RESEARCH ARTICLE

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Competition suppresses shrubs during early, but not late, stages of arid grassland–shrubland state transition

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Abstract

1. Transitions from grass to woody plant dominance, widely reported in arid systems, are typically attributed to changes in disturbance regimes in combination with abiotic feedbacks, whereas biotic mechanisms such as competition and facilitation are often overlooked. Yet, research in semi-arid and subhumid savannas indicates that biotic interactions are important drivers in systems at risk for state transition. We sought to bridge this divide by experimentally manipulating grass-on-shrub and shrub-on-shrub interactions in early and late stages of grassland–shrubland state transition, respectively, and to assess the extent to which these interactions might influence arid land state transition dynamics.

2. Target *Prosopis glandulosa* shrubs had surrounding grasses or conspecific neighbours left intact or killed with foliar herbicide, and metrics of plant performance were monitored over multiple years for shrubs with and without grass or shrub neighbours.

3. Productivity of small shrubs was enhanced by grass removal in years with above-average precipitation, a result not evident in larger shrubs or during dry years. Proxy evidence based on nearest neighbour metrics suggested shrub–shrub competition was at play, but our experimental manipulations revealed no such influence.

4. Competition from grasses appears to attenuate the rate at which shrubs achieve the size necessary to modify the physical environment in self-reinforcing ways, but only during the early stages of shrub encroachment. Our results further suggest that at late stages of grassland-to-shrubland state transitions, shrub–shrub competition will not slow the rate of shrub expansion, and suggest that maximum shrub cover is regulated by something other than density-dependent mechanisms. We conclude that grass effects on shrubs should be included in assessments of desert grassland state transition probabilities and rates, and that desertification models in arid ecosystems that traditionally focus on disturbance and abiotic feedbacks should be broadened to incorporate spatial and temporal variations in competitive effects.

KEYWORDS
Chihuahuan Desert, competition, grassland, shrubland, state transition, woody plant encroachment

1 | INTRODUCTION

The transition from grasslands to plant communities dominated by unpalatable, xerophytic woody plants and bare soil is a common challenge in arid and semi-arid ecosystems, often referred to as "desertification." These transitions are potentially irreversible over time frames relevant to ecosystem management and can have numerous negative consequences for human societies. In the classic desertification model, exogenous drivers such as drought and livestock grazing interact to provide opportunities for woody plants to establish in grasslands (Higgins, Bond, & Trollope, 2000). As woody plants increase in size and abundance, soil resources become spatially heterogeneous, concentrated beneath shrub canopies and depleted in shrub interspaces, thus establishing positive abiotic feedbacks that promote advancement towards a shrubland state (Okin, Gillette, & Herrick, 2006; Schlesinger, Raikes, Hartley, & Cross, 1996; Schlesinger et al., 1990; Ward et al., 2018).

Inherent in the classic desertification paradigm is an assumption that biotic interactions between plants, like competition and facilitation, are negligible in shaping the dynamics of grassland–shrubland transitions. This assumption is grounded in the notion that selection pressures in extreme environments favour adaptations for stress tolerance over competitive ability (Grime 1977; Brooker and Callaghan 1998). Indeed, a Web of Science survey for field-based studies on the mechanisms of desertification revealed that only c. 10% dealt with plant–plant interactions (Table 1). However, the savanna literature tells us that plant competition and facilitation are commonplace in systems at risk of transitioning from grass to woody plant dominance (Moustakas, Kunin, Cameron, & Sankaran, 2013; Sankaran, Ratnam, & Hanan, 2004; Schleicher, Meyer, Wiegand, Schurr, & Ward, 2011; Schleicher, Wiegand, & Ward, 2011; Scholes & Archer, 1997). While the savanna and desertification bodies of literature have developed independently, the former may inform the latter and help explain the observed rates, dynamics and patterns of state change in arid lands.

TABLE 1 Results from Web of Science query for field-based studies in drylands (<600 mm mean annual precipitation) that investigate the mechanisms of desertification

Search term	Desertification
Fields	Environmental Sciences, Ecology
Restrictions	Mechanisms of desertification
	Field-based studies
	Drylands (MAP < 600 mm)
Total results[a]	110
Biotic mechanisms	11
Abiotic mechanisms	101
Livestock grazing	36
Fire	3
Wildlife interactions	4

Note. Details and full results can be found in Appendix S1.
[a]Mechanistic categories are not mutually exclusive (e.g., a given paper may report on abiotic and grazing mechanisms).

Establishment of shrub seedlings in a grassland matrix is a potential demographic bottleneck in which shrub recruitment is constrained by grasses directly through resource competition (Jurena & Archer, 2003) or indirectly by virtue of the fact that grasses provide fuels for fire (Higgins et al., 2007). Once seedlings establish, shrubs become larger with time and resource cycling is amplified within the shrub canopy zone. Litter inputs scale with shrub size; thus, soils beneath shrub canopies typically have elevated nutrient content and rates of water infiltration (Bhark & Small, 2003; Throop & Archer, 2008; Ward et al., 2018) as shrub canopies expand and their shallow, lateral root systems (Gibbens & Lenz, 2001) develop. Additionally, as shrubs become larger, they are better able to capture nutrient-rich aeolian sediments, which then become concentrated beneath shrub canopies and reduced in shrub interspaces (Li, Okin, Alvarez, & Epstein, 2008). However, grasses, with their shallow, dense, fibrous root systems, could compete with shrubs for near-surface soil resources (Kambatuku, Cramer, & Ward, 2013) and reduce percolation of water to deeper depths where shrub taproots occur (Holdo & Brocato, 2015; Knoop & Walker, 1985; Ward, Wiegand, & Getzin, 2013). This could slow shrub growth, with the consequence of lengthening the time required to attain sizes necessary to escape fire effects and begin establishing positive abiotic feedbacks. Alternatively, shrubs establishing within a graminoid matrix could be facilitated as grass patches intercept overland flow, reduce soil evaporation and improve soil water infiltration, especially during periods when grasses are quiescent and not actively using soil moisture (de Dios, Weltzin, Sun, Huxman, & Williams, 2014). Such facilitation could hasten the rate at which shrubs achieve the size and density needed to modify the physical environment in self-reinforcing ways, and helps explain observations that rates of shrub encroachment on sites protected from grazing can be higher than those on grazed sites (Browning and Archer 2011).

While shrub interactions in early stages of grassland–shrubland transition are primarily with grasses, dynamics ostensibly shift to shrub–shrub interactions late in the state transition as grass cover declines and shrub cover increases. Here, density-dependent resource competition would be expected to intensify as woody plant cover increases, particularly when the encroaching woody species overlap in their spatial and temporal niches. Such intra-life form competition would slow shrub growth rates and potentially lead to self-thinning (Sea & Hanan, 2012), thus slowing the rate of transition to shrubland and potentially setting upper limits to maximum woody plant cover/density. Additionally, in cases of monospecific encroachment, shrub–shrub competition would favour intraspecific interference over interspecific competition, which could promote grass–shrub coexistence (Bond, 2008; Scholes & Archer, 1997) and arrest grassland–shrubland transitions. Proxy evidence of interactions between shrubs based on patterns of spatial distribution is relatively common, but with inconsistent outcomes (Browning, Franklin, Archer, Gillan, & Guertin, 2014; Fonteyn & Mahall, 1978; Meyer, Ward, Wiegand, & Moustakas, 2008; Pillay & Ward, 2012). Direct tests of interactions between woody plants, for example via removal experiments (Ansley, Trevino, & Jacoby, 1998; Fonteyn & Mahall, 1981; Kambatuku, Cramer, & Ward, 2011; Mahall, Fonteyn, Callaway, & Schlesinger, 2018; Manning & Barbour, 1988), are less common, represent a narrow range of

biophysical contexts and were not conducted within the context of grassland-to-shrubland state transition dynamics.

Here, we report on two selective removal field experiments conducted along a grassland-to-shrubland state transition gradient in the northern Chihuahuan Desert, USA. One experiment (4 years) was situated in the grassland and grassland/shrubland ecotone portion of the gradient and examined the influence of the historically dominant perennial grass on established shrubs in different life-history stages. The other experiment (5 years) sought to quantify intraspecific shrub-on-shrub interactions and was conducted in the grass/shrub ecotone and shrubland portion of the gradient. We hypothesized that (a) competition, rather than facilitation or neutral interactions, would predominate at the grassland end of the gradient, with grass effects on shrubs diminishing as shrubs become larger; (b) intraspecific, density-dependent interactions would characterize shrub–shrub interactions at the shrubland end of the gradient; and (c) competitive interactions would reduce shrub water-use efficiency (Fernandez-de-Una, McDowell, Canellas, & Gea-Izquierdo, 2016) and increase the magnitude of biological nitrogen fixation (Cramer, Chimphango, Cauter, Waldram, & Bond, 2007; Kambatuku, Cramer, & Ward, 2013). The outcome of tests of these hypotheses will help us understand the extent to which grass-on-shrub and shrub-on-shrub interactions might influence rates and dynamics of grassland-to-shrubland state transitions in arid systems.

2 | MATERIALS AND METHODS

The experiments were conducted at the USDA-Agricultural Research Service Jornada Experimental Range (JER), located approximately 37 km north of Las Cruces, NM, USA (UTM 13S 3,603,596 m N, 334,156 m E; 1,325 m a.s.l.; http://jornada.nmsu.edu/). The Jornada experiences an arid climate (Köppen climate classification BWk). Long-term (1926–2015) mean annual precipitation (PPT) received at gauges near the study site is 241 mm (*SE* ± 9.6, CV = 36%), *c.* 65% of which occurs during the July–October growing season. Summers are warm, with a mean maximum temperature of 36°C in June; January is the coldest month, with mean maximum and minimum of temperatures of 4°C and −6°C, respectively.

The experiments were conducted along a grassland–shrubland continuum. The grassland end of the 3 km × 1 km study area (UTM 13S 334,878 m E, 3,601,198 m N) was dominated by the C_4 perennial grass *Bouteloua eriopoda* (Torr.) Torr., with scattered, relatively small C_3 *Prosopis glandulosa* (Torr.) shrubs, which have the potential to form symbiotic relationships with N_2-fixing microbes (Johnson & Mayeux, 1990; Zitzer, Archer, & Boutton, 1996). Subordinate perennial grasses included *Sporobolus* and *Aristida* species. The opposing end of the gradient (UTM 13S 333,764 m E, 3,604,817 m N) was dominated by relatively large *P. glandulosa* shrubs and bare soil, with minimal grass (*B. eriopoda*, *Sporobolus* spp.) cover. Soils are fine-loamy, mixed, thermic Typic Haplargids and Typic Petrocalcids underlain by a petrocalcic horizon 64–76 cm beneath the surface (Havstad & Schlesinger 2006).

Gibbens and Lenz (2001) excavated *B. eriopoda* and *P. glandulosa* root systems of plants growing on similar soils at the JER. *B. eriopoda* roots were concentrated in the upper 1 m of soil and rarely penetrated the petrocalcic horizon. *P. glandulosa* had dimorphic root systems, with deep tap roots (down to 5 m depth) and coarse, shallow (upper 50 cm of soil) lateral roots that extended many times the canopy diameter. Emerging from these coarse lateral *P. glandulosa* roots are upward-growing secondary roots that terminate as shallow as 4 cm below the soil surface; in some cases, these secondary shrub roots were observed intermingled with *B. eriopoda* grass roots.

2.1 | Grass effects on shrubs

This experiment was conducted in the grassland and grassland/shrubland ecotone portion of the grassland–shrubland continuum. *B. eriopoda* foliar cover declined from 26% in the grassland to 13% in the ecotone, while *P. glandulosa* canopy cover increased from 2% in the grassland to 10% in the ecotone.

Plots (*n* = 60) were established in April–May 2011 and centred upon *P. glandulosa* individuals that were nearest to pins dropped at randomly generated locations within the boundaries of the study area. This resulted in the inclusion of shrubs of various sizes (i.e., life-history stages) in the experiment. The size of each of these focal shrubs was quantified (height, maximum canopy diameter and canopy diameter perpendicular to maximum). Plot size varied as a function of focal shrub size and encompassed all graminoid vegetation within three times the focal shrub maximum canopy diameter. In July 2011, grasses in 30 randomly selected plots were killed by applying a grass-specific foliar herbicide (1.5% sethoxydim [brand name Poast]) in a fine mist with a hand-held sprayer. Herbicide application was repeated as needed in July 2012 and 2013 to minimize grass regeneration. The grass-specific herbicide had no direct visible effects on the shrubs (e.g., no chlorotic, desiccated or lost foliage).

Prosopis glandulosa above-ground annual net primary productivity (ANPP) was estimated by a site- and species-specific allometric equation based on canopy volume (Gherardi & Sala, 2015) at peak biomass in September–October 2011–2013 and 2015.

2.2 | Shrub effects on shrubs

This experiment was conducted in the grassland/shrubland ecotone and shrubland portion of the grassland–shrubland continuum, with *B. eriopoda* foliar cover declining from 13% to 4% and *P. glandulosa* canopy cover increasing from 10% to 18% in the ecotone and shrubland segments, respectively. *P. glandulosa* is the only shrub species to have encroached heavily on sandy soils in the Jornada Basin (Gibbens, McNeely, Havstad, Beck, & Nolen, 2005).

Plots (*n* = 60) centred upon a focal *P. glandulosa* individual were randomly established in fall 2010 as described in the previous section. This resulted in focal shrubs of various sizes with differing conspecific shrub neighbourhoods (fewer, smaller neighbours to more and/or larger neighbours). The size of the focal shrub and that of all conspecific shrub neighbours within 5 m was quantified as per the

previous section. In June 2011, neighbouring shrubs in 30 randomly chosen plots were killed via foliar herbicide solution (0.5% triclopyr [brand name Remedy], 0.5% clopyralid [brand name Reclaim], 5% diesel fuel) applied in a fine mist; shrub skeletons were left intact. The herbicide mixture was effective at defoliating shrubs within 2 weeks of spraying, and no new growth was observed for the remainder of the growing season; the dicot-specific herbicide had no observable direct detrimental effects on graminoid vegetation. Targeted spot spraying was conducted as needed to suppress new basal shoots in 2012 and 2013, after which no regeneration occurred. Focal shrub ANPP was estimated as described above in September–October 2011–2013 and 2015.

Prior to herbicide application on shrub neighbours, proxy evidence for interactions between shrubs was assessed in the context of focal shrub size and the distance to and size of other conspecific shrubs within the 5-m neighbourhood. The sum of the average canopy diameters of the focal shrub and its four nearest neighbours was regressed against the sum of the distances between the focal shrub and its four nearest neighbours (Wiegand, Ward, & Saltz, 2005). A significant positive linear slope was observed for the focal shrub size-neighbour distance relationship would demonstrate that larger shrubs grow further apart from one another than the null expectation, which would constitute proxy evidence for intraspecific competition; a negative slope would be indicative of facilitation; and a zero slope would suggest no interactions between conspecific plants. This analysis was carried out using JMP software (version 13; SAS Institute).

2.3 | Foliar C and N analysis

Treatment effects on shrub water-use efficiency and potential N_2 fixation were assessed by examining $\delta^{13}C$ (Farquhar, Ehleringer, & Hubick, 1989) and $\delta^{15}N$ (Shearer & Kohl, 1986), respectively. We sought to contrast these metrics during a dry year (2012; PPT 50% below the long-term average) and a wet year (2013; PPT 50% above the long-term average). In both experiments, foliar samples were collected for nutrient and isotopic analysis near the end of the growing season in September. Leaves were dried in a forced-air oven at 50°C for 48 hr and then processed at the University of Arizona *Environmental Isotope Laboratory* (https://www.geo.arizona.edu/EIL). Total carbon and nitrogen, as well as $\delta^{13}C$ and $\delta^{15}N$, were measured on a continuous-flow gas-ratio mass spectrometer (Finnigan Delta Plus XL) coupled to an elemental analyser (COSTECH), in which samples were combusted. Standardization was based on acetanilide for elemental concentration, NBS-22 and USGS-24 for $\delta^{13}C$, and IAEA-N-1 and IAEA-N-2 for $\delta^{15}N$. Precision exceeded ±0.10 for $\delta^{13}C$ and ±0.2 for $\delta^{15}N$ (1 s), based on repeated internal standards. ANOVA was used to detect differences in mean values between control and treatment samples (JMP version 13; SAS Institute).

2.4 | ANPP time-series analysis

Overall treatment effects on focal *P. glandulosa* shrub ANPP were analysed in both experiments using repeated measures linear
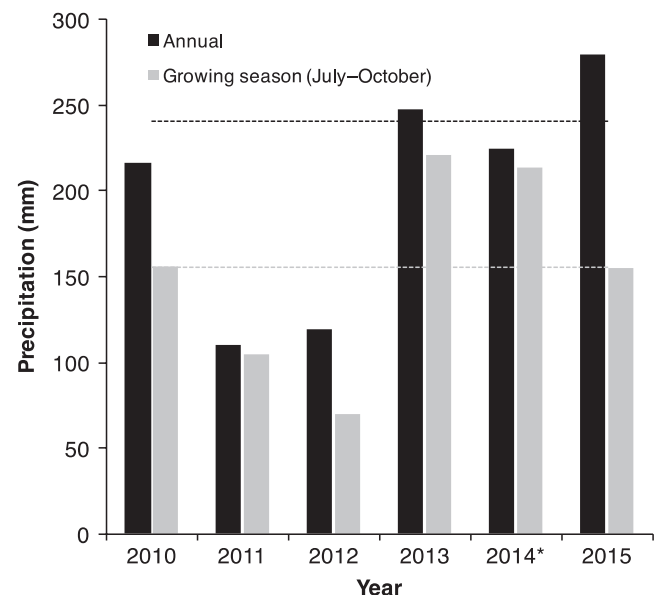
mixed-effects models (JMP version 13; SAS Institute). Shrub removal, year and their interaction were fixed effects, which were all highly significant. Because of the significant neighbour removal × year interaction, interpretations of the main effects are qualified by year.
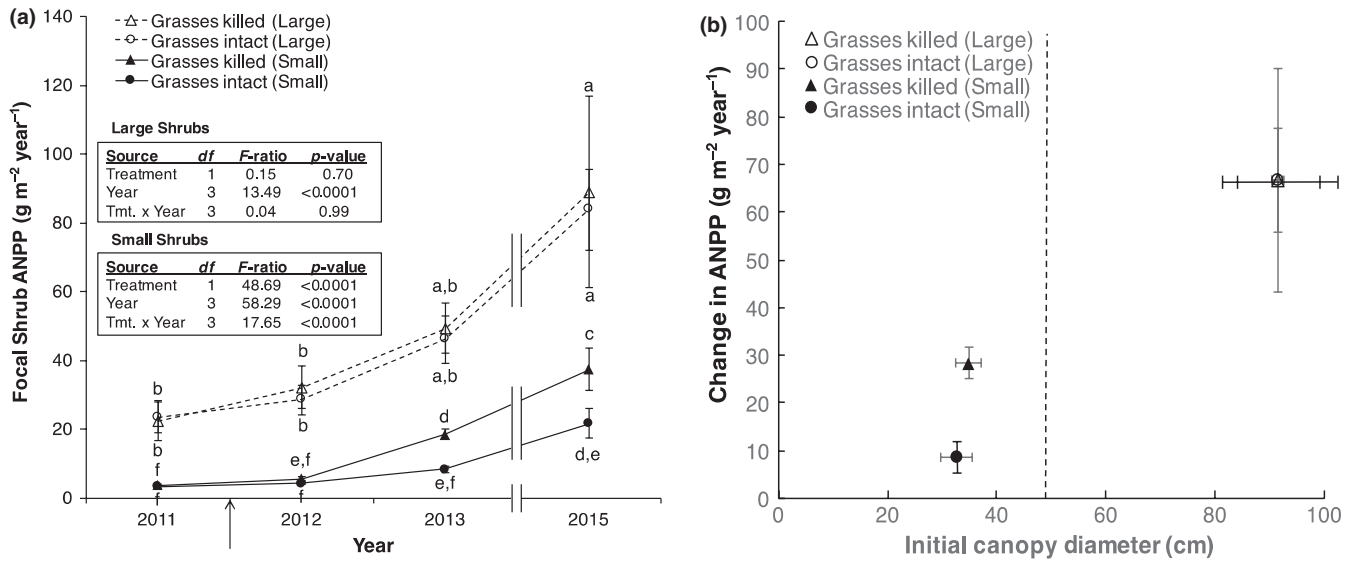
3 | RESULTS

Precipitation varied considerably over the course of the experiments (Figure 1). Dry conditions prevailed in 2011 and 2012, with annual PPT of 54% and 50% that of the long-term (1926–2015) mean, respectively. Growing season (July–October) PPT was similarly low, at 33% and 55% that of the long-term mean in 2011 and 2012, respectively. In contrast, growing season PPT in 2013 and 2014 was 141% and 137% that of the long-term mean, respectively. Annual PPT was 15% above the long-term average in 2015.

3.1 | Grass effects on shrubs

The median canopy diameter of the focal *P. glandulosa* shrubs at the beginning of the experiment was 46 cm. ANPP of focal *P. glandulosa* shrubs increased over the course of the experiment (Figure 2a). Among "large" focal shrubs (defined as those with an initial canopy diameter greater than the median initial canopy diameter), these increases in ANPP were not affected by the killing of grass neighbours in any year. However, among "small" focal shrubs (defined as those with initial canopy diameter less than or equal to the median) ANPP responded positively to grass neighbour removal in years with average to above-average PPT. In 2013, mean shrub ANPP in treatment (grasses killed) plots was elevated to 75% (9.3 g m^{-2} year^{-1}) relative

FIGURE 1 Annual (black) and growing season (July–October, grey) precipitation (PPT) over the course of the experiment. The dashed black and grey lines represent long-term (1926–2015) annual and growing season mean PPT, respectively. (*plot data were not collected in 2014)

FIGURE 2 (a) Focal *Prosopis glandulosa* annual net primary productivity (ANPP) (mean ± *SE*) in plots with grasses killed (triangles) or intact (circles). The arrow between 2011 and 2012 denotes when grass neighbours were killed in treatment plots. Open symbols and dashed lines are focal shrubs with initial canopy diameter greater than the median (46 cm; denoted as "large"); closed symbols and solid lines are focal shrubs with initial canopy diameter less than or equal to the median value (denoted as "small"). Letters denote significant ($p < 0.05$) differences among treatments and dates. Insets summarize ANOVA outcomes. Plot data were not collected in 2014. (b) 2011–2015 change in ANPP (± *SE*) as a function of initial canopy diameter (± *SE*) for large (open symbols) and small (closed symbols) shrubs with their neighbouring grasses killed (triangles) or intact (circles). The dashed vertical line represents the median canopy diameter (46 cm) for all shrubs at the beginning of the experiment (2011)

TABLE 2 ANOVA comparisons of foliar %C, %N, $\delta^{13}C$ and $\delta^{15}N$ isotopic composition (mean ± *SE*) of focal shrubs with grass neighbours intact or removed in 2012 (a dry year) and 2013 (a wet year)

Variable	Year	Shrub size	Grasses intact	Grasses killed	F	df	p
%C	2012	Small	45.1 (0.5)	46.8 (0.4)	6.94	15	0.02
		Large	47.2 (0.5)	48.4 (0.3)	3.08	16	0.09
	2013	Small	49.0 (0.7)	48.4 (0.6)	0.42	6	0.55
		Large	48.6 (0.6)	48.7 (0.6)	0.01	5	0.96
%N	2012	Small	2.8 (0.1)	2.9 (0.1)	0.32	15	0.58
		Large	3.1 (0.2)	3.2 (0.1)	0.37	16	0.55
	2013	Small	2.8 (0.1)	2.8 (0.1)	0.16	6	0.71
		Large	2.8 (0.1)	2.7 (0.2)	0.10	5	0.77
$\delta^{13}C$ (‰)	2012	Small	−25.8 (0.3)	−25.5 (0.2)	0.83	15	0.38
		Large	−25.7 (0.2)	−25.6 (0.2)	0.62	16	0.44
	2013	Small	−26.5 (0.2)	−26.9 (0.2)	1.06	23	0.31
		Large	−26.7 (0.2)	−26.8 (0.2)	0.30	19	0.59
$\delta^{15}N$ (‰)	2012	Small	2.4 (0.3)	2.8 (0.5)	0.56	15	0.47
		Large	4.3 (0.4)	3.1 (0.4)	3.73	16	0.07
	2013	Small	2.6 (0.3)	2.1 (0.4)	0.83	23	0.37
		Large	3.0 (0.4)	2.4 (0.1)	0.60	19	0.45

Note. Treatment and year main effects were not significant ($p < 0.05$); size class was significant only for %N and $\delta^{15}N$.

to that in control (grasses intact) plots ($p < 0.0001$); this difference increased to 20.5 g m^{-2} year^{-1} (97% increase) in 2015 ($p < 0.0001$). Over the course of the experiment, the change in ANPP of shrubs initially larger than the median canopy diameter did not differ between control plots and those that had grass neighbours killed (Figure 2b). Conversely, for shrubs with initial canopy diameters less

than the median value, the 2011–2015 ANPP change was greater for plots with grasses killed than with grasses intact ($p < 0.0001$). Despite the differential ANPP response between control and treatment plots, no significant differences were observed in shrub foliar C, N, $\delta^{13}C$ or $\delta^{15}N$ values under either dry (2012) or wet (2013) conditions (Table 2).
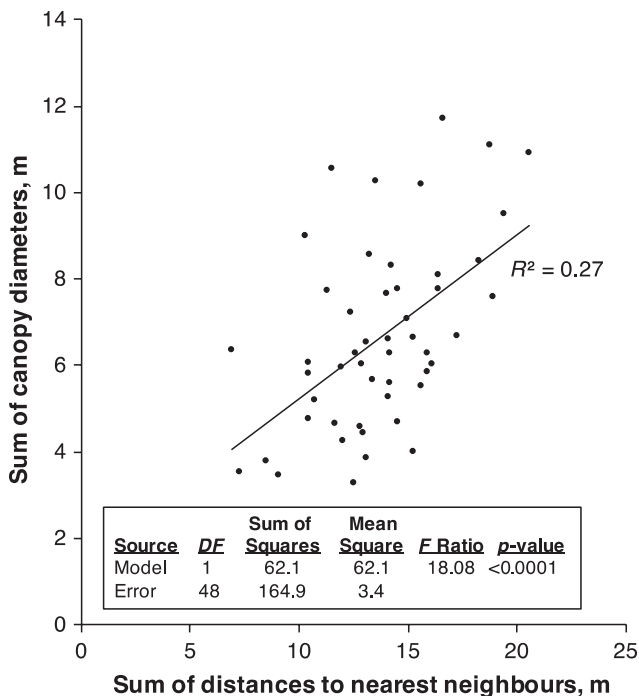
3.2 | Shrub effects on shrubs

The relationship between the size of the focal shrub and the size of and distances to its nearest neighbours was quantified in all plots prior to killing *P. glandulosa* shrubs in the vicinity of the focal shrub in treatment plots. A significant positive linear relationship was observed for the focal shrub size–neighbour distance relationship (R^2 = 0.27, p < 0.0001, Figure 3), suggesting competition among neighbouring *P. glandulosa* shrubs (Wiegand et al., 2005). Experimental results told a different story, however. Following herbicide application in early 2011, focal *P. glandulosa* shrubs showed no differential ANPP response to shrub neighbour removal (Figure 4). This was true regardless of focal shrub initial size. We also observed no significant differences in foliar C, N, δ^{13}C or δ^{15}N values between control and treatment plots in either 2012 or 2013 (Table 3).
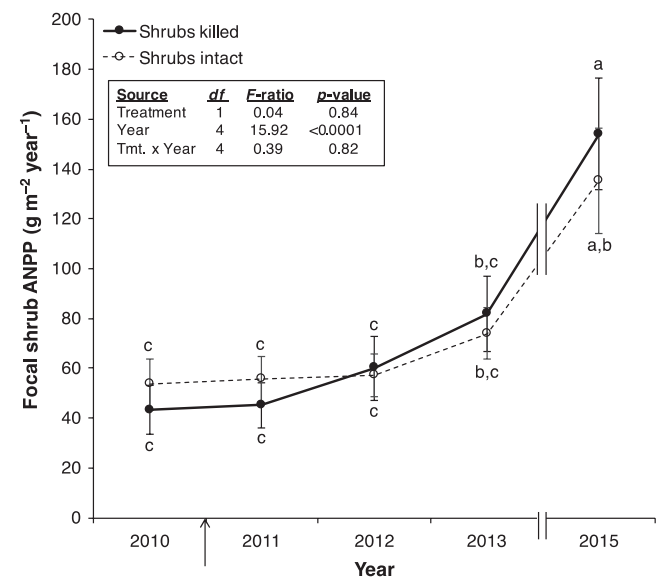
4 | DISCUSSION

4.1 | Grass-on-shrub interactions

Small *P. glandulosa* individuals had higher ANPP when grass neighbours were killed than when grass neighbours were present (Figure 2). This supports the hypothesis that grasses have a competitive, rather than neutral or facilitative, influence on small shrubs in the early stages of their encroachment into arid grasslands. Some of

this competition could have been for above-ground resources (e.g., light) as the height of the smallest shrubs (i.e., <20 cm) was similar to that of grasses (*c*. 30 cm, unpublished field data). However, grasses at this site are sparsely distributed (e.g., <25% canopy cover) with relatively low leaf area index (Gibbens, Hicks, & Dugas, 1996), indicating that competition for light is unlikely to constrain shrub ANPP. Furthermore, the competitive influence of grasses on shrubs was observed only in years with above-average PPT (2013 and 2015). We therefore postulate that competition was primarily for below-ground resources, ostensibly soil water. The spatial niches of grass and small-shrub root systems overlap considerably, making competition for soil resources possible when both plant functional types are active. Shallow lateral roots of *P. glandulosa* shrubs are important for water acquisition (Ansley, Jacoby, & Cuomo, 1990; Ansley, Jacoby, & Hicks, 1991), so it stands to reason that they would compete with grass roots for shallow soil moisture. Furthermore, grasses, with their dense, fibrous root systems, likely utilize shallow soil moisture before it has a chance to percolate to depths where it would be accessible primarily to shrubs (Gherardi & Sala, 2015; Holdo & Brocato, 2015; Ward et al., 2013). Our results are also consistent with observations that in stressful environments, competitive interactions increase with increasing resource availability, as has been found for other Chihuahuan Desert species (Briones, Montana, & Ezcurra, 1998; Pierce, Archer, Bestelmeyer, & James, 2018) and as proposed by the stress-gradient hypothesis (Maestre, Callaway, Valladares, & Lortie, 2009; Miriti, 2006), which argues that interactions between plants shift from net positive (facilitation) to net negative

FIGURE 3 The sum of canopy diameters of the focal *Prosopis glandulosa* shrub and its four nearest conspecific neighbours as a function of the sum of the distances to the four nearest conspecific neighbours to the focal shrub. A positive slope indicates that larger shrubs are further apart from one another, which is indicative of competitive interactions (Wiegand et al., 2005). Inset: ANOVA summary table for the linear regression analysis

FIGURE 4 Mean (± *SE*) annual net primary productivity (ANPP) of focal *Prosopis glandulosa* shrubs with conspecific shrub neighbours killed (filled circles) or intact (open circles). Different letters designate significant (p ≤ 0.05) differences among treatments and dates. Focal shrub size was not a significant factor, so data are pooled across shrub sizes. Inset: ANOVA summary table of main effects. The arrow between 2010 and 2011 indicates when shrub neighbours were killed in treatment plots. Plot data were not collected in 2014

Variable	Year	Shrubs intact	Shrubs killed	F	df	p
%C	2012	47.6 (0.4)	47.1 (0.4)	0.64	27	0.43
	2013	47.1 (0.4)	46.3 (0.4)	2.64	27	0.12
%N	2012	3.1 (0.1)	3.1 (0.1)	0.01	27	0.94
	2013	2.7 (0.1)	2.9 (0.1)	0.71	27	0.41
δ^{13}C (‰)	2012	−25.8 (0.2)	−26.2 (0.2)	2.89	27	0.10
	2013	−26.5 (0.2)	−26.7 (0.2)	0.78	27	0.39
δ^{15}N (‰)	2012	2.6 (0.03)	2.7 (0.3)	0.13	27	0.73
	2013	1.5 (0.4)	2.0 (0.4)	0.71	27	0.41

TABLE 3 ANOVA comparisons of foliar %C, %N, δ^{13}C and δ^{15}N isotopic composition (mean ± SE) of focal shrubs with conspecific shrub neighbours intact or killed in 2012 (a dry year) and 2013 (a wet year)

Note. Shrub size was not significant, so data were pooled across all sizes.

(competition) with decreasing environmental stress. The competitive influence of grasses upon small shrubs that we observed would slow the rate at which those individuals achieve the size necessary to tolerate or escape mortality factors such as fire (Wakeling, Staver, & Bond, 2011) and lengthen the time required for them to begin modifying the physical environment in self-reinforcing ways, such as concentrating resources beneath their canopies (Li et al., 2008).

Prosopis glandulosa and *B. eriopoda* also overlap in portions of their temporal niche at this site primarily during the warm season, but potentially in the cool season as well. It is well-known that *B. eriopoda* (along with other C_4 grasses) are quiescent until monsoonal storms bring PPT during the warm season, while *P. glandulosa* leaf emergence begins much earlier, as soon as temperatures are high enough for them to become metabolically active (Huenneke, Anderson, Remmenga, & Schlesinger, 2002; Kemp, 1983). Under these conditions, shrubs would be positioned to reap the benefits of cool season PPT without competition from dormant grasses. Recent evidence, however, suggests that *B. eriopoda* can generate green shoots much earlier in the year than previously thought (Browning, Karl, Morin, Richardson, & Tweedie, 2017). Accordingly, competition for soil moisture between grasses and shrubs may occur for winter as well as summer PPT—but only if grasses generate leaf area sufficient to use winter PPT to a degree that would influence the abundance of soil water. Under conditions of warmer winters, this would serve to promote resilience of the grassland state as the window of opportunity for shrubs to solely access soil moisture would diminish.

Leaf-level δ^{13}C‰ can serve as an indicator of plant water-use efficiency integrated over the life of a given leaf (Farquhar et al., 1989) and can be influenced by competitive interactions with neighbouring plants (Fernandez-de-Una et al., 2016). Similarly, foliar δ^{15}N‰ can be used as an estimate of the level of biological N_2 fixation that nodulating plants are conducting with their microbial symbionts (Shearer & Kohl, 1986), and competitive interactions with neighbouring plants can modify these values (Cramer et al., 2007). Accordingly, we sought to determine whether removal of neighbouring grasses would result in lower shrub foliar δ^{13}C‰, which would indicate greater water-use efficiency compared to control shrubs competing with neighbouring grasses for soil water. We also predicted that *P. glandulosa* shrubs without grass neighbours would have higher δ^{15}N‰ than control shrubs, which would

be indicative of greater access to soil N pools and a reduced reliance on energetically expensive biological N_2 fixation. Although the presence of grasses reduced ANPP of small shrubs, this did not translate into significant differences in foliar C, N, δ^{13}C‰ or δ^{15}N‰ (Table 2). Our dataset was limited to only one year in which we document a competitive influence of grasses on small-shrub ANPP (2013), and this was a year of above-average growing season PPT (2012 was a dry year, and no treatment effects on shrub ANPP were observed). Thus, soil N and water resources in 2013 may have been sufficiently abundant to mask treatment effects on these metrics of plant performance. The lack of treatment differences in foliar N content suggests that focal shrubs in plots with grass neighbours killed did not receive an indirect "fertilization" effect from decomposing grass root biomass during our study.

While grasses had a competitive effect on small shrubs and may slow the rate of shrub expansion, they had no discernable effect on larger shrubs (Figure 2, Table 3). The lack of a grass effect on large shrubs is consistent with experimental manipulations in mesic savannas (Simmons, Archer, Ansley, & Teague, 2007), although cases of grass competition on adult trees have been documented in other systems (Knoop & Walker, 1985; Sala, Golluscio, Lauenroth, & Soriano, 1989; Stuart-Hill & Tainton, 1989). As shrubs increase in size, their shallow, lateral root systems become increasingly extensive, and *P. glandulosa* at this Chihuahuan Desert site have deep roots that penetrate petrocalcic horizons (Gibbens & Lenz, 2001). Thus, as shrubs become larger, their growth and performance would be expected to become increasingly decoupled from water abundance in the upper horizons and better able to exploit soil resources at depths that grass roots cannot access. Accordingly, shrubs appear capable of escaping the growth-limiting competition from grasses once they reach a critical size (Ward & Esler, 2011; Ward et al., 2013). This, in turn, means that once shrubs have recruited into larger size classes, grass-on-shrub competition is no longer in place to slow their rates of expansion.

Regarding land management, our study provides support for the notion that losses of grass cover due to drought and overgrazing may help to accelerate grassland–shrubland transition. *P. glandulosa* seedling emergence and survival is minimally affected by grass competition in savanna parklands of southern Texas, USA (Brown & Archer, 1999). While a similar relationship between

shrub establishment and grass cover may exist at our Chihuahuan Desert site, shrub growth and eventual dominance after establishment may be reduced if substantial grass cover is maintained via careful grazing management, including rapid adjustments to stocking rates during drought periods (Bestelmeyer et al., 2018). Such resilience management may promote long-term grass–shrub coexistence and mitigate the most pernicious effects of grass–shrub transitions, especially soil erosion.

4.2 | Shrub-on-shrub interactions

As shrub size and density increase and grasses are lost in the later stages of grassland–shrubland transitions, interplay between plants ostensibly shift from grass–shrub interactions to shrub–shrub interactions. When shrub encroachment is predominantly by a single species, as it was at our site, niche overlap in both space and time should become significant as shrubs increase in size and number, and intraspecific competition should consequently intensify. Accordingly, negative correlations between the long-term change in woody plant cover and initial cover would suggest that density-dependent competition slows rates of shrub encroachment (Fensham, Fairfax, & Archer, 2005; Roques, O'Connor, & Watkinson, 2001). Density-dependent competition between woody plants has also been inferred from studies showing a shift from a clumped to regular spatial distribution as stands develop (Goslee, Havstad, Peters, Rango, & Schlesinger, 2003; Phillips & Macmahon, 1981; Wiegand et al., 2005), from analyses of self-thinning (Sea & Hanan, 2012) and from neighbour-removal studies (Ansley et al., 1998; Kambatuku et al., 2011; Mahall et al., 2018). Additionally, continental-scale assessments show that maximum woody plant cover is constrained by mean annual PPT (Sankaran et al., 2005), with competitive interactions among woody plants being inferred as the basis for this limitation.

Despite these numerous lines of evidence that would lead us to expect density-dependent interaction between shrubs, our experimental manipulations did not reveal intraspecific competition. No differences in focal shrub ANPP were seen between plots with conspecific shrub neighbours killed and those with shrub neighbours intact (Figure 4). This was true regardless of focal shrub size. Similarly, and as with grass-on-shrub interactions, no differences were seen in foliar C, N or isotopic compositions of these nutrients between control and treatment plots (Table 3). The lack of shrub–shrub competition indicates that density-dependent interactions are not operating to slow the rate at which shrubs accrue in size and number during grassland–shrubland transitions at this site.

It is not clear why we did not find any evidence of density-dependent interactions between shrubs. In the absence of such competition, it is difficult to explain mechanisms setting the upper limits to shrub cover that occur in relation to PPT (Sankaran et al., 2005). Browning et al. (2014) also failed to detect density-dependent interactions between *Prosopis velutina* shrubs in a Sonoran Desert site and hypothesized that maximum landscape-scale shrub cover may be limited by hydraulic constraints on dryland shrub canopy area. They argue that as shrub size increases, it becomes increasingly

difficult to maintain the continuity of water supply from roots to canopies, increasing the probability of xylem cavitation and causing and partial- or whole-plant canopy dieback. These stress-induced reductions in canopy area represent reductions in landscape cover that would have to be compensated for by recruitment of new plants or growth of smaller plants in the community.

While our experimental manipulations failed to detect competition between *P. glandulosa* shrubs, nearest neighbour analysis suggested density-dependent interactions could be at play (Figure 3). Ours is not the first case in which proxy evidence of competition did not manifest in treatment differences upon removal of neighbouring shrubs. Meyer et al. (2008) documented a similar inconsistency and speculated this was due to the experiment running for too short of a duration. This may have been the case in our study as well. Another potential limitation of our shrub-on-shrub experiment was that intraspecific interactions between shrubs could operate on spatial scales broader than those captured in our design. Lateral roots of large *P. glandulosa* individuals are known to extend >20 m from their origins (Gibbens & Lenz, 2001), so focal shrubs in this experiment could have been influenced by neighbouring shrubs well beyond the removals we made within a 5 m radius of the focal shrub. Nevertheless, the conflicting results we saw between proxy and direct evidence of competition suggest that spatial patterns indicative of plant–plant interactions in rangelands should be interpreted with caution.

5 | CONCLUSIONS

Our field experiments showed that *B. eriopoda* grasses have a competitive effect on small (<46 cm canopy diameter) *P. glandulosa* shrubs, but a neutral effect once canopy areas exceed 46 cm. Our experimental manipulations also indicated that shrubs have a neutral effect on one another. Previous work at this research site has demonstrated that *P. glandulosa* shrubs have a negative (competitive) influence on *B. eriopoda* grasses (Pierce et al., 2018), and that *B. eriopoda* plants can have a negative effect on one another, depending on patch size (Svejcar, Bestelmeyer, Duniway, & James, 2015). Thus, *B. eriopoda* experiences both inter- and intraspecific competition, whereas *P. glandulosa* experiences only interspecific competition, and only in early life-history stages. This asymmetry of competitive pressure provides a nuanced plant–plant interaction perspective that has been largely overlooked and seldom accounted for in explaining or predicting the magnitude and rate of grass loss and shrub proliferation in the context of desertification. The asymmetry also explains why grassland–shrubland transitions have been so difficult to control via grazing management alone. Traditional desertification models focused on disturbance and abiotic feedbacks should be broadened to incorporate these biotic perspectives.

AUTHORS' CONTRIBUTIONS

N.A.P., S.R.A. and B.T.B. conceived the ideas and designed the methods; N.A.P. conducted the research; N.A.P. analysed the data; and N.A.P. and S.R.A. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

All data used in this manuscript are in the Dryad Digital Repository, https://doi.org/10.5061/dryad.7mq2q24 (Pierce, Archer, & Bestelmeyer, 2019).

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