

Seasonal timing of N pulses influences N capture in a saltbush scrub community

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Abstract

Limiting resources are generally available in brief temporal pulses in arid systems. We compared the abilities of dominant shrubs in a saltbush scrub community to capture N from pulses and evaluated whether N capture and partitioning within this community is influenced by the seasonal timing of pulses. Based on previous research in agronomic systems we predicted that the ability of a species to capture N following a pulse would depend on when the pulse occurred in relation to plant growth rate and N demand. Supporting this hypothesis, *Atriplex confertifolia* and *Sarcobatus vermiculatus*, which had greater growth rates early in the growing season compared to *Atriplex parryi*, captured more N from early spring pulses than *A. parryi*. *Atriplex parryi*, which had higher growth rates later in the growing season, captured more N from mid- and late spring pulses than the other species. These temporal differences in N capture among species, however, also depended on the magnitude of the N pulse. These results suggest that temporal variation in N availability may differentially impact competitive abilities of coexisting species and potentially facilitate species coexistence in arid systems.

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1. Introduction

Resource supply rates are dynamic in arid systems and consist of pulses of relatively high resource availability and inter-pulses of low resource availability (Noy-Meir, 1973;

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Goldberg and Novoplansky, 1997). For example, in arid and semi-arid ecosystems nitrogen (N) is often a limiting resource and mainly available to plants in brief pulses following rainstorms and snowmelt. Following prolonged drought, water input stimulates N mineralization from accumulated organic matter (Austin et al., 2004), increases availability of N accumulated from dry deposition (Fenn et al., 2003), and facilitates N flow to roots (Nye and Tinker, 1977). The duration of an N pulse is limited, however, by plant N uptake, microbial immobilization and soil dry down (Nye and Tinker, 1977; Cui and Caldwell, 1997b; Hodge et al., 1999).

While the temporal dynamics of N in arid systems long have been recognized, only recently have there been attempts to understand the potential for such temporal heterogeneity to affect ecological processes. Some studies have demonstrated that pulsed N supply can alter resource capture and competitive ability of coexisting species (Bilbrough and Caldwell, 1997; Cui and Caldwell, 1997a; Gebauer and Ehleringer, 2000). In a number of other studies, however, N pulses have influenced these processes little (Gebauer et al., 2002; Yoder and Caldwell, 2002; Ivans et al., 2003). The basis for these conflicting results is difficult to resolve, in part because little research has focused on understanding the mechanisms that may regulate plant response to N pulses. Such insight is critical, however, to understand how and under what environmental conditions N pulses can be expected to influence ecological processes in arid systems.

In deserts, precipitation events and corresponding N pulses can have a large random component (Noy-Meir, 1973; Loik et al., 2004). As a result, the seasonal timing and magnitude of N pulses is expected to vary greatly from year to year. However, plant N capture depends not only on soil N concentration but also on plant growth rate and plant demand for N (Forde, 2002; Collier et al., 2003). Agronomic and ecological models predict that plants will make physiological and morphological adjustments so resource uptake matches plant growth requirements (Drew and Saker, 1975; Bloom et al., 1985; Gleeson and Tilman, 1992; Gleeson and Good, 2003). Thus, plants should capture more N when pulses occur during periods of high growth rate and capture less N when pulses occur during periods of lower growth rate. This suggests that a species's ability to respond to a pulse is not a fixed ecological characteristic but will vary depending on when the pulse occurs in relation to seasonal plant growth patterns. Moreover, if coexisting species differ in phenology and timing of maximum growth rate, variation in the timing of pulses may differentially impact species N capture and N partitioning.

The broad objective of this field study was to compare the ability of dominant shrubs in a saltbush scrub community to capture N from pulses and to evaluate if N capture and partitioning within this community is influenced by the seasonal timing of pulses. The plant community selected for this study lies on the ecotone between the Great Basin and Mojave Deserts of North America. Although annual precipitation is generally low in this system, previous studies have documented that primary production in this and similar saltbush scrub communities is N limited (Drenovsky and Richards, 2004; Snyder et al., 2004; James et al., 2005). Two of the three dominant species in this system, *Atriplex confertifolia* S. Watson (Torrey & 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 warm desert communities of the Mojave. In general, Great Basin species initiate shoot and root growth at lower soil and air temperatures than Mojave Desert species (Caldwell, 1985; Comstock and Ehleringer, 1992). Consequently, in this community

A. confertifolia and *S. vermiculatus* should achieve higher growth rates earlier in the growing season than *A. parryi*. Thus, we hypothesized that *A. confertifolia* and *S. vermiculatus* would demonstrate a greater ability to exploit N pulses earlier in the growing season relative to *A. parryi* and conversely that *A. parryi* would demonstrate a greater ability to capture N from pulses occurring later in the growing season compared to the other two shrubs. To test these predictions we: (1) quantified seasonal patterns of soil N dynamics for three growing seasons in our shrub community to document the temporal heterogeneity of soil N availability, (2) evaluated the potential of the three study shrubs to deplete soil N in early spring following natural N pulses, and (3) by applying experimental pulses labeled with ^{15}N , we determined how seasonal variation in timing of N pulses influences the ability of the coexisting species to capture N.

2. Materials and methods

2.1. Study site and species

The study was conducted in the Owens Valley, California, USA, (36°N , 118°W ; c.a. 1085 m elev.). Sampling was conducted at two sites, one at the north-east side of Owens (dry) Lake and one on the south-west side of Owens Lake. We included multiple sites within the community to increase the scope of our sampling and develop stronger inferences about the general patterns of soil inorganic N dynamics and species responses within our community. Vegetation at both study sites is co-dominated by the three study species (Dahlgren et al., 1997). Other common species at the study sites include *Distichlis spicata* (L.) E. Greene and *Suaeda moquinii* (Torrey) E. Greene. Soils at both sites are classified as Torripsamment, with no horizonation and a sand content ranging from 69% to 94%. Mean annual precipitation at Haiwee, CA 20 km south of Owens Lake averages 172 mm. The majority of precipitation falls in winter and spring as rain, however, there is substantial year-to-year variation in amount and timing of precipitation (Fig. 1).

2.2. Soil inorganic N sampling and analysis

To quantify the seasonal patterns of soil N dynamics in our study system (objective 1), five to eight soil samples were taken under the edge of plant canopies at random locations in the community at approximately monthly intervals during the spring growing seasons of 2002–2004 and once during the fall of 2002 and 2003. To evaluate the potential of the three species to deplete soil N following natural N pulses (objective 2), five to eight soil samples were taken under the edge of the canopy of randomly selected plants of the three dominant shrub species 10 days after the first large (>5 mm) precipitation event occurring in early spring 2003 (16 March) and 2004 (26 February). In addition, soil samples also were taken under the three species once during fall 2002 and 2003. For each soil sample, three subsample cores were removed from the 0–10 cm soil depth, homogenized and sifted to remove the >2 mm coarse fraction, and stored at 5°C until extracted in the lab. Approximately 50 g of soil from each sample was extracted with 2 M KCl. The extracted inorganic N was measured colorimetrically following Forster (1995) for NH_4^+ and Miranda et al. (2001) for NO_3^- . There were no significant differences in soil inorganic N concentrations between sites so soil samples from both sites were pooled by for analysis.

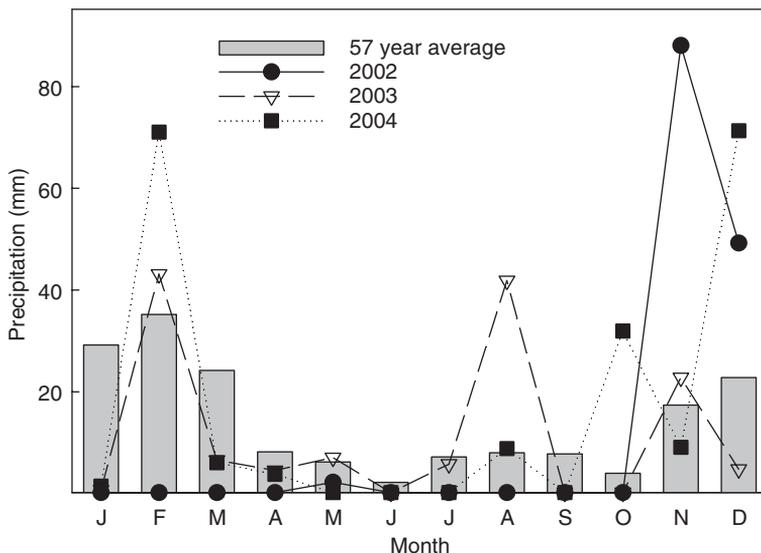


Fig. 1. Long-term (57 year) average monthly precipitation and mean monthly precipitation during the study period recorded at record at Haiwee, CA 20 km south of the study site.

2.3. Experimental N pulses labeled with ^{15}N

To determine how seasonal variation in timing of N pulses influences the ability of the coexisting species to capture N (objective 3), experimental N pulses were applied at the southwest site three times during the spring 2002 growing season (early-, mid-, and late spring) by applying 5 g N m^{-2} as $10\text{ at}\% \text{ K } ^{15}\text{NO}_3$ in a simulated 20 mm rain event. Different plants were used for each experimental N pulse. For each species, similar-sized shrubs (canopy dimensions ca. $20 \times 20 \times 35\text{ cm}$) were selected to receive the experimental N pulses. Applying N at a high rate and removing water limitations allowed us to quantify inherent differences in the ability of a species to capture N from pulses. N pulses were applied to five plants of each species during each pulse. Leaf tissue was sampled at six random locations in the canopy immediately before and 20 days after label application. Leaves were rinsed with deionized water, dried at 60°C to a constant mass, and ground. Samples were analysed for ^{15}N on an isotope ratio mass spectrometer (Fisons Instruments, Beverly, MA). Although roots were not sampled pot studies with these species have demonstrated that over 80% of the N acquired from a pulse is allocated to leaves (James et al., unpublished) suggesting our leaf measurements are a good indicator of whole-plant response. Calculations of ^{15}N uptake followed Nadelhoffer and Fry (1994) where ^{15}N acquisition ($\text{mg } ^{15}\text{N kg leaf}^{-1}$) = $m_f \times (N_f - N_i) / (N_{\text{lab}} - N_i)$. Here, m_f is leaf N concentration (mg kg^{-1}), N_f , and N_i are the final and initial at% ^{15}N of the sample and N_{lab} is the at% ^{15}N of the labeled solution.

2.4. Seasonal patterns of plant growth

Cumulative stem length of new stems produced each growing season was used as an index for shrub phenology growth rate. Early in the growing season of 2002 and 2003 four budding shoots (subsamples) were marked on five randomly selected plants of each species.

These stems were repeatedly measured through the growing season and the subsamples averaged for each time period. Similar growth measurements were made on shrubs selected to receive experimental N pulses. For these plants, measurements were made prior to each experimental N pulse and 20 days after the last pulse.

2.5. Statistical analysis

Data were analysed using ANOVA. Assumptions of ANOVA were evaluated using Shapiro–Wilk test for normality and Levene’s test for homogeneity of variance. If these assumptions were violated, ANOVA models were weighted by the inverse of the variance (Neter et al., 1990). Following ANOVA, differences between treatments were determined using the Ryan–Einot–Gabriel–Welsch multiple range test (SAS, 2001).

3. Results

3.1. Environmental conditions during the study period and plant growth

A significant drought occurred during the first growing season of the study (spring 2002). Total crop year precipitation in 2002 (Sept 2001–August 2002) was 35 mm or only 20% of the 57-year mean. Essentially no precipitation occurred during winter 2001 or spring and summer 2002 (Fig. 1). Large precipitation events, however, in late winter, spring, and summer 2003 resulted in a 2003 crop year precipitation of 245 mm, which was 40% greater than the long-term average. Crop year precipitation in 2004 was 120 mm, approximately 70% of the long-term average.

The Great Basin shrubs, *A. confertifolia* and *S. vermiculatus* obtained higher growth rates earlier in the growing season than the Mojave shrub *A. parryi* when air and soil temperatures were still relatively cool (Fig. 2). Although sampling in 2003 was not conducted early enough to estimate the timing of new stem growth, earlier sampling in the 2004 growing season indicated that *A. confertifolia* and to some degree *S. vermiculatus* initiated shoot growth earlier in the growing season than *A. parryi*.

3.2. Soil inorganic N concentrations

Soil inorganic N pools were generally very low in the community, averaging $\sim 3 \text{ mg kg}^{-1}$ across all sampling dates, and were dominated by NO_3^- -N (Fig. 3). While soil inorganic N pools tended to vary seasonally within years as expected, the magnitude of this variation was highly dependent on year ($p < 0.0001$) (Fig. 3). In general, spring sampling periods (March–May) typically had higher concentrations of available N than summer sampling periods (June–August).

3.3. Species response to natural resource pulses

Soil inorganic N concentrations were not significantly different in soils beneath *A. parryi* and *S. vermiculatus* in fall 2002 prior to the large N pulse (soils under *A. confertifolia* were not sampled) (Fig. 4). Following the N pulse induced by the first naturally occurring rain event in spring 2003 (March 16, 6.2 mm), soil NO_3^- differed significantly between the three species with soil NO_3^- levels being higher under *A. parryi* canopies than those of *A. confertifolia* and

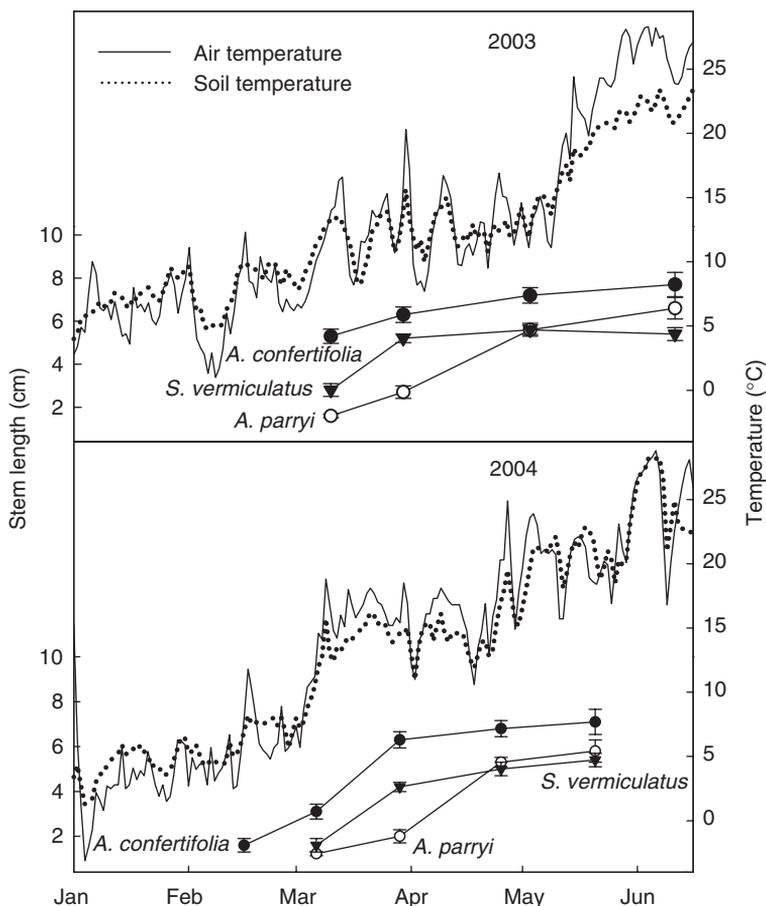
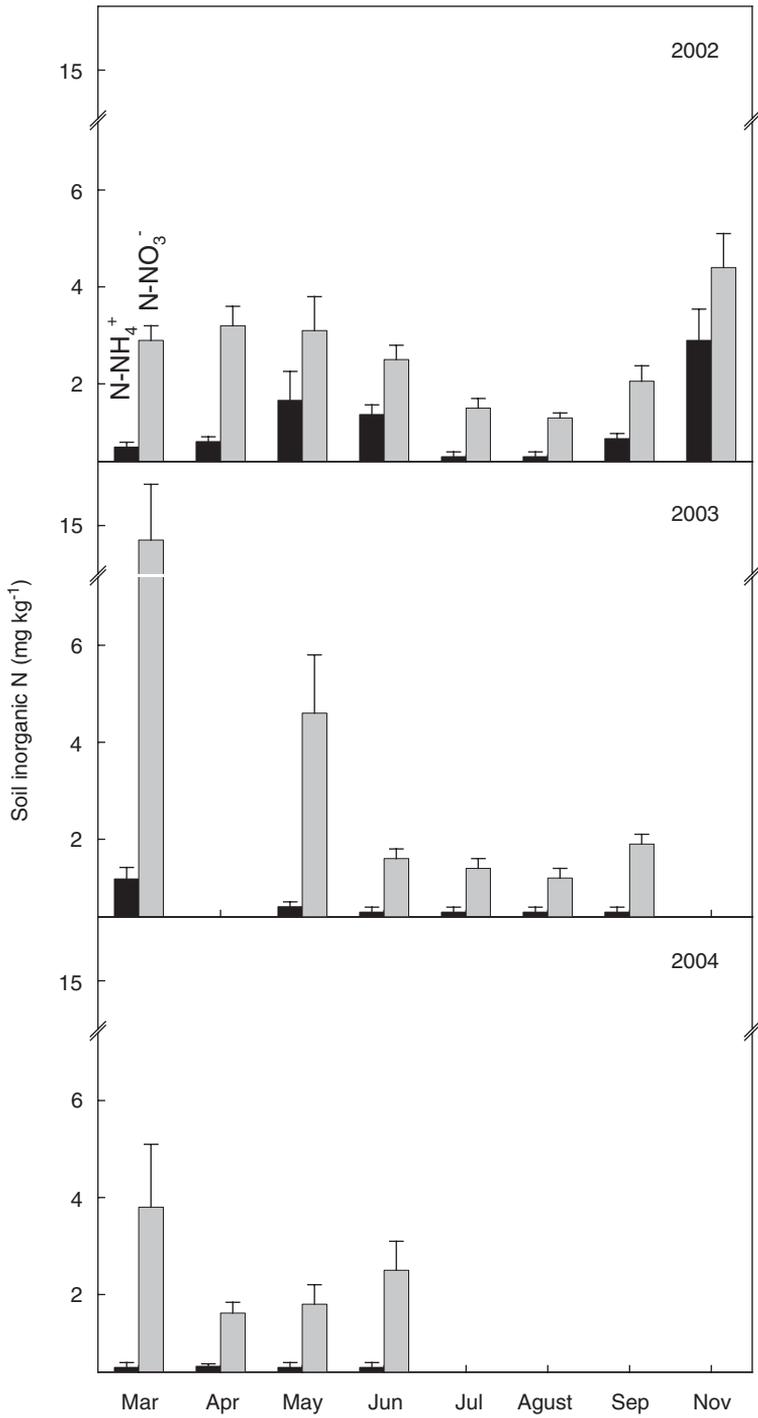


Fig. 2. Seasonal pattern of stem growth of the three study species (mean \pm S.E., $n = 5$). Also shown on the right Y-axis is daily mean air and soil temperature in 2003 and 2004. Air temperature was recorded at a height of 1.5 m and soil temperature at a depth of 15 cm at the Owens (dry) Lake North CIMIS weather station (<http://www.cimis.water.ca.gov/cimis/data.jsp>) 15 km north-east of the study site.

S. vermiculatus. Soil inorganic N levels did not differ among the three species in fall 2003 and differences in soil N among species following the first naturally occurring rain event in spring 2004 (26 February, 56.8 mm) were small and likely not biologically significant.

3.4. Species response to experimental N pulses

Atriplex confertifolia and *S. vermiculatus* had higher growth rates than *A. parryi* during the early spring experimental N pulses but had lower growth rates than *A. parryi* during the mid-spring pulse (Fig. 5, line graphs). Both *A. confertifolia* and *S. vermiculatus* captured the greatest amount of N from early spring pulses (Fig. 5, bar graphs). Later in the growing season, the ability of these species to obtain N from pulses declined. In contrast, N capture by *A. parryi* was lowest during the early spring pulse and maximal during the mid-spring pulse.



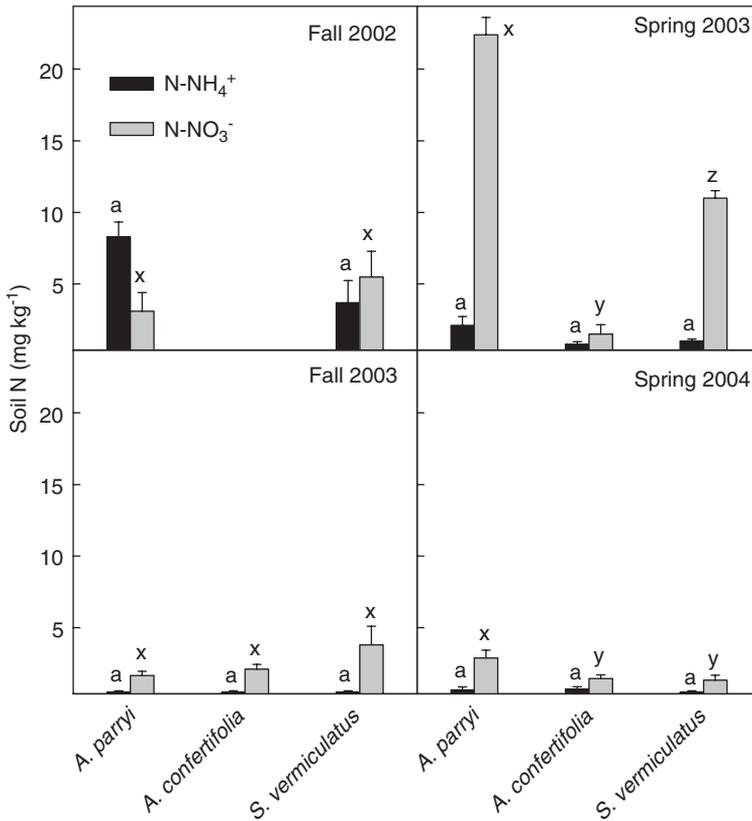


Fig. 4. Soil inorganic N concentrations under the canopy of the three study species (mean ± S.E., $n = 5-8$). Soils under *A. confertifolia* were not sampled in fall 2002. Letters indicate significant differences in soil N concentration within a chemical form of N (i.e. $N-NO_3^-$ or $N-NH_4^+$) ($p < 0.05$).

4. Discussion

Temporal variation in N availability is a ubiquitous feature of arid systems. In our saltbush scrub community soil N generally was greatest in early spring when water availability was high and tended to decrease in summer and fall as seasonal drought progressed (Fig. 3). Seasonal variation in N availability has been demonstrated in a number of arid systems (Mazzarino et al., 1998; Xie and Steinberger, 2001; Peek and Forseth, 2003). Our results also demonstrate that the magnitude of temporal variation in N availability can be greater between years than within years, depending on precipitation patterns (Fig. 3). For example, in 2002 when crop year precipitation was only 20% of the

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 Fig. 3. Soil inorganic N concentrations in the community during spring 2002, 2003, and 2004 growing season and summer and fall 2002 and 2003 (mean ± S.E., $n = 5-8$). Soil samples were taken at random locations under plant canopies in the community. Note y-axis break between 7 and 12 mg kg⁻¹. Soils were not sampled between July and November 2004.

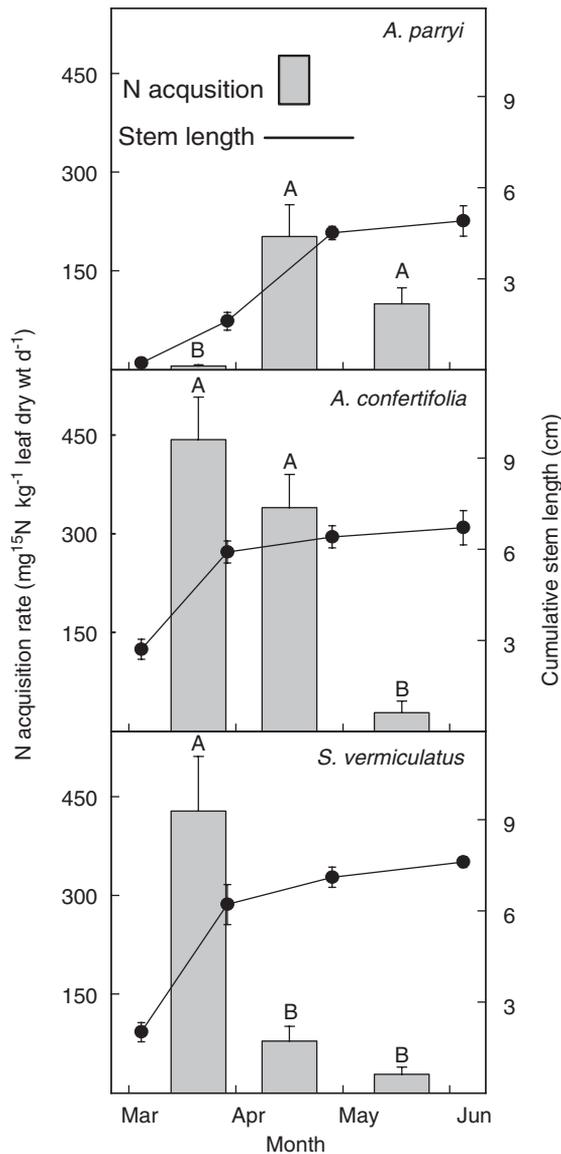


Fig. 5. Nitrogen acquisition rates of the three study species following early, mid, or late spring N pulses (bar graph, mean \pm S.E., $n = 5$) in relation to seasonal stem growth (line graph, mean \pm SE, $n = 5$). Different letters indicate significant difference in N capture within a species among pulses ($p < 0.05$).

long-term average, soil inorganic N concentration varied little between spring and summer months (ca. 3–1 mg kg⁻¹). During the same time period in the subsequent higher rainfall year (2003), however, soil inorganic concentration increased close to 15 mg kg⁻¹ and then declined during the summer dry period to concentrations similar to those observed in 2002. Large precipitation inputs following drought may stimulate mineralization of accumulated labile plant material, producing substantial N pulses (Austin et al., 2004). During

consecutive years of relatively high precipitation, however, these labile soil carbon pools may become depleted and the magnitude of N mineralized dampened. This may be one reason why soil inorganic N levels in 2004 were comparable to soil inorganic N levels observed during the 2002 drought even though precipitation in 2004 was over three-fold greater. A similar phenomenon has been demonstrated on a shorter time-scale in laboratory studies. In these experiments, repeated wet–dry cycles reduced labile carbon pools and caused a decline in N mineralization and soil respiration (Fierer and Schimel, 2002; Mikha et al., 2005).

Although temporal variation in N availability has been widely documented, few studies have evaluated how the seasonal timing of pulses impacts plant N capture. Our seasonal soil N measurements under the three study shrubs suggest that they differ in their ability to deplete soil N following early spring pulses. While soil N levels during fall 2002 and 2003 were generally comparable among the study species, following the large N pulse induced by the first naturally occurring rain event in spring 2003, soil NO_3^- levels were almost ten- and two-fold greater under *A. parryi* canopies than under those of *A. confertifolia* and *S. vermiculatus*, respectively. The N pulse induced by the first naturally occurring rain event in spring 2004, however, was much lower in magnitude than the N pulse induced by the first naturally occurring rain event in spring 2003, and large differences in soil N among the study shrubs were not observed. Although the cold desert shrubs *A. confertifolia* and *S. vermiculatus* consistently achieved higher growth rates earlier in the growing season than *A. parryi* (Fig. 2), these seasonal differences in growth rate among the study species only corresponded to differences in ability to deplete soil N following a large pulse. Therefore, our hypothesis that greater growth rates and N demand by the cold desert shrubs would result in greater N capture from early spring pulses by the cold desert shrubs relative to *A. parryi* was only partially supported. It appears that during small N pulses, such as the one induced by the first naturally occurring rain event in spring 2004, plant N capture may be more limited by low N supply rates to the root system than the capacity of the root system to capture N (Jackson and Caldwell, 1996). As a consequence, even if some species have a greater physiological capacity to capture N early in the growing season than others due to higher growth rates and N demand (Jeuffroy et al., 2002) this may not translate into large differences in N capture among species following a pulse if N capture is limited relatively more by soil N supply than uptake capacity per unit root.

Although seasonal soil N measurements provided some evidence that N capture during a pulse depended partially on plant growth rate and N demand, experimental manipulation of N pulses was necessary to evaluate how pulse timing may influence N capture and partitioning among dominant shrubs in this system. Consistent with the observed patterns of soil N depletion in early spring, N capture from early spring experimental N pulses by the cold desert shrubs was close to 18-fold greater than N capture by *A. parryi*, which corresponded with their higher growth rates during this period (Fig. 5). During the early spring pulses *A. confertifolia* and *S. vermiculatus* exhibited higher growth rates than *A. parryi*. As growth rates of the cold desert species declined during the growing season there was a corresponding decline in their ability to capture N from pulses. N capture by *A. confertifolia* and *S. vermiculatus* was over ten-fold lower following late spring N pulses relative to early spring N pulses. These findings are largely consistent with previous research in the Great Basin which demonstrated shrubs and grasses have a greater ability to utilize early spring N pulses than N pulses occurring later in the growing season (Bilbrough and Caldwell, 1997; Ivans et al., 2003; James and Richards, 2005). In contrast,

the Mojave Desert shrub *A. parryi* achieved maximum growth rate during the mid-spring pulse, and N capture by *A. parryi* was on average 25-fold greater during the mid- and late spring pulses relative to the early spring. These results demonstrate that in this community there is not a consistent hierarchy among coexisting species in ability to capture N from pulses. Instead, our results indicate that pulse N capture by a species strongly depends on plant growth rate during the pulse.

Desert ecologists are increasingly interested in understanding the degree to which resource pulses can influence ecological processes in arid systems (Goldberg and Novoplansky, 1997; Loik et al., 2004; Schwinning et al., 2004). Taken together, our results indicate that the impact of temporal variation in N availability on some ecological processes, such as competition and resource partitioning, will depend on the degree to which coexisting species differ in seasonal timing and rate of growth. Current models of competitive interactions predict that physiological traits allowing rapid capture of a limiting resource or depletion of a limiting resource to low levels will be important determinants of competitive ability (Grime, 1977; Tilman, 1988). Our results demonstrate that when coexisting species differ in seasonal timing and rate of growth both the rate at which a species can capture N from a pulse and the extent to which a species can deplete N following a pulse, depends strongly on the seasonal timing of a pulse. If such environmental variation impacts the competitive ability of a species, then competitive hierarchies in any given year could change based on the temporal N dynamics. Temporal variation in N availability, therefore, also may facilitate species coexistence in these pulse-driven systems by altering competitive advantages over time (Chesson et al., 2004). Further work with plants in different competitive environments is needed to fully assess the ecological consequences of this heterogeneity for survival, competitive ability and diversity maintenance.

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