areas were five and 20 times greater, respectively, in live than in open. Dead Ashe juniper basal area was greatest in the dead treatment, with three and four times that observed in open and live, respectively. Soil organic matter content was greater in live and dead treatments than in open, soil K was greater in live than in open, soil Ca was greater in dead than in live, and soil moisture was greatest in open and lowest in dead. Soil temperature was greatest in September 2015 and lowest in September 2016. Soil moisture was lowest in September 2015 and greatest in September 2016.

Emergence and survival

Emergence of shin oak seedlings was significantly lower in open treatment plots than in live or dead (Fig. 2; $P < 0.001$, ($R^2_{(m)} = 0.570$, ($R^2_{(c)} = 0.890$). Further modeling of this observation was unsuccessful: The best emergence model (global) only explained 9.2% of the variation (($R^2_{(c)} = 0.092$) with 6.5% explained by the fixed factors (($R^2_{(m)} = 0.065$; Appendix S1: Table S4). In open plots, seedling emergence was negatively associated with gap size (GLM: Emergence ~ log(Gap size), $P = 0.002$, $R^2 = 0.894$).

From 6 to 22 months post-planting, seedling survival in all treatments declined, with complete mortality in the four largest canopy gaps around the open plots by 22 months (Fig. 2). At 34 months post-planting, the number of surviving seedlings appeared to increase significantly in the dead treatment (Fig. 2); this observation was later found to be due to counting multiple stems of the same individual. When we harvested seedlings in October 2017, we discovered that what appeared to be separate plants were stems growing from the same root. We then carefully excavated around the base of all seedlings to confirm the number of individuals and ensure an accurate final seedling count and used these

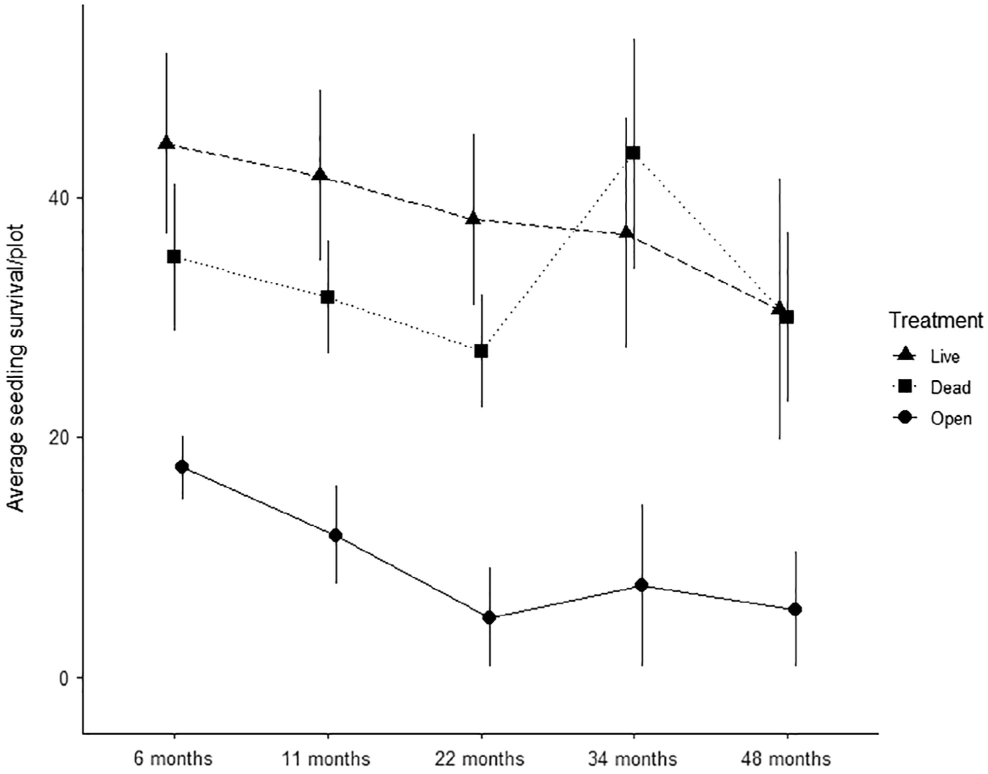


Fig. 2. Shin oak seedling emergence (May 2014) and survival in three habitat treatments (live juniper-oak canopy, dead juniper-oak canopy, open invasive grassland) across six plots (count ± SE). Shared letters indicate no significant difference.

numbers in our models. By the end of the study, total seedling survival was significantly greater in live and dead treatments at ~15%, compared with 2.8% in open (Fig. 2; $P < 0.001$, ($R^2_{(m)}$ 0.649, ($R^2_{(c)} = 0.954$). We also found that survival in open plots was negatively associated with gap size; no seedlings survived in gaps >220 m^2 by the end of the study (GLM: Survival ~ Gap size, $P < 0.001$, $R^2 = 0.996$). The best survival model (global) explained 55% of the variation in the data (($R^2_{(c)} = 0.546$) with 34% explained by the fixed factors and their interactions (($R^2_{(m)} = 0.337$). The global model including both abiotic and biotic factors received the most support (Table 1), and the significant covariates were living Ashe juniper basal area, living plateau live oak basal area, proportion shrub cover, and percentage of soil organic matter (Table 2). The probability of seedling survival increased as each of these covariates increased (Fig. 3a).

Table 1. Model selection of shin oak seedling survival and ectomycorrhizal colonization in response to biotic and abiotic parameters

Model	K	AIC_c	ΔAIC_c	ω_i
Survival				
Global	**8**	**2201.4**	**0**	**0.93**
Biotic	6	2206.6	5.2	0.07
Abiotic	4	2300.5	99.1	0.00
Null	2	2344.4	143	0.00
Ectomycorrhizal colonization				
Biotic	**6**	**50.32**	**0**	**0.73**
Global	8	52.32	2	0.27
Null	2	66.02	15.7	0.001
Abiotic	4	68.69	18.37	0.001

Notes: AICc, Akaike's second-order information criterion; K, number of parameters; ΔAICc, difference between model AICc and best model AICc; ωi, AIC weight. Biotic model includes living Ashe juniper basal area, living plateau live oak basal area, dead Ashe juniper basal area, and shrub cover. Abiotic model includes soil P and organic matter. Global model includes all factors in the biotic and abiotic models. Bold indicates the most supported (best) models.

Table 2. Parameter values for AICc "best" model factors affecting survival probability or ectomycorrhizal colonization of shin oak seedlings

Model parameter	β	SE	LCL	UCL	*P*
Global (survival)					
Intercept	−6.99	0.83	−8.62	−5.36	<0.01
Living juniper BA	**0.09**	**0.04**	**0.01**	**0.17**	**0.02**
Living oak BA	**0.06**	**0.03**	**0.001**	**0.12**	**0.02**
Dead juniper BA	0.16	0.2	−0.23	0.55	0.43
Shrub cover	**32.46**	**5.38**	**21.91**	**43.01**	**<0.01**
Organic matter	**0.41**	**0.16**	**0.1**	**0.72**	**0.01**
Soil P	0.15	0.09	0.33	0.03	0.09
Biotic (ectomycorrhizal colonization)					
Intercept	−0.74	1.45	−3.87	2.39	0.62
Living juniper BA	**0.65**	**0.16**	**0.30**	**1.00**	**<0.01**
Living oak BA	**0.26**	**0.1**	**0.04**	**0.48**	**0.02**
Dead juniper BA	1.42	0.75	−0.20	3.04	0.08
Shrub cover	41.84	25.41	−13.05	96.73	0.12

AICc, Akaike's second-order information criterion; β, beta coefficient; LCL, lower 95% confidence interval; SE, standard error; UCL, upper 95% confidence interval. Bold indicates significant factors with a 95% CI that does not include zero.

Growth and ectomycorrhizal colonization

Seedling height in the dead and open treatments was twice that in live, and rooting depth was 1.5–2 times deeper in dead and open, respectively, than in live (Table 3; Appendix S2: Fig. S2). Root biomass and shoot biomass were four to five times greater in dead and open, respectively, than in live (Table 3; Appendix S2: Fig. S3).

On average, the total number of ectomycorrhizal root tips per seedling in live was 1.8 and 1.5 times greater than those in dead and open, respectively (Table 3). However, there was considerable variation between plots (Fig. 4). Ectomycorrhizal colonization density (tips/g root biomass) in live was five times greater than in dead and three times greater than in open (Table 3). The best ectomycorrhizal colonization model was the biotic set (Table 1), which explained 83% of the variance between seedlings (adjusted $R^2 = 0.83$). The significant covariates were living Ashe juniper and plateau live oak basal areas (Table 2), and as with seedling survival, ectomycorrhizal colonization increased as the basal area of these trees increased (Fig. 3b).

Foliar nutrition

The 12 measured foliar nutrients were best represented by five PCA axes (73.9% of the variance; Appendix S1: Table S5). Axis 1 (25.72%) separated live and dead treatments, and was positively correlated with five foliar nutrients (N, S, P, Cu, and K), dead Ashe juniper BA, seedling height, rooting depth, and % grass cover, and negatively correlated with two foliar nutrients (Ca and Mg), % leaf litter, % canopy cover, soil Mg, and living tree BA (Fig. 5; Table 4). Axis 2 (17.8%) was positively correlated with three foliar nutrients (Ca, Mn, and Zn) and negatively correlated with foliar C (Fig. 5; Table 4). Axis 3 (11.9%) separated live and open treatments and was positively correlated with three foliar nutrients (Cu, K, and Mg), soil Mg, and % canopy cover, and negatively correlated with three foliar nutrients (S, Fe, and B), root biomass, total biomass, and % grass cover (Fig. 5; Table 4). No measured abiotic or biotic variables were correlated with Axes 2, 4, or 5 (Table 4). Axes 4 and 5 each represented less than 10% of the variance (Table 4). Further examination of foliar nutrient levels based on the results of the PCA indicated that foliar B, C, Cu, K, and Zn did not vary significantly among treatments.

DISCUSSION

Shin oak seedling emergence and survival was facilitated by the presence of canopy in a semiarid juniper-oak woodland. Both living and dead canopy supported seedling survival after four years; however, the seedlings growing under each treatment had very different characteristics (Fig. 6). Seedlings under living canopy were smaller, had greater ectomycorrhizal colonization, and increased foliar Ca, Mg, and Mn. Dead canopy supported larger seedlings with deeper roots, taller shoots, less ectomycorrhizal colonization, and increased foliar N, P, and S. Seedling survival in open gaps was extremely low, and gap size had a strong negative effect. Thus, planting shin oak acorns under existing canopy appears to be a more useful oak regeneration strategy in semiarid regions than canopy clearing.

Emergence and survival

Emergence under canopy was more than twice that in open gaps. Oak seedlings depend on

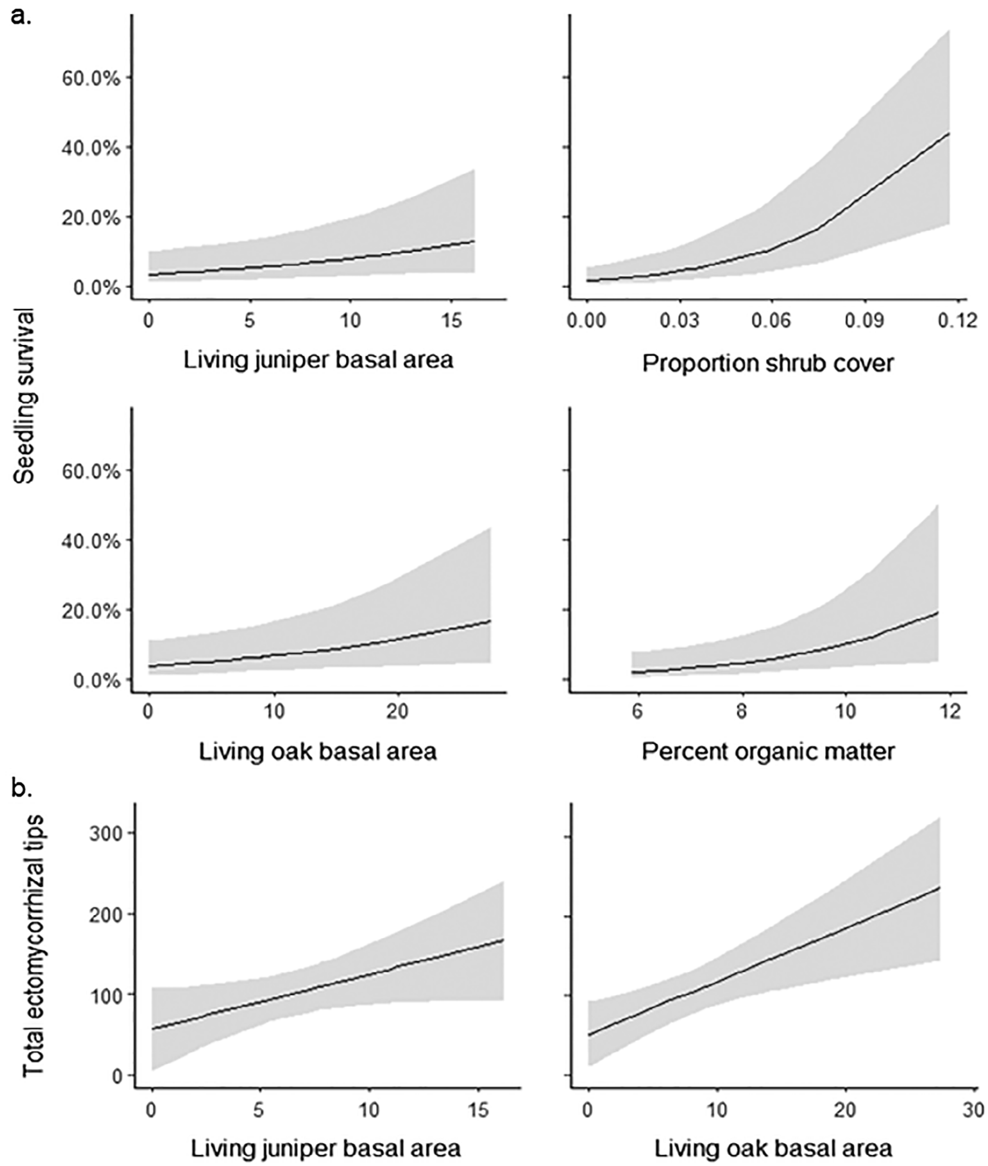


Fig. 3. Biotic and abiotic factors affecting shin oak seedlings based on significant model coefficients for (a) survival, global model, and (b) ectomycorrhizal root tips, biotic model. Solid line indicates modeled response; shading indicates 95% confidence interval.

acorn reserves during their first year but become more dependent on external resources as seed reserves are depleted (Gómez-Aparicio et al. 2008, Pérez-Ramos et al. 2010), which is likely the reason seedling emergence was not well explained by any of the measured variables in our models. Lower emergence in open plots may be attributed to competition with invasive King Ranch bluestem, which can be a contributing factor in oak mortality (Montes-Hernández and López-Barrera 2013). Canopy cover in the live plots effectively shaded out King Ranch bluestem and may have provided indirect facilitation of the seedlings by reducing competition (Cuesta et al. 2010). While we did not see evidence of acorn predation, and the density of feral hogs and white-tailed deer was low in our study area, canopy cover can protect seedlings from

Table 3. Differences in shin oak seedling growth and ectomycorrhizal (EcM) root tip responses between habitat treatments using linear mixed models

	Treatment mean (± SE)							
Response	Live	Dead	Open	df	F	P	$R^2_{(m)}$	$R^2_{(c)}$
Height (cm)†	7.56 (0.47)b	15.75 (1.44)a	12.27 (1.43)a	2,67.5	24.90	<0.001	0.397	0.452
Depth (cm)	22.78 (1.50)b	36.77 (1.80)a	40.57 (4.91)a	2,67.3	22.08	<0.001	0.378	0.430
Total biomass (g)†	1.52 (0.17)b	6.49 (1.07)a	7.68 (1.95)a	2,64.3	24.55	<0.001	0.412	0.428
Shoot biomass (g)	0.35 (0.04)b	1.30 (0.27)a	1.77 (0.48)a	2,62.5	16.17	<0.001	0.319	0.319
Root biomass (g)	1.10 (0.13)b	5.16 (0.84)a	5.92 (1.57)a	2,64.5	23.58	<0.001	0.401	0.420
EcM root tips (count)‡	167.30 (30.8)a	94.30 (21.6)b	110.80 (23.8)b	2,66.0	328.82	<0.001	0.149	0.985
EcM density (tips g^{-1})†	178.90 (34.0)a	35.40 (10.6)b	57.30 (29.6)b	2,66.6	20.68	<0.001	0.321	0.468

Notes: Model form (Response) ~ (Canopy treatment) + (1|Plot). Means that do not share a letter were significantly different ($\alpha = 0.05$).

† Data $\log_e$ transformed to achieve normality.

‡ Count data analyzed using a generalized linear model with a Poisson distribution and log link, trigamma method for R^2.

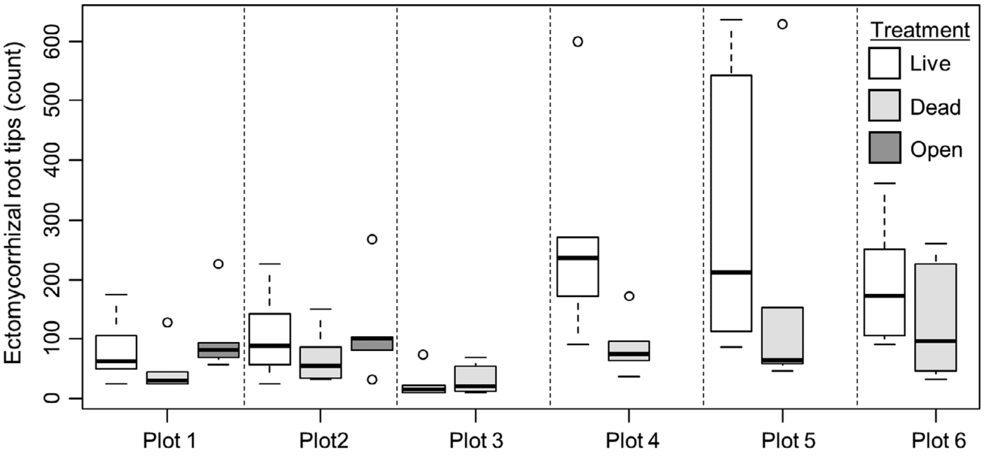


Fig. 4. Boxplot showing differences in the number of ectomycorrhizal root tips per shin oak seedling between plots and treatments ($n = 5$ seedlings per treatment per plot). Box indicates median plus interquartile range; circles indicate extreme values (greater/<1.5 times the upper/lower interquartile range).

ungulate herbivory (Castro et al. 2004, Russell and Fowler 2004) and so could have contributed to lower emergence in the open plots.

Survival was fivefold higher under canopy and increased with shrub cover, tree basal area, and soil organic matter. By the end of the second year, only the two open plots with the smallest canopy gaps (152 and 220 m^2) had live seedlings, with five times as many growing in the smallest canopy gap; the remaining three plots with larger gaps (346–478 m^2) had only desiccated seedlings. In contrast, we occasionally saw desiccated seedlings in the dead canopy plots but rarely under the live canopy, and live seedlings persisted in all canopy plots by the end of our study. Multiple studies in ecosystems that experience light, heat, and drought stresses have reported shade as the primary mechanism enhancing seedling survival of woody plants and that the importance of this facilitative effect increases with abiotic stress (Castro et al. 2004, Gómez-Aparicio et al. 2004, 2008, Valladares et al. 2005, Padilla and Pugnaire 2006, Quero et al. 2006, Sánchez-Gómez et al. 2006, Puerta-Piñero et al. 2007, Christian et al. 2008, Badano et al. 2011, Montes-Hernández and López-Barrera 2013, Caldeira et al. 2014). In our system, late summer was a critical period for seedling survival due to high temperatures and low rainfall, with significantly lower soil temperatures observed under

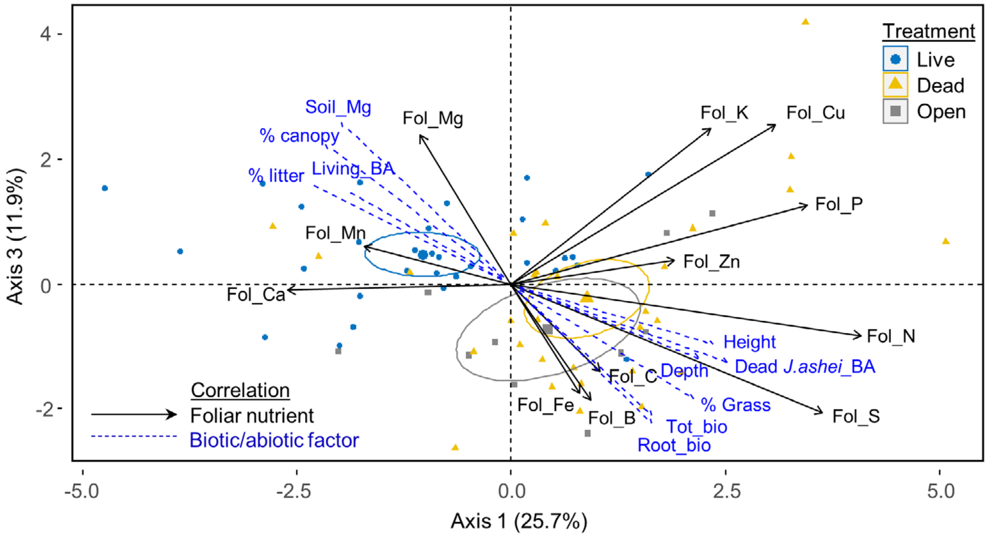


Fig. 5. Foliar nutrient biplot of principal component analysis Axes 1 and 3 for four-year-old shin oak seedlings with 95% confidence ellipses for each treatment (n = 5 seedlings per treatment per plot). Points indicate individual seedlings; arrow length indicates strength of correlation.

living canopy, presumably due to shading. Soil organic matter concentrations were significantly higher under canopy, which can further improve microclimatic conditions by increasing soil fertility (Padilla and Pugnaire 2006), but these effects appear to be secondary to reduced radiation (Gómez-Aparicio et al. 2005). Hence, our results suggest that the main benefits of canopy are the amelioration of drought stress and reduction in solar radiation, which can cause photoinhibition of photosynthesis and leaf overheating (Valladares 2003).

Growth and ectomycorrhizal colonization

Seedlings under living canopy generally had smaller and more compact roots and shoots. Seedlings under dead canopy or in open gaps had deeper root systems that grew into and through several layers of solid rock and were commonly intertwined with roots of Ashe juniper, oaks, and other species. Seedling growth in general was negatively correlated with increased soil nutrient concentrations, which were highest under the live canopy except for Ca. Other studies have found a limited response of seedling growth to soil nutrients compared with light and other factors (Long and Jones 1996, Gómez-Aparicio et al. 2005, Pérez-Ramos et al. 2010). Light-mediated growth limitations have been reported as the main negative effect of facilitation by nurse plants in arid and Mediterranean systems (Sánchez-Gómez et al. 2006, Puerta-Piñero et al. 2007, Montes-Hernández and López-Barrera 2013, Caldeira et al. 2014), and may change seedling resource allocation strategies (Villar-Salvador et al. 2012), but this may be an acceptable trade-off for increased survival (Gómez-Aparicio et al. 2006, Pérez-Ramos et al. 2010). In our study, the slower growth observed under living canopy could allow seedlings to employ a sit-and-wait strategy (e.g., Greenberg et al. 2001), whereas development of deep roots in dead canopy and gap conditions may be critical for summer survival in these more open habitats (Padilla and Pugnaire 2007). This increase in primary root depth under dead canopy and in open gaps may also be a growth response triggered by limited availability of key soil nutrients including N and P (Lambers et al. 2006, Giehl et al. 2014, Robbins and Dinneny 2015).

Ectomycorrhizal colonization was highest on seedlings under living canopy, and the basal areas of live Ashe juniper and oaks were the best predictors of ectomycorrhizal root tip counts. Mycorrhizal fungi play an important role in nutrient and water uptake and transport, with

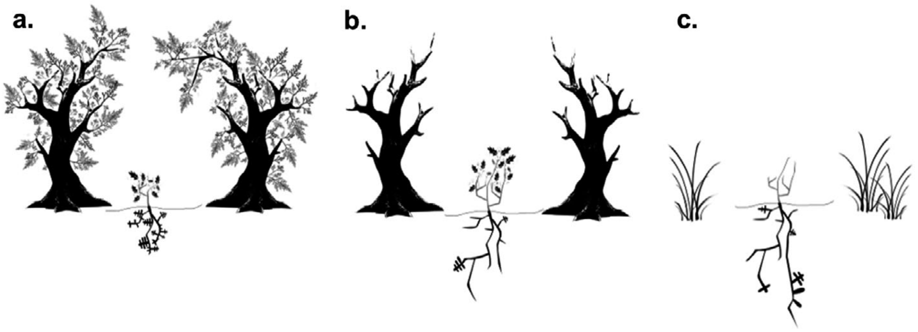
Table 4. Correlations between shin oak seedling foliar nutrients or additional measured variables and principal component analysis (PCA) axes

PCA Factor	Axis 1 (25.72%)		Axis 2 (17.83%)		Axis 3 (11.87%)		Axis 4 (9.52%)		Axis 5 (8.91%)	
	r	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*
Foliar										
Fol_N	0.835	<0.001								
Fol_S	0.742	<0.001	0.247	0.039	−0.424	<0.001				
Fol_P	0.706	<0.001	0.326	0.006	0.258	0.031				
Fol_Cu	0.631	<0.001			0.523	<0.001				
Fol_K	0.476	<0.001	−0.325	0.006	0.512	<0.001			−0.310	0.009
Fol_Zn	0.390	<0.001	0.454	<0.001			0.582	<0.001	−0.280	0.019
Fol_Mn	−0.350	0.003	0.474	<0.001					0.344	0.004
Fol_Ca	−0.533	<0.001	0.591	<0.001			0.399	<0.001		
Fol_Fe			0.430	<0.001	−0.358	0.002	−0.422	<0.001	−0.563	<0.001
Fol_B			0.420	<0.001	−0.382	0.001	0.274	0.022	0.456	<0.001
Fol_Mg			0.355	0.003	0.487	<0.001	−0.515	<0.001	0.295	0.013
Fol_C			−0.764	<0.001	−0.285	0.017			0.313	0.008
% Cover										
% Canopy	−0.442	<0.001			0.459	<0.001				
% Litter	−0.480	<0.001								
% Grass	0.436	<0.001			−0.378	0.001				
Basal area										
Dead juniper	0.514	<0.001								
All living	−0.391	<0.001								
Soil										
Soil_Mg	−0.405	<0.001			0.528	<0.001				
Seedling										
Height	0.482	<0.001								
Depth	0.450	<0.001								
Total bio					−0.430	<0.001				
Root bio					−0.456	<0.001				

Note: For Axis 1 (25.72%), live vs. dead $r^2 = 0.266$, $P < 0.001$. For Axis 3 (11.87%), live vs. open $r^2 = 0.137$, $P = 0.007$.

the fungal hyphae providing access to mineral nutrients and water from soil and rock, which would otherwise be unavailable to their host plant, in exchange for carbon in the form of sugars (Gorzelak et al. 2015, Pickles and Simard 2017). This symbiotic relationship improves plant health and reduces susceptibility to drought (Smith and Read 2008, Ochoa-Hueso et al. 2017, Pickles and Simard 2017). Consistent with our findings of increased survival and ectomycorrhizal colonization under living canopy, Deniau et al. (2018) observed a net positive effect of ectomycorrhizal fungi on oak seedlings under canopy of close relatives. These observations are also consistent with findings from temperate (Bennett et al. 2017) and Mediterranean (Teste et al. 2017) systems, which have demonstrated that plant–soil feedbacks are typically positive for ectomycorrhizal seedlings grown under ectomycorrhizal hosts. Lower ectomycorrhizal colonization and/or colonization density in open gaps and under dead canopy corresponds to the observation of Ibañez et al. (2015) that plant stress from high light levels can reduce carbon assimilation and investment in mycorrhizal associations.

We noted that surviving seedlings in the two smallest open gaps had comparable total ectomycorrhizal colonization to seedlings under the adjacent living canopy and greater total colonization than seedlings under the adjacent dead canopy. In both cases, the roots of the seedlings in these open gaps were found to be in close association with other living oak roots. The roots of surviving seedlings in the smallest gap were entangled with a large plateau live oak root growing underneath the plot (from a mature tree located ~13 m away), whereas surviving



	a. Live	b. Dead	c. Open
Emergence (plots)	23% (6/6)	18% (6/6)	9% (6/6)
Survival (plots)	15% (6/6)	15% (6/6)	2% (2/6)
Seedling size	Small	Large	Large
EcM root tips	Many	Few	Many
Foliar nutrients	Mg, Mn, Ca	N, P, S	S, Fe

Fig. 6. Shin oak seedling responses to each habitat treatment. (a) Live juniper-oak canopy: small seedlings, high ectomycorrhizal root tip density; (b) dead juniper-oak canopy: large, deep-rooted seedlings, fewer ectomycorrhizal root tips; (c) open invasive grassland: large, deep-rooted seedlings, low ectomycorrhizal root tip density, low survival.

seedlings in the other small gap were adjacent to roots connected to a plateau live oak shinnery. Lower colonization under dead canopy may have been due to a lack of living ectomycorrhizal mycelium, leading to increasing reliance on resistant propagules with increasing distance from living trees (Teste et al. 2009, Southworth 2012, Ibañez et al. 2015).

Although junipers are believed to associate exclusively with arbuscular mycorrhizal fungi (Bush 2008), many oaks can associate with both arbuscular and ectomycorrhizal fungi (Southworth 2012, Ibañez et al. 2015). Hence, there is the potential for shared arbuscular mycorrhizal fungi to link Ashe juniper with oak seedlings via common mycorrhizal networks (Selosse et al. 2006), which may facilitate oak seedling survival while they begin to form associations with ectomycorrhizal fungi. Alternatively, oak seedlings may be stimulated to form more ectomycorrhizal associations as a response to competition from juniper roots; however, if competition were a significant factor, we would not expect to see positive survival responses to the presence of juniper. We recommend future research into host interactions of arbuscular and ectomycorrhizal fungi in juniper-oak forests.

Foliar nutrition

Foliar nutrient content indicated that seedlings followed different growth strategies. The largest seedlings were found under dead canopy and in open gaps; dead canopy seedlings had higher foliar N, P, and S, which play critical roles in plant growth (Hawkesford et al. 2012). Seedlings under live canopy were slower-growing and had higher foliar Ca, Mg, and Mn content, which suggest tougher and more photosynthetically active leaves; Ca contributes to the stability and integrity of cell membranes, whereas Mg and Mn are major components of chlorophyll (Liu et al. 1997, Marschner 2012). Seedlings in open gaps had the greatest levels of foliar Fe and had higher foliar S than seedlings under live canopy; elevated foliar Fe may be an indicator of drought stress (Broadley et al. 2012, Tripathi et al. 2018). Soil nutrient concentrations were highest under live canopy (except for Ca), but Mg was the only foliar nutrient that increased with increasing soil concentration. Foliar nutrient concentrations provide further support for a sit-and-wait strategy under living canopy, where seedlings invest in structure and nutrient acquisition at the expense of growth, while seedlings under dead canopy or in open gaps adopt a strategy of rapid growth to improve their chances of survival in the relatively more extreme conditions.

CONCLUSIONS

Our findings suggest that juniper-oak canopy benefits shin oak seedling regeneration by ameliorating stressful abiotic conditions, particularly shading to reduce high light levels and temperatures during hot, dry summers. Unlike studies of oak regeneration in the eastern United States (McShea and Healy 2002, Johnson et al. 2005, Arthur et al. 2012), we found little evidence of competition. Instead, the semiarid woodlands of the eastern Edwards Plateau appear to more closely resemble those of Mediterranean regions. In these drier climates, canopy trees and shrubs facilitate regeneration by restricting herbivory (Russell and Fowler 2004), reducing solar radiation (Castro et al. 2004, Gómez-Aparicio et al. 2004) and evaporation (Nagra et al. 2016), increasing soil infiltration (Lindley 2005), enriching soil nutrients (Padilla and Pugnaire 2006), and providing access to soil fungal communities (Ochoa-Hueso et al. 2017). Based on recent climate projections, environmental conditions are predicted to become more arid in locations such as central Texas, with more frequent and severe droughts leading to increased tree mortality (Johnson et al. 2017, Schwantes et al. 2017). Given that facilitative effects typically increase with abiotic stress (Gómez-Aparicio et al. 2004), we anticipate that the importance of nurse trees and shrubs in enhancing oak regeneration will become even more critical, although multiple simultaneous stressors may reduce their impact (Andivia et al. 2017). While our study focused on oak regeneration, we recommend further exploration of nurse-plant effects in these ecosystems to examine the importance of facilitative relationships during later life stages (e.g., Reisman-Berman 2007, Cavard et al. 2011, Forrester et al. 2011).

Despite their global distribution, relatively few oak regeneration studies have been conducted in semiarid ecosystems. Our results suggest that retention of canopy trees and shrubs, living or dead, plays an important role in oak regeneration in juniper-oak woodlands. We conclude that oak restoration in these ecosystems benefits from canopy retention, which provides shade, nutrients, protection from browsing, and access to mycorrhizal fungi. Where canopy has been removed, oak seedling regeneration may be enhanced by employing shade cloth and fencing to reduce solar radiation and protect from browsing damage (Benayas et al. 2005), and by encouraging growth of nurse trees and shrubs for the same purpose. Planting acorns under live and dead canopy, and potentially in small gaps (<150 m^2) near large trees of native species, appears to be an effective, low-cost, and sustainable strategy for promoting oak regeneration in drought-prone ecosystems.

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