

Influence of temporal heterogeneity in nitrogen supply on competitive interactions in a desert shrub community

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Abstract Soil nutrients in arid systems are supplied to plants in brief pulses following precipitation inputs. While these resource dynamics have been well documented, little is known about how this temporal heterogeneity influences competitive interactions. We examined the impacts of the temporal pattern of N supply on competitive intensity and ability in an N-limited desert shrub community. At our field site, the three codominant shrubs, *Atriplex confertifolia*, *A. parryi*, and *Sarcobatus vermiculatus*, differ in seasonal growth patterns, with *A. confertifolia* and *S. vermiculatus* achieving higher growth rates earlier in the growing season than *A. parryi*. We predicted that these timing differences in maximum growth rate may interact with temporal variation in N supply to alter competitive abilities over time. Seedlings of the two *Atriplex* species were planted either individually in field plots or as target plants surrounded by neighbor seedlings. After one year of establishment, the same amount of ^{15}N was applied to plots either as early spring pulses, mid spring pulses or continuously through the second growing season. Competitive effects were observed under continuous and pulsed N supply. Averaged across all target–neighbor treatments, competitive intensity was ~1.8-fold greater when N was pulsed compared to

when N was supplied continuously, but overall, the outcome of competitive interactions was not influenced by N pulse timing. While the timing of resource supply did not differentially influence the competitive abilities of coexisting species in this system, the temporal pattern of resource supply did alter the intensity of competitive interactions among species. While additional studies in other systems are needed to evaluate the generality of these results, this study suggests that competitive intensity may not necessarily be a direct function of productivity or resource availability as traditionally assumed. Instead, the intensity of competitive interactions in resource-poor systems may depend upon the temporal pattern of resource supply.

Keywords *Atriplex* · Great Basin · Nitrogen isotopes · Resource pulses · *Sarcobatus*

Introduction

In resource-rich environments, competitive interactions are thought to strongly influence plant community structure and dynamics (Grime 1977; Tilman 1988; Goldberg 1990). Current models of plant community organization, however, differ strongly in how the magnitude of competition is predicted to change along resource gradients. Grime (1977) proposed a tradeoff between traits associated with competitive ability and traits related to stress tolerance. In this model, competitive ability is conferred by traits allowing rapid resource capture while stress tolerance is associated with traits allowing conservative resource use. Because traits associated with stress tolerance deplete only small amounts of resources, this model predicts that competitive intensity will be low in infertile environments. In contrast, Tilman (1988) proposed a tradeoff in ability to compete for

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different limiting resources where an increase in ability to compete for one resource decreases the ability to compete for other resources. Here, competitive ability is not conferred by traits allowing rapid resource capture but rather is based on ability to deplete resources. Therefore, competitive intensity is predicted to be similar in fertile and infertile habitats. Although these models have been tested extensively, empirical data have not consistently supported either model (Goldberg et al. 1999). Consequently, the importance of competition in structuring communities in resource-poor environments is still poorly understood.

Most investigations of plant interactions in resource-poor systems have assumed that resource supply rates are constant. While overall resource availability may be low in these systems, resources fluctuate between pulses of relatively high resource availability and interpulses of low resource availability (Noy-Meir 1973; Goldberg and Novoplansky 1997). For example, soil nitrogen (N) is often limiting in arid and semi-arid systems and only available to plants in brief pulses following precipitation events. The duration of an N pulse, however, is limited by a number of biotic and abiotic factors, including plant uptake, microbial immobilization, volatilization/denitrification, and soil dry-down (Cui and Caldwell 1997; Hodge et al. 1999; Austin et al. 2004; James and Richards 2006). In these systems, plant growth depends on a species' ability to rapidly capture brief N pulses (Bilbrough and Caldwell 1997) which can, in turn, influence survivorship during periods of low resource supply (Toft and Fraizer 2003). This suggests that competitive intensity in resource-poor systems may be a function of temporal patterns of resource supply and the degree to which limiting resources are reduced during a pulse by neighbor plants relative to other biotic and abiotic processes (Goldberg and Novoplansky 1997).

In addition to influencing the magnitude of competitive interactions in resource-poor plant communities, pulse timing may differentially affect the competitive abilities of coexisting species. Several studies have demonstrated that the ability of a plant to capture N from pulses is greatest when the pulses coincide with periods of high growth rate and N demand (Bilbrough and Caldwell 1997; James and Richards 2005, 2006). This suggests that the competitive effects of a species may be highly variable over time and depend partly on the seasonal timing of N pulses. If coexisting species differ in seasonal patterns of growth rate and N demand, then temporal variation in N supply has a strong potential to alter the outcome of competitive interactions.

The broad objective of this study was to determine how the temporal pattern of N-supply influences competitive interactions in an N-limited desert shrub community. The plant community selected for this study lies on the ecotone between the Great Basin and Mojave Desert of North America. Two of the three dominant shrub species in this

system, *Atriplex confertifolia* S. Watson (Torrey and Frémont) and *Sarcobatus vermiculatus* (Hook.) Torrey, are widely distributed throughout the cold desert communities of the Great Basin and Colorado Plateau. The third dominant species, *Atriplex parryi* S. Watson, is distributed throughout the warmer Mojave. In this community, *A. confertifolia* and *S. vermiculatus* achieve higher growth rates and N uptake rates earlier in the growing season than *A. parryi* (James et al. 2006; James and Richards 2006). We predicted that (1) competitive intensity will be greater under pulsed N supply than when the same amount of N is supplied at a low rate continuously through the growing season. Based on the expectation that the ability of a species to acquire N and suppress N capture of competing plants will be greatest during periods of high growth rate, we also predicted that (2) the competitive effects of *A. confertifolia* and *S. vermiculatus* neighbors on *A. parryi* target plant N capture will be greater when pulses occur in early spring compared to when pulses occur in mid-spring, and (3) the competitive effects of *A. parryi* neighbors on *A. confertifolia* target plant N capture will be greater in mid-spring compared to early spring.

Materials and methods

Study site, common garden installation and experimental design

The study was conducted in the Owens Valley, CA, USA (36° 21' N, 118° W; 1,087 m elev.). Annual precipitation in Independence, CA, approximately 45 km north of the site, averages 134 mm, with the majority of the precipitation falling in winter and spring as rain. Soils at the site are classified as Torripsamment and range from 69 to 94% sand (Dahlgren et al. 1997). Inorganic N levels at the site are low throughout most of the year (ca. 1–3 mg kg⁻¹ in the 0–5 cm soil layer) and limit plant growth (James et al. 2005). The first precipitation inputs following prolonged drought, however, can increase inorganic N to around 15 mg kg⁻¹ (James et al. 2006).

A common garden was established by clearing a 25 × 25 m area within the existing shrub community. Field plots (36 cm diameter, spaced 1 m apart) within the garden were set up in winter 2003. A plastic lining was buried 45 cm deep around the outside of each plot to restrict lateral movement of the N pulses and maintain a uniform below-ground competitive environment where the majority of the fine roots of these three study species are distributed (Fernandez and Caldwell 1975; Donovan et al. 1996; Dahlgren et al. 1997). Treatments were applied in a complete factorial design (two target species × four neighbor treatments × three temporal patterns of N supply) replicated in

seven blocks for a total of 168 plots. The two target species used in this study were *A. confertifolia* and *A. parryi*. The four neighbor treatments included a single target plant grown alone or with two individuals of *A. confertifolia*, *A. parryi* or *S. vermiculatus*. The plants used in this experiment were transplanted in spring 2003 as three-month-old seedlings raised from seed collected at the site. The biomass, phenology and spacing of seedlings planted in the experimental plots were representative of naturally occurring seedling and juvenile plants in the native population (Breen 2005; James et al. 2005, 2006). Seedlings were kept well-watered after planting. Any seedlings that died within two weeks of transplanting were replaced. After this second planting, a severe windstorm killed 30 of the 420 seedlings planted. While mortality was not treatment-specific, these seedlings were not replaced because they would have been of substantially different size and age than the seedlings planted at the start of the experiment. Plots with any seedling mortality were not included in the final analysis because they differed in seedling density. During the first growing season plants received two 1-L applications of one-eighth-strength modified Hoagland's solution and were watered approximately twice a month to facilitate establishment. During summer 2003, plots were watered heavily several times to leach the majority of inorganic N out of the root zone. The plants were allowed to grow for one year before the temporal N supply treatments were applied.

During the 2004 growing season experimental plots were randomly assigned to receive experimental N pulses either three times in early spring (27 February–10 March), three times in mid-spring (22 April–6 May), or as a series of small pulses continuously (approximately twice a week) throughout the growing season (27 February–15 June). A drip irrigation system was used to supply N in the continuous treatment. A separate drip irrigation system was used to lightly water the plots assigned to early and mid-spring N pulses so that soil water content remained comparable among the three N supply treatments. The same total amount of water (25 l) and N (330 mg) were applied to all treatments. Experimental N pulses were applied as 3.2 atom% $^{15}\text{NH}_4^+\text{NO}_3$. The labeled N in the pulse treatments was distributed evenly across the plot and produced a wetting front approximately 40 cm deep. The drip irrigation system used to supply the labeled N in the continuous N supply treatment was placed in the center of the plot to maintain a relatively constant but low concentration of N to a depth of 40 cm. The rate and pattern of N application were expected to produce an N concentration of $\sim 7 \text{ mg kg}^{-1}$ in the pulsed treatments and $\sim 1.5 \text{ mg kg}^{-1}$ in the continuous N supply treatment (based on the inorganic N concentrations in the soil after leaching, mass of N added to the volume of soil in each plot, and soil bulk density). These soil N levels are within the range over which inor-

ganic N concentrations can vary in this system (James et al. 2006).

Harvest

Plants were harvested sequentially by block starting on 23 June 2004 and ending on 25 June 2004. The canopy of the target plant in each plot was cut at the soil surface and divided into stems and leaves. The soil within each plot was excavated intact to a depth of 45 cm and the root system of the target plant was recovered by gentle washing. The root system was separated into woody and nonwoody roots for analysis. Leaves and nonwoody roots of the target plant were dried at 65 °C for one week and then weighed. A subsample of leaves and nonwoody roots were triple-rinsed with distilled water, dried at 65 °C and then finely ground for ^{15}N analysis. Leaf and root N concentration and ^{15}N enrichment were measured by continuous flow direct combustion and mass spectrometry at the UCD Stable Isotope Facility. Leaf and root ^{15}N pools were summed to determine target plant ^{15}N capture under different temporal patterns of N supply and neighbor environments. Calculations of ^{15}N content followed Nadelhoffer and Fry (1994), where ^{15}N content (mg plant^{-1}) = $m_f \times [(N_f - N_i)/(N_{\text{lab}} - N_i)]$ and m_f is mass of the N pool (mg), N_f , and N_i are the final and initial atom% ^{15}N of the sample and N_{lab} atom% ^{15}N of the labeled solution.

Statistics

The ability of different neighbor species to suppress N capture by the two target *Atriplex* species [competitive effect sensu Goldberg (1990)] was quantified per block using the natural-log-transformed response ratio (lnRR), where $\ln\text{RR} = \ln(^{15}\text{N}$ capture by target species i growing with neighbor j under N supply treatment k / ^{15}N capture by target species i grown alone under N supply treatment k) (Hedges et al. 1999; Novoplansky and Goldberg 2001; Suding et al. 2004). Values of lnRR are symmetric around zero, with negative values indicating competition and positive values indicating facilitation. The statistical properties of lnRR have been examined in detail by Hedges et al. (1999) and have been shown to have major advantages over other potential metrics of competitive intensity. A t -test for mean of $\ln\text{RR} = 0$ was conducted to determine if the competitive effects of neighbors on target plant N capture were significantly different from zero (SAS 2001). The effect of different neighbor environments and temporal patterns of N supply on lnRR and ^{15}N capture of target species were analyzed by ANOVA (SAS 2001). Because the assumptions of homogeneity of variance were not met for ^{15}N and lnRR data the ANOVA models were weighted by the inverse of the variance (Neter et al. 1990). Leaf ^{15}N data were not

normally distributed and were $\log(x + 1)$ -transformed before analysis. Following ANOVA, linear contrasts were used to evaluate the effects of neighbors and temporal pattern of resource supply on plant ^{15}N capture and to test our hypotheses about how competitive effects may change with different neighbor species under different temporal patterns of N supply.

Results

Effect of neighbors and temporal patterns of N supply on target plant N capture

Capture of ^{15}N by the two *Atriplex* target species was influenced differently by the pattern of N supply, as indicated by a significant N supply pattern \times target species interaction (Table 1). While N capture by target plants was generally lower under continuous resource supply than pulsed resource supply ($P = 0.001$) (Fig. 1a,b), in the absence of neighbors, N capture by *A. confertifolia* target plants was influenced less by the temporal pattern of N supply than *A. parryi* target plants. The effect of neighbors on *A. parryi* and *A. confertifolia* target plant N capture depended on the temporal pattern of N supply and neighbor plant identity. Neighbor plants had minimal effects on *A. parryi* and *A. confertifolia* target plant N capture in the continuous N supply treatment ($P = 0.508$ and 0.068 , respectively), but significant negative effects on target plant N capture when N was pulsed ($P = 0.002$ and 0.023 , respectively).

Table 1 ANOVA results (*df*, *F* and *P*) assessing the effects of N supply pattern, target species and neighbor species on competitive intensity ($\ln\text{RR}$) and ($\log_{10} + 1$) plant ^{15}N capture

Source	<i>df</i>	$\ln\text{RR}$		Plant ^{15}N	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Model	23	1.19	0.278	2.32	0.003
Block	6	0.71	0.643	0.65	0.6917
N supply pattern	2	3.38	0.039	2.17	0.121
Target	1	3.16	0.079	21.81	<0.001
Neighbor	2	3.49	0.035	3.90	0.024
N supply pattern \times target	2	2.21	0.117	4.23	0.018
N supply pattern \times neighbor	4	0.23	0.923	0.54	0.709
Target \times neighbor	2	0.12	0.886	0.13	0.882
N supply pattern \times target \times neighbor	4	0.73	0.577	1.15	0.338
Error	72				
Total	95				

Data are presented in Figs. 1 and 2

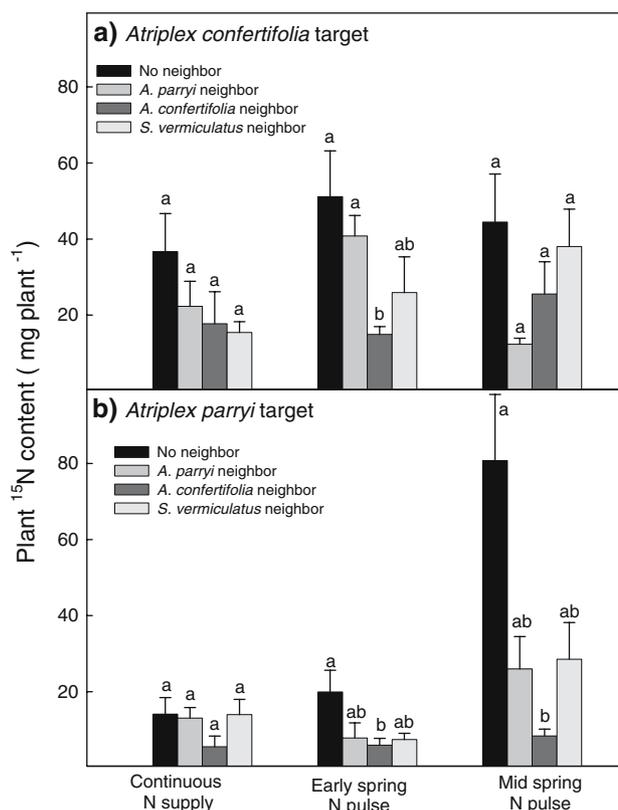


Fig. 1a–b Effect of temporal pattern of N supply and neighbors on ^{15}N capture by **a** *A. confertifolia* and **b** *A. parryi* target plants (mean \pm SE, $n = 5–7$). Bars with different letters indicate significant differences within N supply treatments ($P < 0.05$, Tukey's studentized range test)

Effect of temporal patterns of N supply on competitive interactions

Competitive effects of neighbors on target plant N capture were observed under both continuous and pulsed N supply (*t*-test for mean of $\ln\text{RR} = 0$, $P < 0.05$; Fig. 2a,b). However, the competitive effect of neighbors on target plant N capture was influenced by the pattern of N supply (Table 1), with competitive effects generally being greater under pulsed compared to continuous N supply ($P = 0.018$). The effect of neighbors on target plant N capture depended to some extent on the timing of the N pulse and identity of the neighbor species. For example, the competitive effect of *A. parryi* neighbors on *A. confertifolia* targets tended to be lower under early spring pulses compared to mid-spring pulses ($P = 0.119$), while the competitive effect of *S. vermiculatus* neighbors on *A. confertifolia* targets was largely similar under early and mid-spring N pulses ($P = 0.716$). The competitive effect of *A. confertifolia* and *S. vermiculatus* neighbors on N capture by *A. parryi* target plants did not differ significantly between early or mid-spring N pulses ($P = 0.471$ and 0.521 , respectively). Averaged

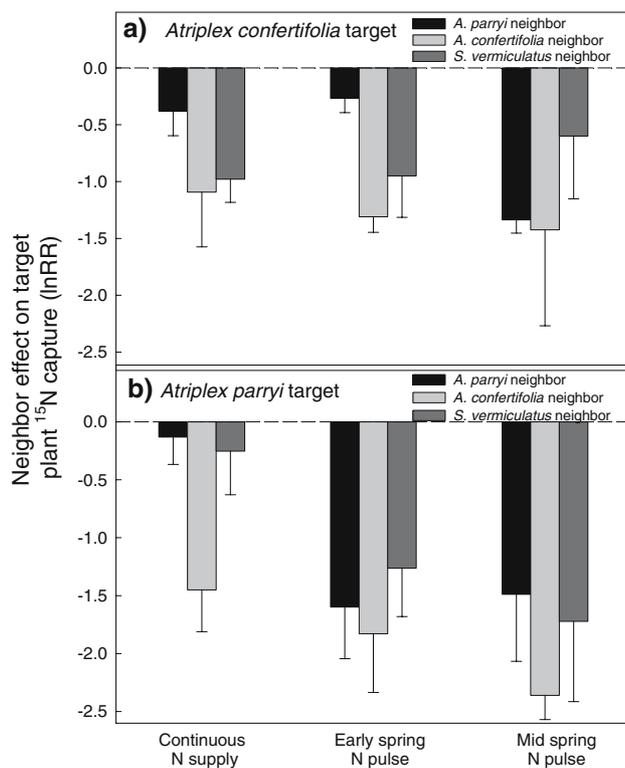


Fig. 2a–b Competitive effects of different neighbor species on **a** *A. confertifolia* and **b** *A. parryi* target plant ^{15}N capture under different temporal patterns of N supply (mean \pm SE, $n = 5\text{--}7$). More negative values indicate greater competitive effects of neighbors. The dashed line indicates $\ln\text{RR} = 0$ (i.e., no competitive effect)

across the different temporal patterns of N supply, competitive effects on target plant N capture did not differ between intraspecific and interspecific neighbors ($P = 0.788$).

Discussion

Competitive effects were observed under continuous and pulsed N supply. Averaged across the different target–neighbor treatments, however, competitive intensity was around 1.8-fold greater when N was pulsed compared to when N was supplied continuously (Fig. 2a,b). These results support our first hypothesis and suggest that the intensity of competitive interactions in arid systems may be linked to the magnitude and temporal pattern of N supply. For example, during prolonged dry periods in arid systems, microbial decomposition of litter is inhibited and a portion of the microbial biomass may be killed, resulting in substantial accumulation of labile soil organic matter with a low C:N (Kieft et al. 1987; Austin et al. 2004). When these dry soils are wetted and conditions for microbial growth improve, rapid microbial decomposition of this low C:N substrate can result in high rates of N mineralization, low rates of immobilization, and a large pulse of plant-available

N (Austin et al. 2004). Under these conditions, N supply to the root system of a target plant would likely be less limited by rates of N mineralization and diffusion and more limited by the abundance of neighbor plants and ability of neighbors to preempt N. Therefore, as the annual N supply to a plant becomes increasingly restricted to brief pulses, competition intensity would be expected to increase. However, if the labile organic matter pool becomes depleted following frequent wet–dry cycles, or if precipitation inputs increase relatively more than labile soil organic matter inputs, the C:N of the microbial substrate will increase, resulting in higher rates of N immobilization and lower rates of N mineralization (Fierer and Schimel 2002; Mikha et al. 2005). A decline in labile soil organic matter also can increase rates of gaseous N loss, particularly as coarse, high-pH desert soils dry (Schlesinger and Peterjohn 1991; Schaeffer and Evans 2005). Under these conditions, the N supply to the root system of a target plant would likely be more limited by biotic and abiotic soil processes and less limited by the abundance of neighbor plants, resulting in a decrease in competition intensity.

Based on previous studies of individual plant responses, we predicted that competitive effects of neighbors on target plant N capture would depend on when the N pulse occurred relative to target and neighbor plant growth rate. The outcome of competitive interactions in this system was not significantly influenced by the seasonal timing of the N pulse, in contrast to our prediction. For example, we predicted that the ability of *A. confertifolia* and *S. vermiculatus* to suppress *A. parryi* N capture would decrease during mid-spring pulses compared to early spring pulses. Previous studies have shown that *A. parryi* has greater growth rates in mid-spring compared to early spring, and in this study individually planted *A. parryi* plants captured more N from mid-spring pulses compared to early spring pulses (Fig. 1b). In this experiment, the competitive effects of *A. confertifolia* and *S. vermiculatus* neighbors on *A. parryi* target plant N capture did not differ between the early and mid-spring pulse (Fig. 2b). This suggests that when the temporal pattern of N supply varies in this system, differences in timing of maximum growth rate among shrubs may have a limited impact on the outcome of competitive interactions. Other plant traits may be more important than growth rate in influencing competitive interactions when resources are pulsed. For example, previous studies on individual plants have suggested that rapid physiological adjustment of existing roots may be one of the most important traits allowing plants to exploit short-duration nutrient pulses (BassiriRad and Caldwell 1992; Cui and Caldwell 1997). Measurements on individual plants in this system have shown that even though *A. parryi* demonstrates a greater relative increase in root N uptake capacity from early spring to mid-spring compared to *A. confertifolia*, *A.*

confertifolia maintains greater absolute root N uptake rates than *A. parryi* following a pulse, regardless of pulse timing (James and Richards 2006). This difference in root uptake capacity could be one reason that *A. confertifolia* neighbors had greater competitive effects on *A. parryi* targets under all resource supply treatments compared to the competitive effects of *A. parryi* neighbors on *A. confertifolia* targets (Fig. 2a,b).

Although plants in arid and semi-arid systems experience pronounced annual and interannual variations in resource supply (Noy-Meir 1973), only a handful of studies have evaluated how the pattern of resource supply influences competitive interactions. A recent pot study has demonstrated that the temporal pattern of resource supply alters competitive interactions between juvenile and adult grasses in arid systems (Jankju-Borzelabad and Griffiths 2006). Consistent with these results, our findings suggest that competitive intensity in arid systems may be influenced as much by the temporal pattern of resource supply as by total resource quantity. Other research, however, suggests species from these systems do not compete for pulsed resources but may instead compete for resources at depth (Gebauer et al. 2002; Yoder and Caldwell 2002). The degree to which the temporal pattern of resource supply alters competitive interactions may depend on the limiting resource and the position in the soil profile where limiting resources are primarily extracted. For example, some resources such as N are restricted to upper soil layers, which have substantially greater temporal variation in resource availability than lower soil layers (Noy-Meir 1973). When N is limiting, as in our system, temporal fluctuations in resource supply may have a large effect on species interactions. When water is limiting and competing plants primarily extract water at depth, resource pulses restricted to shallow soil layers may barely influence competitive interactions.

Much research in community ecology has centered on understanding how the intensity of plant interactions changes along productivity gradients (Goldberg and Barton 1992; Goldberg et al. 1999). Traditionally the focus of this research has been on evaluating if competitive intensity decreases or remains the same as resource availability declines (Goldberg and Novoplansky 1997). This field study was a first step in evaluating if the intensity of competitive interactions in resource-poor systems could be influenced by the temporal pattern of resource supply. Results from this initial study showed an overall increase in competitive intensity when N was pulsed compared to when the same amount of N was distributed continuously through the growing season. This trend, however, was not observed in all target \times neighbor species combinations. For example, the competitive effect of *A. parryi* plants on *A. confertifolia* target plant N capture did not increase when N

pulses were applied in early spring when the growth rate of *A. parryi* was low. This suggests that resource pulses may not increase competitive intensity if pulses occur when competing neighbors have a limited ability to deplete resources.

While we did find an overall increase in competition intensity with nitrogen pulsing, caution in interpreting our findings is needed since this study was conducted at one site in one year with only three species. Future work with other species in other study systems is needed to examine the generality of these findings. In addition, other factors may modify the degree to which resource pulsing alters competitive interactions in arid systems, including abiotic stress, size-asymmetric competition, and the potential for microbial communities to positively or negatively affect plant resource capture (Fowler 1986; Donovan and Richards 2000; Bever 2002). An understanding of these interactions is ultimately needed to determine the degree to which resource pulses can alter plant community dynamics in resource-poor systems.

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