Nitrogen acquisition from different spatial distributions by six Great Basin plant species

Sara E. Duke  
*Utah State University*

Martyn M. Caldwell  
*Utah State University*

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Supplies of soil resources to plants are characterized by spatial heterogeneity and temporal variation in many natural environments (Grime 1994). Plant characteristics that allow plants to acquire resources from spatially or temporally variable nutrient supplies can differ among species and likely depend on the evolutionary history of the species (Grime 1977, Chapin 1980, 1988, Aarssen 1983, Tilman 1986). Rapid acquisition of nutrients from pulses requires the presence of an active root system to take up nutrients when they first become available (Campbell and Grime 1989, Campbell et al. 1991). Utilization of a nutrient-enriched soil patch is commonly associated with the ability of a plant to elevate root physiological uptake capacity and proliferate roots in these local zones (Drew and Saker 1975, Jackson and Caldwell 1989). Plant communities composed of species that vary in growth form and size have been postulated to exhibit different strategies for acquiring nutrients when resources are not uniform in space or time (Campbell and Grime 1989, Grime 1994). Coexisting species that potentially compete for the same resources are thought to segregate...

Sagebrush-steppe communities of the semi-arid Intermountain West receive moisture primarily from late fall through spring. Summers are warm and dry. Plant nutrient availability corresponds with soil moisture in fall and spring and is greatly reduced in summer months as soils dry (Nye and Tinker 1977, Crawford and Gosz 1982, Barber 1995).

Phenological differences among species can result in different degrees of temporal coupling between nutrient uptake and its use for growth and reproduction. For example, in the sagebrush-steppe, perennial tussock grasses and winter annuals initiate growth in early spring from overwintered tillers that began growth in the fall (Nowak and Caldwell 1984). Tiller growth accelerates and seed production occurs in late spring and early summer, followed by death of annuals or dormancy of perennials in early to midsummer. The shrubs *Artemisia tridentata* and *Chrysothamnus nauseosus* initiate belowground growth early in the spring (Fernandez and Caldwell 1975), but vegetative growth first begins in early summer and flowering occurs in late summer (Bilbrough and Caldwell 1997). Thus, within a sagebrush-steppe community the timing of nutrient acquisition in spring and its subsequent use by different species can vary considerably.

Recently, Bilbrough and Caldwell (1997) investigated the ability of 6 species common to the Great Basin to procure nitrogen (N) from nitrogen-rich pulses at different times during the spring growing season. Plant growth was monitored throughout the growing season for each species. They concluded that most species exhibited a greater growth advantage by the onset of summer when they received a single 4-day pulse of N in the spring than when they received the same quantity of nitrogen applied over 10 weeks in the spring. The species differed as to how effectively they acquired N from the pulses, but there were only small differences in the timing when pulses were best utilized among the species. Therefore, temporal niche separation of N acquisition among the species during spring was apparently limited (McKane et al. 1990, Bilbrough and Caldwell 1997).


Our objective was to evaluate the ability of 6 Great Basin species representing 3 life forms to acquire N from different spatial distributions. The relative capability of species for coarsescale and fine-scale foraging of nutrients is one aspect of potential spatial niche separation among coexisting species (Campbell et al. 1991, Grime 1994). We evaluated this potential by comparing the ability of these species to acquire N from (1) locally enriched patches, (2) a uniform distribution surrounding the plant, and (3) enriched areas at a distance of 35–45 cm. Due to phenological differences among the selected species, it was necessary to create spatial patterns of N that would persist over a sufficiently long period of time in the spring such that all species would have the opportunity to experience N applications when they were active. We used an 15N-labeled ammonium-loaded clinoptilolite zeolite as a slow-releasing N source (Ming and Mumpton 1989). The 6-week experimental period overlapped active growth stages of all 6 species (Bilbrough and Caldwell 1997). We focused on total quantity of N acquired from zeolite applications and translocated to current year’s leaf and the proportion of the leaf N pool that this newly gained N represented.

**METHODS**

The research was conducted in spring 1995 at Utah State University Green Canyon Research Center, located approximately 4 km northeast of Logan, Utah (41°45’N, 111°48’W, 1460 m elevation). Annual precipitation in Logan comes largely as snow in the winter, but spring months receive 44 mm of rain on average.

Our experiment was conducted in large, unlined, sand-filled plots (5 m x 18 m, 1 m deep)
where plants were exposed to field conditions. There were 4 sand pits each planted with 6 species common to the Great Basin of the Intermountain West and used in earlier studies (Bilbrough and Caldwell 1997). The 4 perennial species were planted in 1992 as monoculture subplots within each sand plot. Subplots with perennial species were ~15 m × 1.5 m and were arranged parallel to each other along the length of the sand plots. Subplots with annual species were located at the end of each sand plot. Within each species subplot were 4 separate experimental units (approximately 1.5 m² for perennials and 0.5 m² for annuals; Fig. 1). Experimental treatments had been applied to the perennial species’ experimental units in previous years. Each species had received N (but no ¹⁵N) in the form of a pulse the previous 2 years, and these N pulses were applied to various experimental units at different times during the spring (Bilbrough and Caldwell 1997). For each species, we used 2 prior experimental units from each subplot in each sand plot (i.e., n = 8 experimental units). Prior treatments were included in the ANOVA as an experiment factor. The ANOVA factor PRIOR and all interaction terms with this factor were not statistically significant for any response variable for any species. Furthermore, N tissue concentrations between plants from different prior treatment experimental units were not statistically different. Therefore, we believe our N acquisition results were not strongly influenced or confounded by these prior N applications.

Perennial shrubs were transplanted as small seedlings and perennial tussock grasses as clumps of tillers in 6 parallel rows within each subplot. We staggered plants in adjacent rows with consistent spacing between all plants, creating a uniform distribution (Fig. 1). Spacing between plants necessarily varied because of size differences of the growth forms. The indigenous shrubs Artemisia tridentata ssp. vaseyana (Rydb.) Beetle and Chrysothamnus nauseosus (Pallas) Britt. were planted at an interplant distance of 25 cm. The introduced and indigenous perennial tussock grasses Agropyron desertorum (Fisch. ex Link) Schult and Pseudoroegneria spicata (PURSH A. Löve), respectively, were planted at 20-cm spacing. After 2 years, however, the interplant distance was approximately 15 cm in perennial grass subplots. In early March 1995 seeds of the introduced exotic annual grasses Bromus tectorum (L.) and Aegilops cylindrica Host. were planted at 5-cm spacing in two 0.5-m² experimental units within each sand plot (Fig. 1B). Because plants were growing in sand, they required light watering daily. To maintain some background nutrient availability in these sand cultures, we applied a 20% Hoaglands solution (with 5% N) through the drip irrigation system which was positioned between plant rows. After a 45-minute watering period, the entire surface of the sand was wetted.

Fig. 1. Diagram of plant location and N-amendment placement in experimental units (EU). Represented here are (A) a perennial grass EU, and (B) an annual grass EU. Spacing among shrub plants was 25 cm, 20 cm among perennial grass plants, and 5 cm among annual grass plants. Each dot represents an individual plant. Solid-line circles represent patch applications and solid-line rectangles represent uniform applications; dashed circles represent potential target plants to be harvested. Shrub EUs were similar in layout and treatment application to perennial grass EUs. The Uniform Treatment in the shrub EU covered 2 plants in adjacent rows; otherwise treatment coverage was the same as in perennial grass EUs.
Plants showed no signs of nutrient stress this year or in previous years.

We utilized the mineral clinoptilolite zeolite to create local areas of increased nitrogen availability. Clinoptilolite zeolite is composed of a crystalline lattice with a very high surface area that is negatively charged with an affinity for NH$_4^+$ (Ming and Mumpton 1989). Pulverized zeolite can easily be “loaded” with NH$_4^+$ by soaking in concentrated NH$_4$Cl solution, allowing the internal sites to become occupied by the cation NH$_4^+$. We soaked 200 g of crushed zeolite for 7 days on a shaker table in a 2% $^{15}$NH$_4$Cl-labeled 1-M NH$_4$Cl solution. We then repeatedly rinsed the zeolite with deionized distilled water to remove the chloride. Zeolite was oven-dried for 3 days and stored in a desiccator. Following the “loading” process, 1 g of dry NH$_4^+$-loaded zeolite contained 2.3 mg of N. Zeolite released the NH$_4^+$ + $^{15}$NH$_4^+$ in exchange for other cations, such as Ca$^{2+}$, K$^+$, and Mg$^{2+}$ in our diluted Hoaglands solution; thus, it was effective in creating a long-term nutrient patch in this sand system, since zeolite would release N slowly over time and remain localized.

Due to plant size differences (e.g., 3-year-old shrubs versus 3-week-old annual seedlings), we used different quantities of NH$_4^+$-loaded zeolite and created different size application areas for each growth form. The quantity of zeolite used for each growth form was based on the spacing of plants such that uniform applications were approximately equal to previous years’ background nitrogen fertilization (0.043 g N m$^{-2}$). Patches for shrubs were applied to 9.5-cm-diameter circular areas with 1.65 g zeolite placed on the surface in the space equidistant between 3 plants (Fig. 1A). Uniform applications were 900 cm$^2$ with the same quantity of zeolite covering the soil surface; this included 2 shrubs in separate rows (modification of uniform application in Fig. 1A). These application rates correspond to 5.3 g N m$^{-2}$ and 0.042 g N m$^{-2}$ for the patch and uniform treatments, respectively. Perennial grass circular patches were 7 cm in diameter to which 1.1 g of zeolite was applied over the surface in the space equidistant between 3 plants. Uniform applications were 600 cm$^2$ with the same amount of zeolite and encompassed 3 plants in 2 adjacent rows (Fig. 1A). Application rates for perennial grasses corresponded to 6.6 g N m$^{-2}$ and 0.042 g N m$^{-2}$ for the patch and uniform treatments, respectively. Patches in annual plots were 4.5 cm in diameter and uniform applications were 300 cm$^2$, each with 0.55 g zeolite, corresponding to application rates of 8.0 g N m$^{-2}$ and 0.042 g N m$^{-2}$, respectively (Fig. 1B).

Patch and uniform zeolite applications were created within each experimental unit on 3 May 1995. Plants were harvested 14–20 June. This experimental period was long enough for zeolite to release much of the $^{15}$N-labeled ammonium (J.L. Boettinger unpublished) and overlapped the growth period of all 6 species (Billbrough and Caldwell 1997). In each perennial species experimental unit, 2 plants adjacent to the patch (Patch Treatment), 2 plants within the uniform area (Uniform Treatment), and 1 plant 35–45 cm away from both applications (Distant Treatment) were harvested. Tissues for the 2 individuals harvested from Patch and Uniform Treatments were not pooled for N analysis. Two or 3 plants were between the Distant Treatment plant and zeolite applications in each experimental unit (Fig. 1). Immediately following harvest, aboveground tissue for shrubs was partitioned into current year’s growth and prior years’ growth. Perennial grasses were separated into living tiller material and seed. For the annual grasses there was only leaf tissue.

Soil cores were taken from the interspace among plants in the Patch and Uniform Treatments and adjacent to the single distant plant to assess local root morphological parameters. Cores for shrubs and perennial grasses were 10 and 7.5 cm in diameter, respectively, slightly larger than the diameter of patch treatments. All soil cores were 20 cm deep. Roots were separated from the soil cores and washed free of sand and other debris. All plant material was processed immediately, frozen in liquid N$_2$ in the field, and kept on dry ice until processing.

Plant material was freeze-dried for 48 hours and then weighed. A subsample of roots was rehydrated overnight and root length for each sample was assessed using a Comair root length scanner (Melbourne, Australia). The current year’s leaf material was then finely ground. Total nitrogen content and $^{15}$N enrichment of leaf and root tissues were determined by a continuous flow direct combustion mass-spectrometer (ANCA 2020 system, Europa Scientific Inc., Cincinnati, OH). Nitrogen acquired
by plants from the experimental treatments was determined based on $^{15}$N enrichment in the leaf tissue in excess of background $^{15}$N (which we assumed to be constant at 0.36599 atomic %). Total N in the tissue was estimated based on total tissue mass and tissue concentration. Since zeolite was 2% enriched with $^{15}$N, we could calculate the proportion of total tissue N derived from our treatments. Mass of N acquired from treatments and translocated into current year’s growth was calculated as the proportion of treatment-derived N multiplied by total tissue N for each plant.

Statistical Analysis

Statistical analyses were performed at the species level to test for differences among N levels in treatment plants. Comparisons among species and growth forms were qualitative. We performed all analyses as a randomized block design with prior pulse treatments and distribution treatments (Patch, Uniform, and Distant) as fixed effects in the model. Tests for normality were performed on each response variable. Proportion data were transformed with a modified log transformation, and amounts of total N acquired were transformed with a square root transformation to approximate normality. ANOVA analyses were performed on transformed variables using a mixed-model analysis (Proc Mixed; SAS 1993) for the variables proportion of N acquired, mass of N acquired, and specific root length. P-values presented for explicit comparisons of means among treatments were Bonferroni adjusted. Means and standard errors for each variable were back-transformed for graphical presentation of the data. Statistical power was low for this experiment because of small sample sizes; therefore, we did not adhere to a strict interpretation of statistical significance for P-values ≤ 0.05. P-values are presented in the results, allowing readers to form their own conclusions.

There was high variability in the quantity of N acquired between the 2 Artemisia plants within each experimental unit of our Patch Treatments, and this contributed to large standard errors for this variable. We therefore defined a new variable, total N acquired by the 2 plants harvested for each treatment, by summing the mass of N acquired from the treatment applications for the 2 plants in the Patch and the 2 plants in the Uniform Treatments within each experimental unit. We analyzed this new variable in the same manner as described above.

Results

All 6 species acquired N from patch and uniform applications. The proportion of N in leaf tissue derived from zeolite applications was greater for annual species (Figs. 2a, b) than for perennials (Figs. 3a, b, 4a, b). The proportion was significantly greater for both species of annual plants adjacent to patches (0.20 and 0.28 for Aegilops and Bromus, respectively, $P = 0.0001$) than for these annuals within the uniform distribution (0.06 and 0.12, respectively, $P = 0.0001$, Figs. 2a, b). For the annual species, nitrogen acquired by plants adjacent to patches and within uniform applications was significantly greater than N acquired by Distant-Treatment plants ($P \leq 0.03$). A similar pattern was apparent for the mass of N procured. Aegilops and Bromus plants both acquired a greater quantity of N from localized patches than from the uniform application ($P = 0.0001$, Figs. 2c, d). Distant-Treatment plants did acquire N from the applications ($P = 0.001$), although significantly less than Patch- and Uniform-Treatment plants ($P = 0.0001$).

For the perennial grasses, Agropyron Patch-Treatment plants exhibited a significantly greater proportion of new N in leaf tissues and also a greater mass of acquired N than Uniform- and Distant-Treatment plants ($P = 0.002$ and $P = 0.001$, Figs. 3a, c, respectively). However, proportions of N in the leaf tissue and mass of N acquired from applications were not significantly different among the 3 treatments for Pseudoroegneria ($P = 0.25$ and $P > 0.26$, Figs. 3b, d, respectively). This suggests that zeolite-N applications were utilized with equal effectiveness by all Pseudoroegneria plants within the experimental unit regardless of their proximity to the application area.

The 2 shrubs also differed in their acquisition of N from the treatments. There were no differences in average mass of leaf N acquired by plants from the 3 treatments for Chrysothamnus ($P = 0.64$, Fig. 4d). Artemisia exhibited significant differences among treatments for both the proportion of N and the quantity of N derived from zeolite applications ($P = 0.05$ and $P = 0.06$, Figs. 4a, c, respectively). Patch-Treatment plants acquired a greater mean
quantity of N than did Uniform- or Distant-Treatment plants \((P = 0.12, \text{Fig. 4c})\). But Distant-Treatment plants for both shrub species had a significant quantity of application-derived N in their leaf tissues (Figs. 4c, d).

In the *Artemisia* data plant-to-plant variability within treatments was particularly large. Of the 2 plants harvested in Patch Treatments, one often acquired a much greater quantity of N than its neighbor. Analysis performed on total N acquired by the 2 plants revealed that *Artemisia* procured more N from the Patch than from the Uniform Treatment \((P = 0.005)\). Such high plant-to-plant variability within treatment pairs was not apparent for any other species; therefore, the same analysis was not warranted.

**Root Proliferation**

There were no differences in root mass within soil cores between the patch- or uniform-application areas and the unamended soil for any of the species. However, specific root length (SRL), root length per mass, did differ among treatments for one species. *Artemisia* was the only species that showed a significant increase in SRL in the Patch Treatment compared with the Distant \((P = 0.01)\) and Uniform Treatments \((P = 0.08, \text{Fig. 5})\).

**DISCUSSION**

At least one species of each growth form obtained a greater quantity of N from patches than from the uniform distribution: *Artemisia*, *Agropyron*, and both annual grass species (Figs. 2, 3, 4, 6). The shrub *Artemisia* and the tussock grass *Agropyron* both utilized the concentrated patch better than the uniform application (ratio of N acquired from patch:uniform > 2, Fig. 6), whereas the shrub *Chrysothamnus* and the tussock grass *Pseudoroegneria* utilized N from the patch and uniform applications equally (ratio of N acquired from patch:uniform ~1, Fig. 6). Thus, for the perennial species, effective acquisition of a localized source of N did not simply correspond with growth form (Campbell et al. 1991).
Root characteristics that provide the capacity to utilize spatially concentrated N patches may not necessarily be the same as those that enable effective utilization of an N pulse. Our study and that of Bilbrough and Caldwell (1997) conducted in the same sand-plot system provide the opportunity to compare the ability of these species to utilize patches and pulses of N. Five of 6 species we tested were common to both studies. Bilbrough and Caldwell (1997) used another aggressive exotic annual grass, *Teanatherum caput-medusae*, for their N-pulse study rather than *Aegilops cylindrica* as used in our study. Of the species tested for capacity to utilize N pulses here, all except *Chrysothamnus* exhibited a growth advantage when they received a 4-day concentrated pulse of N compared to a 10-week continuous-control N application; however, this varied in degree (Fig. 7). It appears from our results and those of Bilbrough and Caldwell (1997) that *Bromus* has the ability to effectively procure N from both concentrated pulses and patches. The 2 annual grasses not common to both studies, *Aegilops* and *Teanatherum*, behaved similarly to *Bromus* in effectively acquiring N from patches and pulses, respectively. These 3 exotic annual grasses have similar growth habit and phenology and are common aggressive weeds in agricultural fields and rangelands (Donald and Ogg 1991, Young 1992, Billings 1994). Their flexibility in effectively using patches and early pulses of N may contribute to their effectiveness in competing with Great Basin perennials.

Both perennial grasses appeared capable of translating N acquisition from spring pulses into a significant growth advantage (Fig. 7); however, these 2 grass species differed in their capacity to procure N from patches, as mentioned above (Fig. 6). *Agropyron* proved to be facile in exploiting patches while *Pseudoroegneria* did not respond to patches, but appeared to possess a more broadly distributed active root system (Fig. 3). It was better able to take advantage of N in distant patches than was *Agropyron*. Shrub species behaved differently in their ability to utilize both N pulses and patches. *Artemisia* responded well to both pulses and patches, while *Chrysothamnus* acquired little N from different spatial distributions and did not respond to pulses. In a similar vein, *Chrysothamnus* was not able to utilize soil moisture in upper soil layers derived from summer precipitation events (Ehleringer et al. 1991, Lin et al. 1996). In general, it appears this species is rather unresponsive to resource opportunities in upper soil layers. In contrast, *Artemisia* effectively utilized N pulses.
in the spring (Bilbrough and Caldwell 1997), and roots in upper soil layers remained responsive to pulses of moisture following periods of drought (Ehleringer et al. 1991, Lin et al. 1996). Based on its ability to obtain N effectively from all 3 distributions, Artemisia apparently has a broad distribution of roots capable of both coarse- and broad-scale nutrient foraging. Although the 2 shrub species occur in similar habitats and have a generally similar general growth form and phenological progression, they appear to be functionally different in use of shallow soil resources (Ehleringer et al. 1991, Donovan and Ehleringer 1994, Lin et al. 1996, Bilbrough and Caldwell 1997).

The ability to allocate a large proportion of actively absorbing roots in nutrient-rich soil volumes should be of advantage in acquiring N from such patches. Campbell et al. (1991) found that dominant species that captured the most mineral resources were those exhibiting high belowground potential growth rates. These fast-growing species were not, however, particularly precise in allocating roots to resource-rich patches. Grime (1994) maintained that slower-growing species with high precision in allocating roots to resource-rich patches would be subdominant species that retain their position in the community by their precision in root foraging. However, in our study relative growth rates of the species were not inversely correlated with precision in foraging. Fast-growing species in our study, such as the annual grasses and Artemisia, exhibited a high precision in foraging in that they clearly acquired the greatest proportion of N from enriched patches. Also, both perennial grasses in our study have similar growth rates (Caldwell et al. 1991, Bilbrough and Caldwell 1997) but differ strikingly in their precision of foraging.

Results from our large, outdoor sand-culture experiment allow us to identify potential patterns of spatial soil resource use by these co-occurring Great Basin species. We do not suggest that these are necessarily the tactics employed by these species in nature. However, our results do identify differences among species use of localized nutrient patches and precision of foraging. Differences in spatial use of mineral resources may contribute to spatial niche separation in Great Basin communities. However, temporal niche separation expressed in the ability of these species to utilize pulses of N through time is not necessarily correlated with spatial foraging patterns.

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