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Plant nitrogen capture in pulse-driven systems: interactions between root responses and soil processes

J. J. JAMES and J. H. RICHARDS
Department of Land, Air, and Water Resources, University of California, Davis, CA 95616-8627, USA

Summary

1 Soil resources are heterogeneously distributed in natural systems. In arid systems, for example, soil nitrogen (N) is often supplied in pulses. Mechanisms influencing the ability of a species to exploit N pulses through the season, however, are poorly understood despite the strong potential for temporal variation in N supply to impact growth, survival and competitive interactions in these systems.

2 We examined how plant physiological and soil processes interacted to influence the ability of two dominant perennial *Atriplex* species to capture N from pulses occurring at different times in the growing season.

3 ^{15}N-labelled pulses were applied to the two *Atriplex* species in early and mid spring. Sequential time harvests were used to quantify changes in plant ^{15}N content, root length, root length relative growth rate, root N inflow rates, microbial biomass ^{15}N, soil water content and soil inorganic ^{15}N pools. Path analysis and structural equation modelling were used to quantify the relative importance of different root parameters for plant N capture from pulses and to evaluate the degree to which these root responses interacted with soil processes to influence plant N capture.

4 Plant N capture was greatest when pulses coincided with high root length relative growth rates. Declining availability of total inorganic N through a pulse had a limited effect on N capture. This was partly because soil NH_4^+ pools were removed from the soil system four times faster than soil NO_3^- pools, allowing sufficient NO_3^- supply to roots, although total inorganic N pools declined. Microbial immobilization rates did not change significantly through a pulse and did not influence plant N capture during a pulse. Instead, plant N capture during a pulse was limited by total root length and uptake capacity per unit root length, which in turn was affected by plant N demand and soil water content.

5 Understanding interactions between root responses, soil processes and pulse timing provides insight into mechanisms underlying competitive interactions and diversity maintenance in pulse-driven systems.

Key-words: *Atriplex*, Great Basin, nitrogen isotopes, path analysis, resource pulses

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Introduction

Soil resource heterogeneity is a ubiquitous feature of natural systems (Stark 1994; Gross *et al*. 1995; Farley & Fitter 1999). Accordingly, much research has centred on understanding the mechanisms enabling plants to capture resources in variable soil environments and how these responses differ between species. The majority of this work, however, has focused on plant response to spatial heterogeneity, and substantially less is known about plant responses to temporal resource heterogeneity (Hodge 2004), despite the strong potential for such variation to impact growth, survival and competitive interactions in many systems.

For example, in arid and semi-arid ecosystems nitrogen (N) is limiting and mainly available to plants

Present address and correspondence: Jeremy J. James, USDA-Agricultural Research Service, Eastern Oregon Agricultural Research Center, 67826-AHwy 205, Burns, OR 97720 USA (tel. +1 541 573 8911; fax +1 541 573 3042; e-mail jeremy.james@oregonstate.edu).

in brief pulses following precipitation events. Following prolonged drought, water input stimulates N mineralization from accumulated organic mater (Austin *et al.* 2004), increases availability of N accumulated from dry deposition (Fenn *et al.* 2003) and facilitates N flow to roots (Nye & Tinker 1977). The duration of a pulse is limited, however, by plant N uptake, microbial immobilization and soil dry-down (Nye & Tinker 1977; Cui & Caldwell 1997; Hodge *et al.* 1999). Consequently, plant growth and survival in these environments should be closely linked to the ability of a species to capture N rapidly during brief periods of high N availability.

In addition to the short duration of resource pulses, the seasonal timing of precipitation events and subsequent N pulses in arid systems can have a large random component (Noy-Meir 1973). A growing body of research demonstrates that the relative abilities of coexisting species to capture N from pulses can depend on seasonal timing of pulses, with some species capturing more N from pulses occurring early in the growing season and others capturing more N from pulses occurring later in the growing season (Bilbrough & Caldwell 1997; Gebauer & Ehleringer 2000; James & Richards 2005). This suggests that timing of N pulses could differentially affect growth, survival and competitive ability of coexisting species in arid systems.

Despite the clear potential for variation in the seasonal timing of N pulses to influence ecological processes, little is know about what plant and soil processes influence the magnitude of plant N capture from pulses. On the most basic level, simulation models predict that plant N capture during a pulse will be related to the length of existing roots, rate of new root growth, N uptake rate per unit root length and N supply to the root surface (Barber 1995). Additionally, agronomic models predict that the timing of N inputs in relation to relative growth rate will influence the ability of a plant to exploit a pulse (Jeuffroy *et al.* 2002). New root growth rates are high when whole-plant relative growth rate is greatest, thus increasing the volume of soil explored (Aanderud *et al.* 2003). Additionally, uptake rates per unit root length may be elevated during periods of high growth owing to greater plant N demand (Schenk 1996) and as a result of production of new roots with high uptake capacity (Volder *et al.* 2005). Furthermore, microbial biomass and community composition can change rapidly following water inputs (Austin *et al.* 2004; Saetre & Stark 2004) and it is widely expected that microbes will compete with plants for N during a pulse (Hodge *et al.* 2000; Ivans *et al.* 2003). Little is known, however, about immobilization patterns following N pulses in deserts and the potential impact these could have on plant N capture. Although a number of plant and soil processes can directly affect plant N capture, it is likely that interactions among multiple factors ultimately determine plant response to an N pulse.

The broad objective of this field study was to evaluate how plant physiological and soil processes interact to influence the ability of two dominant perennial *Atriplex* species to capture N from pulses occurring at different times in the growing season. We first compared the ability of two *Atriplex* species to exploit pulses of N at different times in the growing season. Using sequential plot harvests, we quantified short-term (hours–days) and long-term (weeks) changes in plant N capture, root growth, root N inflow rates, soil inorganic N pools and microbial biomass N following ^{15}N-labelled pulses. Second, using path analysis and structural equation modelling, we quantified the relative importance of different root parameters for plant N capture from pulses and evaluated the degree to which these root responses interacted with changes in soil water content, soil N concentration and microbial N immobilization to influence plant N capture. Based on previously developed agronomic models of crop growth rate and N uptake, and mathematical models of soil nutrient supply and uptake by roots, we hypothesized that:

1. Both the amount of root length present and N inflow rate per unit root length would be important mechanisms for N capture during a pulse. Inflow rates, however, would be relatively more important for N capture immediately following a pulse when soil water content and N concentration are high, while root length density would be more important for N capture later in a pulse as soil water and N were depleted.

2. Root length and N inflow rates, and consequently plant N capture from a pulse, would be affected by the growth rate of the root system; higher growth rates would increase rooting density but also should increase N inflow rates through greater plant N demand.

3. The effect of microbial N immobilization on plant N capture would vary through a pulse; because of high growth rates of microbial biomass but rapid turnover times, immobilization would be greatest immediately following a pulse but would then decline through the pulse.

Materials and methods

STUDY SPECIES, STUDY SITE AND COMMON GARDEN INSTALLATION

The experiment was conducted in a saltbrush scrub community in the Owens Valley, California, USA, which is located on the south-western edge of the Great Basin (36°21.5′ N, 118° W; 1085–1087 m elevation). Vegetation at the study site is co-dominated by the two *Atriplex* study species. *Atriplex confertifolia* S. Watson (Torrey & Frémont) is widely distributed throughout the cold desert communities of the Great Basin and Colorado Plateau while *A. parryi* S. Watson is regionally dominant throughout the warmer Mojave. Both species are C4, winter deciduous, halophytic shrubs and have very similar canopy morphology, litter chemistry and root structure. These chenopod shrubs are non-mycorrhizal. Measurements of cumulative stem length of naturally

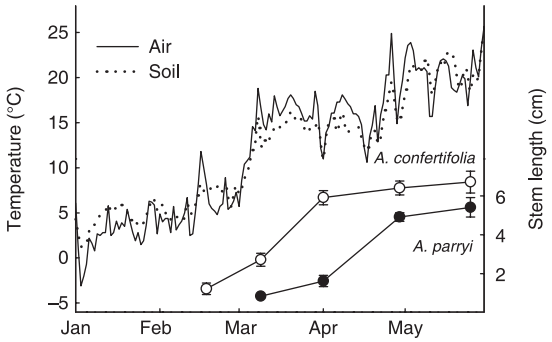

Fig. 1 Daily mean air (1.5 m height) and soil (0.15 m depth) temperature between January and June 2004, and pattern of seasonal stem growth (mean ± SE, $n = 5$ per species) of naturally established plants of the two study species. Temperature data are from the Owens Lake North CIMIS weather station (http://wwwcimis.water.ca.gov/cimis/data.jsp) approximately 15 km north-east of the study site.

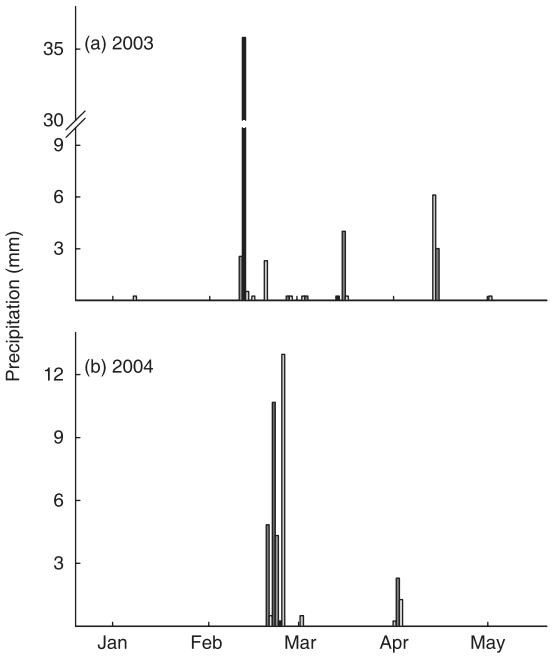

Fig. 2 Distribution of daily precipitation events (mm) between January and June during the (a) 2003 and (b) 2004 growing seasons recorded at the Owens Lake North CIMIS (see Fig. 1) weather station.

established shrubs in 2004 (mean ± SE, $n = 6$) demonstrate that in this ecotonal plant community between the Great Basin and Mojave, the cold desert species, *A. confertifolia*, initiates spring shoot growth when air and soil temperatures are relatively low, achieving a high growth rate much earlier in the growing season than *A. parryi* (Fig. 1). *Atriplex parryi* initiates growth approximately 1 month later in the spring and also achieves maximal growth rate much later in the growing season than *A. confertifolia*.

Soils at the site range from 69% to 94% sand (0.05–2 mm) (Dahlgren *et al*. 1997). Annual precipitation at the site averages 150 mm, with the majority of precipitation falling in winter and spring as rain. There is, however, substantial year-to-year variation in the amount and timing of precipitation, and typical of arid systems these inputs tend to be clustered into a few discrete events (Fig. 2). Available soil N at our study site limits plant growth and is very low throughout most the year (*c*. 1–3 mg kg^{-1}) (James *et al*. 2005) but can increase following precipitation inputs, to levels ranging from 8 mg kg^{-1} to more than 15 mg kg^{-1}, mainly as NO_3^- (Z. Aanderud, J. James & J. Richards, unpublished data).

A common garden was established by clearing a 25 × 20 m area within the existing shrub community. In winter 2003, 192 plots spaced 0.5 m apart were installed in the garden. For each plot a hole was augered and lined with a large plastic barrier (30 cm diameter × 30 cm deep). The bottom of the barrier was perforated with holes allowing roots to grow vertically and water to drain. Using these barriers allowed the upper 30 cm of the root system to be removed intact and quantified. The barriers also prevented the lateral movement of added ^{15}N so that a mass balance of ^{15}N could be determined for each plot. The sandy soil excavated from each plot was sifted with a 5-mm-mesh sieve to remove large pieces of plant material and stones and then used to refill the holes to a depth of 5 cm below the soil surface. To reduce heterogeneity in organic matter content between plots, the remaining 5 cm was filled with surface soil collected under mature canopies of the two *Atriplex* species growing at the site. Collected soil was homogenized for each block and used for the 5-cm surface soil layer of each plot. Three-month-old seedlings of each species, raised from seed collected at the site, were planted in the 192 plots; half the plots (96) were randomly assigned to receive an *A. confertifolia* seedling and another 96 plots were randomly assigned to receive an *A. parryi* seedling. Seedlings that died within a month of transplanting were replaced. After seedlings were established plots were watered heavily several times to leach NO_3^- out of the root zone. Seedlings were allowed to grow for 1 year before treatments were applied.

EXPERIMENTAL DESIGN AND ^{15}N PULSE APPLICATION

In winter 2004, seedlings of each species were assigned, based on size, to one of eight blocks. The 12 seedlings of each species in each block were then randomly assigned to receive a ^{15}N pulse in early spring (28 February) or mid spring (21 April) and to a harvest time (see below). Experimental N pulses were applied as a simulated 10-mm rain event labelled with 120 mg N as 10 at.% $^{15}NH_4{}^{15}NO_3$. This rate was expected to produce an N pulse close to 10 mg kg^{-1} (16.9 kg ha^{-1}) based on the inorganic N concentrations in the soil after heavy leaching, mass of N added to the volume of soil in each plot and soil bulk density. This rate is within the range of the amount of inorganic N available during natural pulses in this system. During the early spring pulse, five

harvests were made and sampling took place at 1, 2, 12, 21 and 28 days. The mid spring harvests were conducted at 0.3 (i.e. 8 h), 0.5, 1, 2, 8 and 16 days. Standard statistical comparisons with ANOVA, consequently, were limited to species and harvest time effects within a pulse. Path analysis and structural equation modelling, however, can be used to analyse the interrelationships among the response variables despite the different sampling intervals (see Statistical analysis and path model development section below).

HARVEST MEASUREMENTS

Soil N pools and volumetric water content

At each harvest time, three, 5.1-cm-diameter soil cores were collected from the 0–30-cm-depth layer in each plot. Root length in these cores was not measured because of the need for immediate processing to quantify inorganic and microbial N pools. These three cores were homogenized and two 70-g subsamples were placed in plastic bottles. One subsample (control) was immediately extracted with 0.2 M K_2SO_4 while 1 mL of liquid chloroform was added to the other subsample (fumigated) and the lid closed tightly to make an airtight seal. After 24 h exposure to chloroform the sample was aired for 1 h and then extracted. Preliminary studies demonstrated N recovered from this liquid fumigation technique did not differ from N recovered from vacuum fumigation for this soil ($P = 0.323$). Inorganic N was measured in the control sample and total dissolved nitrogen (TDN) was measured in control and fumigated samples following Forster (1995) for NH_4^+ (using the Berthelot reaction), following Miranda *et al.* (2001) for NO_3^- (using vanadium to reduce nitrate to nitrite) and following Cabrera & Beare (1993) for TDN (using persulphate oxidation). Microbial ^{15}N was estimated as chloroform-labile ^{15}N [$(TDN_{fum}) - (TDN_{cont})$]. Extracts for ^{15}N analysis were prepared by diffusion following Stark & Hart (1996). ^{15}N enrichment was measured by continuous flow direct combustion and mass spectrometry at the University of California Davis Stable Isotope Facility (UCD-SIF). Volumetric soil water content was quantified using standard gravimetric techniques and corrected for soil bulk density.

Plant N pools and root measurements

At each harvest the entire plant canopy was cut at the soil surface and divided into leaves and stems. The plastic barrier was excavated intact, sliced open and the entire root system was recovered by gentle washing. The root system was separated into taproot, woody roots and non-woody roots. Non-woody lateral roots generally consisted of 2–3 branches. Approximately 44% of the lateral root length had a diameter of 0.1–0.5 mm, 40% had a diameter of 0.5–1 mm and 16% had a diameter of 1–2 mm. This harvest and sampling approach did not allow us to quantify potential differences in physiology between non-woody roots of different age or branch order and probably underrepresented the smallest lateral roots (Pregitzer *et al.* 2002; Volder *et al.* 2005). In addition, non-woody root length may have been underestimated if new root production and subsequent decomposition occurred in a time frame shorter than our harvest intervals (Stevens *et al.* 2002). Such root turnover is not likely to affect results of the short-term harvests (0.3–2 days), but may have a small influence on the later harvests.

Non-woody roots were stored in 5% ethanol at 4 °C until scanned for length with WinRHIZO (Regent Instruments Inc., Saint-Foy, Canada) to determine root length density (RLD; km m^{-3}) (Bouma *et al.* 2000). After scanning, roots were triple rinsed with distilled water, dried at 65 °C, weighed to determine specific root length (SRL; km kg^{-1}) and then finely ground. Root N concentration and ^{15}N enrichment were measured by continuous flow direct combustion and mass spectrometry. A similar processing and analysis procedure was used to determine leaf N concentration and ^{15}N enrichment. ^{15}N content in leaves and roots was determined using a mass balance equation following Nadelhoffer & Fry (1994).

Growth rates and root ^{15}N inflow rates

Root length relative growth rate (RGR) was calculated per block as: $RGR = [\ln(L_f) - \ln(L_i)]/(t_f - t_i)$ where L_f and L_i are root length of all non-woody roots harvested at the beginning (L_i) and end (L_f) of each pulse within each block. To integrate ^{15}N inflow rates from measurements spanning several days, we followed the calculations of Drew & Saker (1975) where $d^{15}N/dt$ (nmol ^{15}N m^{-1} root day^{-1}) $= [(N_2 - N_1)/(t_2 - t_1)] \times [(\ln(L_2) - \ln(L_1))/(L_2 - L_1)]$. Here, N is plant ^{15}N content (mg) of two plants (N_1 and N_2) harvested at different times (t_1 and t_2; days) within each block and L is total length of all non-woody roots (m) of the same two plants (L_1 and L_2) harvested at different times (t_1 and t_2).

STATISTICAL ANALYSIS AND PATH MODEL DEVELOPMENT

Effects of species and harvest time for plant ^{15}N capture, root responses and soil N pools were analysed separately for the early and mid spring pulse with ANOVA. Assumptions of ANOVA were evaluated using the Shapiro–Wilk test for normality and Levene's test for homogeneity of variance. When these assumptions were violated, data were weighted by the inverse of the variance (Neter *et al.* 1990). Because of unequal sample size due to plant death (12 out of 192 seedlings), ANOVA was run as an unbalanced design and factor effects were evaluated using Type III sums of squares. Linear contrasts were used to compare treatments.

We used path analysis to investigate the processes underlying our experimental data of plant ^{15}N capture (Mitchell 1992). Path analysis does not allow determination

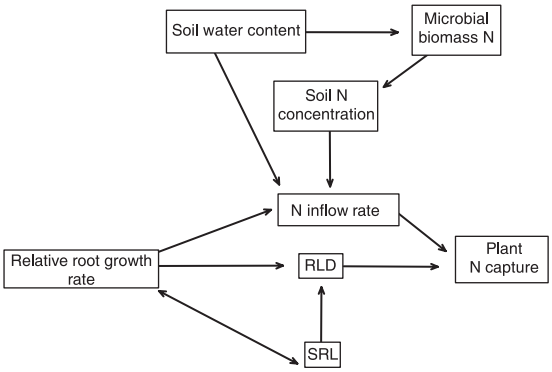

Fig. 3 Hypothesized causal relationships (path model) of direct and indirect effects of root length relative growth rate, root length density (RLD), specific root length (SRL), N inflow rate, soil N concentration, soil water content and microbial N immobilization on plant N capture. Single-headed arrows indicate a direct causal relationship and double-headed arrows indicate unanalysed correlations.

of causation among the variables. Theory and previous experimental results, however, can be used to construct a conceptual model (path diagram) of expected causal and non-causal interrelationships. Our path model (Fig. 3) integrates previously developed root models of nutrient flow to roots and plant nutrient capture in relation to root length, growth rate, physiology and morphology (Barber 1995) with agronomic models and empirical work describing growth-rate-regulated nutrient uptake. This model also includes the expectation that microbial communities will compete directly with plants for soil N during a pulse.

Plant ^{15}N capture from a pulse was expected to be directly affected by the amount of root length and the inflow rate per unit root length (Fig. 3) (Barber 1995). Based on the experimental set-up, we assumed that soil volume was constant. Accordingly, root length was measured as RLD (km root m^{-3} soil). In our model, RLD could increase during a pulse due to the rate that new root length is added to the root system (root length Rgr; m m^{-1} day). RLD also could increase further if thinner roots were produced (smaller radius) which have greater SRL (m root g^{-1} root). We assumed that changes in growth rate were not causally linked to changes in SRL but were instead correlated with root age. We did not measure other changes in architecture that also could change RLD, such as branching frequency and angle (Fitter 1994). We assumed that ^{15}N inflow rate per unit root length followed Michaelis–Menten kinetics, depending on the ^{15}N concentration at the root surface, maximum uptake capacity (I_{max}) and ion affinity (K_m) (Barber 1995). We expected that ^{15}N inflow rates would increase with root length growth rate because of higher plant N demand (Schenk 1996; Jeuffroy *et al*. 2002). Additionally, inflow rates also could increase with root length growth rate if younger roots with higher N uptake capacity are produced (Volder *et al*. 2005). We assumed that the bulk soil concentration of available ^{15}N ($^{15}NH_4^+ + {}^{15}NO_3^-$) would affect ^{15}N concentration at the root surface and, consequently, ^{15}N inflow rate. Likewise, we assumed that volumetric soil water content could directly affect ^{15}N inflow rate by altering the supply rate of ^{15}N to the root surface due to effects on mass flow and diffusion (Nye & Tinker 1977). Also included is the potential for soil dry-down to decrease root N uptake capacity (BassiriRad & Caldwell 1992; Matzner & Richards 1996). Although a similar effect of soil water on root growth could be expected, we did not expect to be able to detect these effects within the relatively short sampling period. Microbial communities, however, have been shown to respond rapidly to pulsed water inputs (Austin *et al*. 2004), so we predicted that soil water content would affect the amount of ^{15}N immobilized and that this would alter bulk soil ^{15}N, with improved water status increasing net immobilization.

Prior to analysis, N inflow rate and plant N capture data were log transformed to normalize data distributions and linearize relationships with other variables. Multicollinearity among predictor variables was screened by calculating variance inflation factors (VIFs). In all cases, VIFs for the predictor variables were less than 3; therefore, it is unlikely that multicollinearity had a strong impact on our results (Myers 1990). Path coefficients, their significance level and the fit of the structural model to the data were evaluated using structural equation modelling with the CALIS procedure in SAS. The total correlations between independent and dependent variables were decomposed into direct and indirect effects with direct effects indicated by single-headed arrows in the path diagram (Fig. 3). Indirect effects occurred when a variable was linked to a dependent variable through one or more intermediary variables. The path coefficients correspond to the standardized partial regression coefficients. We used CALIS to compare the predicted covariance matrix based on the specified model with the observed covariance structure from our data to evaluate the fit of the model. We used the Goodness of Fit Index (GFI), χ^2 statistic, and Normed Fit Index (NFI) as indices of model fit. A statistically significant χ^2 suggests a poor fit while values of GFI and NFI > 0.9 are generally considered as an indication of good agreement between the matrices (Hatcher 1994; Schumacker & Lomax 2004).

Results

PLANT N CAPTURE

Atriplex confertifolia captured more ^{15}N than *A. parryi* following early and mid spring N pulses ($P < 0.001$). Both species, however, acquired more total ^{15}N from the mid spring pulse than from the early spring pulses (Fig. 4). Nitrogen capture by *A. confertifolia* and *A. parryi* increased 1.9- and 5.7-fold, respectively, during the mid spring pulse relative to the early spring pulse. Likewise, while both species were able to capture

Table 1 Volumetric soil water content and percentage of ^{15}N recovered in plant (leaf + non-woody roots), microbe and soil N ($^{15}NO_3^- + {}^{15}NH_4^+$) pools in the plots for the two study species following early and mid spring N pulses (mean ± SE, n = 4–8)

Harvest (days)	Water content (%)	^{15}N recovered (%)			
		Plant	Microbe	Soil	Total
Early spring pulse					
Atriplex confertifolia					
1	15.5 ± 1.2	0.3 ± 0.1	4.9 ± 0.9	69.0 ± 6.9	74.3 ± 7.4
2	13.6 ± 0.7	0.3 ± 0.1	6.8 ± 1.0	70.3 ± 2.6	77.2 ± 2.0
12	8.15 ± 0.6	2.0 ± 0.3	7.3 ± 0.9	45.3 ± 3.3	54.4 ± 3.1
21	8.48 ± 0.6	7.4 ± 1.6	6.0 ± 0.3	47.9 ± 4.3	61.3 ± 4.7
28	5.8 ± 0.4	9.1 ± 1.7	5.9 ± 0.5	42.8 ± 5.7	63.5 ± 6.3
Atriplex parryi					
1	14.5 ± 0.9	< 0.1	5.3 ± 1.2	71.0 ± 6.7	76.3 ± 6.8
2	15.9 ± 1.3	< 0.1	6.1 ± 1.1	69.2 ± 5.4	77.3 ± 5.7
12	8.4 ± 0.6	0.2 ± 0.1	8.4 ± 1.1	68.4 ± 7.2	77.0 ± 7.9
21	7.0 ± 0.3	0.7 ± 0.2	6.0 ± 0.4	58.0 ± 8.2	51.0 ± 11.8
28	7.6 ± 0.4	1.7 ± 0.7	8.8 ± 0.6	66.4 ± 5.5	76.2 ± 4.0
Mid spring pulse					
Atriplex confertifolia					
0.3	13.4 ± 0.8	3.8 ± 0.8	8.4 ± 0.6	62.0 ± 3.1	73.3 ± 3.4
0.5	13.4 ± 0.7	3.1 ± 0.4	8.3 ± 1.2	43.1 ± 6.1	54.5 ± 6.1
1	10.5 ± 0.6	5.3 ± 0.8	7.2 ± 1.9	45.4 ± 16.0	54.0. ± 4.0
2	10.0 ± 0.6	6.7 ± 1.3	6.9 ± 1.3	39.3 ± 4.8	52.3 ± 7.3
8	3.9 ± 0.6	11.6 ± 1.6	7.2 ± 1.7	33.5 ± 5.6	50.9 ± 9.2
16	3.5 ± 0.7	15.4 ± 2.2	6.3 ± 1.8	41.8 ± 6.0	62.2 ± 6.8
Atriplex parryi					
0.3	14.3 ± 0.6	0.3 ± 0.1	8.3 ± 0.7	65.9 ± 12.0	73.9 ± 9.6
0.5	13.3 ± 1.0	0.3 ± 0.0	6.5 ± 1.1	58.9 ± 8.4	67.6 ± 8.6
1	13.8 ± 0.5	1.9 ± 0.3	7.4 ± 1.2	54.8 ± 11.0	64.7 ± 9.1
2	11.7 ± 1.1	3.3 ± 1.0	9.8 ± 1.5	66.4 ± 7.4	81.1 ± 7.5
8	6.8 ± 1.0	7.7 ± 1.4	6.1 ± 1.8	48.1 ± 3.4	61.1 ± 2.9
16	4.9 ± 0.7	10.8 ± 1.4	6.3 ± 1.7	51.9 ± 9.1	69.9 ± 11.0

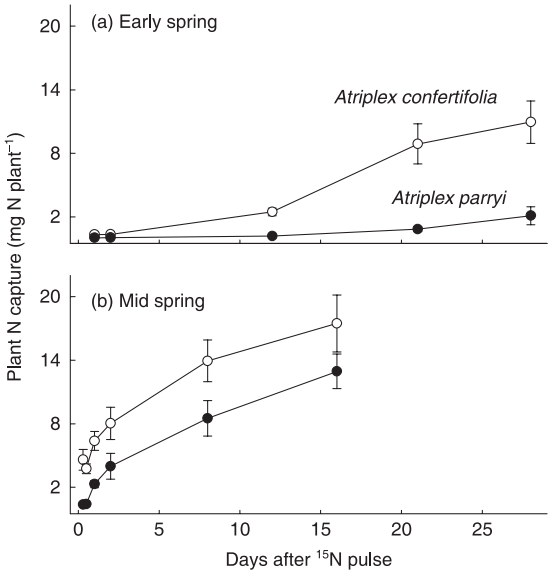

Fig. 4 N capture by the two study species following experimental ^{15}N pulses in (a) early spring and (b) mid spring (mean ± SE, n = 4–8 for each harvest). Note that spacing between harvest times differed between the early and mid spring pulses as described.

a significant amount of ^{15}N within 1 day after early and mid spring N pulses (t-test comparing plant ^{15}N content before and 1 day after a pulse, P = 0.046 and P < 0.001 for *A. parryi* and P = 0.005 and P < 0.001 for *A. confertifolia*) the amount of ^{15}N captured within 1 day was greater following the mid spring N pulse than the early spring N pulse for both species. These temporal patterns of plant ^{15}N capture following early and mid spring N pulses were reflected in percentage recovery of ^{15}N in the plant biomass (leaves + non-woody roots) (Table 1). Across species, recovery of ^{15}N in plant biomass averaged 5.3% following an early spring pulse and increased up to 13% following a mid spring pulse. For both species the majority of ^{15}N (85%) was allocated to leaves vs. non-woody roots (data not shown). Recovery of ^{15}N in stem and woody root tissue, analysed on a subset of samples, was low (0.3–1.1 mg ^{15}N per plant), increasing total recovery by around 2%.

ROOT RESPONSES

For both species root length RGR was greater during the mid spring pulse than during the early spring pulse (P < 0.05) (Fig. 5). Whereas *A. confertifolia* had greater root length RGR than *A. parryi* during the early spring pulse (P = 0.034), root length RGR did not differ between the two study species during the mid spring pulse (P = 0.381). SRL did not differ between the study species during either the early or the mid spring pulses (species × harvest time × pulse, P = 0.311). SRL for *A. parryi* was 56 ± 5.0 km kg^{-1} and 49 ± 2.8 km kg^{-1} for *A. confertifolia* (mean ± SE). RLD of *A. confertifolia*

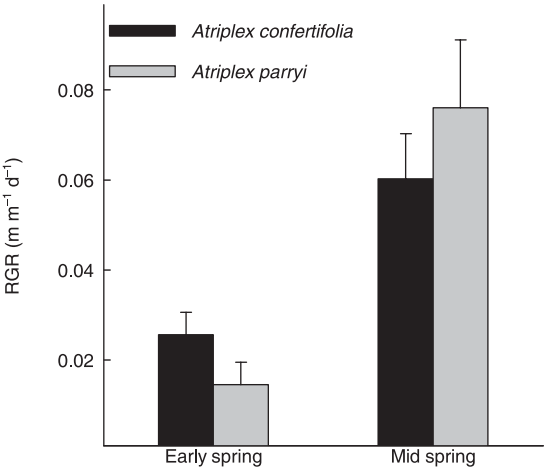

Fig. 5 Root length relative growth rates (RGR) for the two study species averaged across the early and mid spring N pulses. Calculations of RGR were made per block using total non-woody root length of the experimental plants harvested at the beginning and end of each pulse (mean ± SE, $n = 8$).

was significantly greater than *A. parryi* during the early and mid spring N pulses ($P < 0.0001$; Fig. 6a,b). RLD of both study species increased through both pulses ($P < 0.05$) and was greater during the mid spring than the early spring pulse ($P < 0.05$). For both study species, ^{15}N inflow rates were highest during the mid spring pulse (Fig. 6c,d). ^{15}N inflow rate per unit root length was not significantly different between the study species during harvest days 1, 2 and 12 of the early spring pulse ($P > 0.1$). ^{15}N inflow rate for *A. confertifolia* during harvest days 21 and 28 was on average 2.8-fold higher than for *A. parryi*, although this difference was only marginally significant ($P = 0.058$). *Atriplex confertifolia* N inflow rates were 30% higher than those of *A. parryi* through the first 2 days of the mid spring N pulse but inflow rates between the study species were similar 8 and 16 days following the pulse.

SOIL N POOLS AND ^{15}N RECOVERY

Leaching plots repeatedly prior to planting and during the first growing season resulted in very low soil inorganic N concentration prior to initiating experimental N pulses (Fig. 7). Application of the experimental N pulses increased soil NO_3 six-fold and soil NH_4^+ four-fold. Although we applied equal amounts of NO_3^--N and NH_4^+-N, by the first harvest (1 day in early spring and 0.3 days in mid spring) soil NH_4^+ concentration was significantly lower than soil NO_3^-. Assuming first-order kinetics, the half-life ($t_{1/2}$) of NH_4^+ following the early spring pulse was 6.9 days whereas the $t_{1/2}$ for soil NO_3^- was greater than 30 days. Following the mid spring pulse, the $t_{1/2}$ of NH_4^+ and NO_3^- were 1.3 and 4.9 days, respectively.

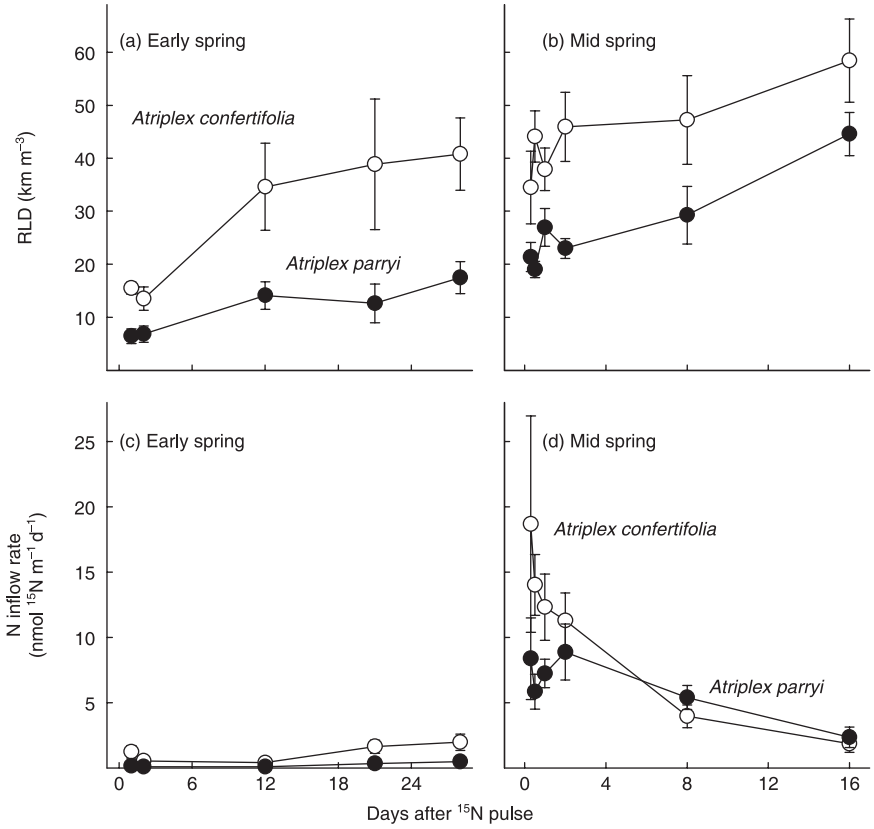

Fig. 6 Root length density (RLD) (a, b) and root N inflow rates (c, d) of the two study species during the early spring and mid spring ^{15}N pulses (mean ± SE, $n = 4$–8 for each harvest). Root N inflow rates were calculated using root length and ^{15}N content of experimental plants harvested at different times within each block.

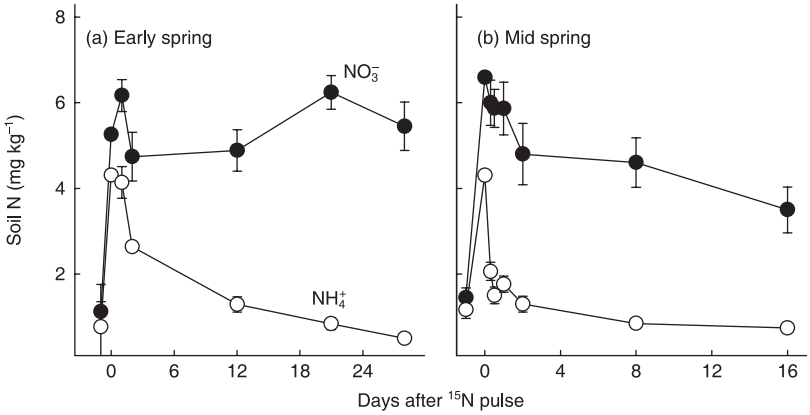

Fig. 7 Extractable soil NO_3^- and NH_4^+ following (a) early spring and (b) mid spring experimental N pulses. Data for both study species were pooled for each harvest time (mean ± SE, n = 8–16 for each harvest). Percentage of extractable soil ^{15}N ($^{15}NO_3^- + {}^{15}NH_4^+$) recovered in the study plots for each species is shown in Table 1.

Total ^{15}N recovery in the experimental plots averaged 75% immediately following a pulse, but recovery declined about 10% through both the early and the mid spring pulses (Table 1). The majority of ^{15}N was recovered in the extractable soil ^{15}N pool ($^{15}NH_4^+ + {}^{15}NO_3^-$) regardless of pulse timing or species. Extractable soil ^{15}N declined significantly following a pulse ($P < 0.05$), except for the early spring *A. parryi* plots in which there were changes in the extractable soil ^{15}N pool among harvest times but no significant decline through time ($P = 0.332$). Microbial biomass N represents a significant pool of ^{15}N and was typically larger than or comparable with the plant ^{15}N pool several days following a pulse. Although the microbial ^{15}N pools on average were larger during the mid spring pulse than during the early spring pulse, this difference was small (*c.* 20%) and microbial ^{15}N pools did not change significantly during the duration of either experimental N pulse ($P > 0.05$).

PATH ANALYSIS

The set of model fit indices indicated that the model fit the data to a reasonable level but that model modifications could significantly improve the fit between the sample variance–covariance matrix and the predicted variance–covariance matrix. The fit indices (GFI, χ^2, NFI) for the model describing short-term interactions (0.3–2 days) between root and soil parameters among the variables were 0.086, 61 (d.f. = 15, $P < 0.001$) and 0.83, respectively. Indices for the model describing long-term interactions (8–28 days) were 0.80, 56 (d.f. = 15, $P < 0.001$) and 0.68, respectively. When paths were constrained to include only root responses, the model fit improved substantially for both models: GFI for both models was > 0.98, χ^2 was not significant ($P > 0.45$) and NFI was > 0.95. This indicates that additional paths or unmeasured parameters affecting our soil variables may be contributing to the poor fit of the full model. Although we address some of these aspects in the discussion, we did not constrain our full model when calculating the strength and significance of path coefficients as we proposed this model a priori (Petraitis *et al*. 1996).

Nevertheless, the parameters we did include in the model explained 83% and 53% of the variation in plant ^{15}N capture over the short (Fig. 8a) and long term (Fig. 8b), respectively. RLD and ^{15}N inflow rate had strong and significant paths to plant ^{15}N capture both immediately following a pulse and over the long term. However, the path for ^{15}N inflow rate was relatively stronger than the path for RLD immediately following a pulse, although this strength difference lessened over the long term. The direct paths from root length RGR to RLD and ^{15}N inflow rate were strong and significant during the short and long term. The indirect path from root length RGR to plant ^{15}N capture was 0.63 over the short term and 0.53 over the long term. Over the short term, none of the soil parameters (water, inorganic N or microbial biomass N; Table 1) had a significant direct or indirect path to ^{15}N inflow rate, and consequently had minimal effects on plant ^{15}N capture. Over the long term, volumetric soil water content had a strong and significant path to ^{15}N inflow rate and an indirect path to plant ^{15}N capture of 0.28. Other soil parameters had minimal direct or indirect paths to ^{15}N inflow rate. Overall, the unexplained variability of the response variables (U) tended to be greatest for the soil parameters.

Discussion

THE IMPORTANCE OF PULSE TIMING FOR PLANT N CAPTURE

Although the importance of nutrient pulses for plant nutrient budgets has been extensively demonstrated (Jonasson & Chapin 1991; Fransen *et al*. 1998; Bowman & Bilbrough 2001), few studies have evaluated how seasonal timing of nutrient pulses impacts plant nutrient capture and growth. In this study, both *A. confertifolia* and *A. parryi* captured more N from the mid spring

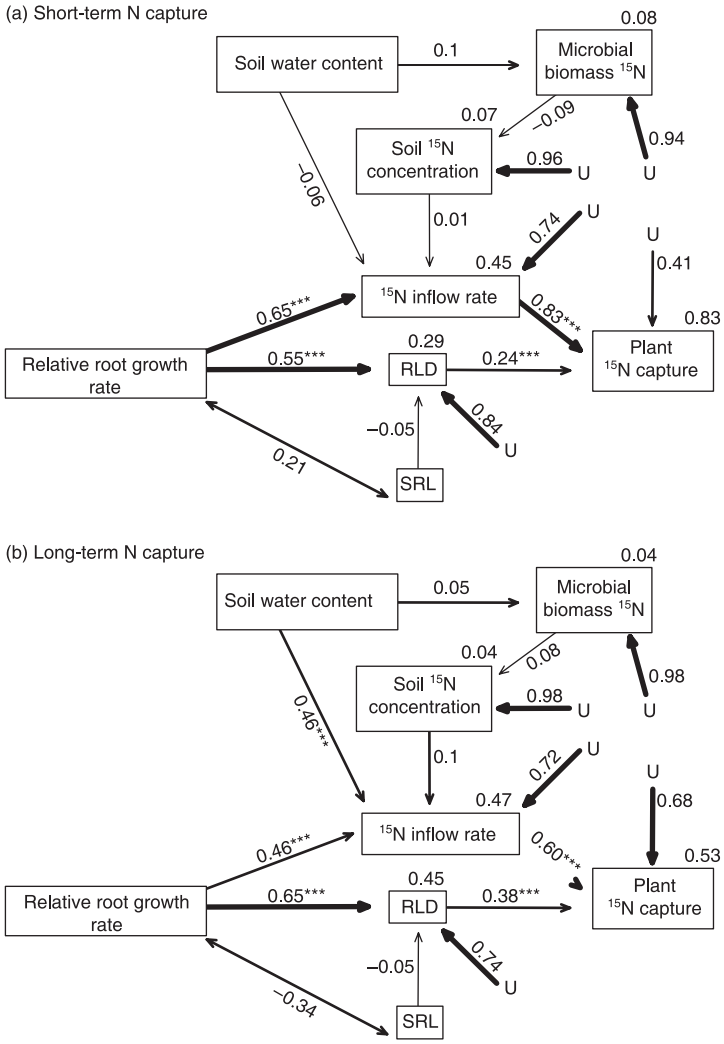

Fig. 8 Path model of hypothesized causal relationships among root and soil parameters predicted to influence plant N capture from pulses. RLD is root length density and SRL is specific root length. Parameters were quantified through sequential time harvests following experimental ^{15}N-labelled pulses. Path model (a) describes the strength and significance of the causal relationships for short-term (0.3–2 days) N capture and model (b) describes the relationships for long-term (8–28 days) N capture. Single-headed arrows indicate a hypothesized direct causal relationship and double-headed arrows indicate unanalysed correlations. For each effect path, standardized path coefficients are given and the magnitude of the effect is also indicated by the thickness of the line. Significance of the path coefficients is indicated as: $*P < 0.05$, $**P < 0.01$, $***P < 0.0001$. The residual variables (U) indicate the contribution of all unmeasured or unknown factors to the response variables. Numbers in bold are the total variance explained (r^2) for each dependent variable.

pulse than from the early spring pulse (Fig. 4). Although *A. confertifolia* captured more N than *A. parryi* from both pulses, the proportional increase in N capture from the early spring pulse to the mid spring pulse was greater for *A. parryi* than for *A. confertifolia*. The importance of pulse timing for plant N capture is consistent with previous observations in cold deserts. In the Great Basin, growth of tussock grasses and annual grasses was greatest when N pulses occurred in early spring, whereas growth of sagebrush was greatest when N pulses occurred in mid spring (Bilbrough & Caldwell 1997). Likewise, on the Colorado Plateau, N capture by the perennial shrubs *Coleogyne ramosissima* and *Ephedra viridis* was greatest when pulses occurred early in the growing season, while N capture by the herbaceous perennial *Cryptantha flava* was greatest when pulses occurred later in the growing season (Gebauer & Ehleringer 2000).

In addition to demonstrating that the magnitude of N capture can depend on pulse timing, our results also show that the rate of pulse exploitation can vary with pulse timing. For example, the proportion of total N captured within 1 day following the early spring pulse was 2% for *A. confertifolia* and less than 1% for *A. parryi.* By contrast, the proportion of total N captured within 1 day following the mid spring pulse was over 45% for *A. confertifolia* and over 40% for *A. parryi*. Thus, our observations contribute to the emerging view that the seasonal timing of N pulses probably has significant ecological consequences in arid systems; not only does the rate and total amount of N capture depend on the timing of a pulse but it

seems that in a number of desert systems, coexisting species may differ in relative abilities to capture N from pulses depending on when the pulse occurs in the season. Path analysis provides insight into interactions among the major mechanisms driving these plant responses.

INTERACTING ROOT AND SOIL PROCESSES INFLUENCE N CAPTURE FROM PULSES

RLD and N inflow rate were both strong drivers of short-term and long-term N capture from a pulse (Fig. 8a,b). Because soil volume was constant in our experiment, higher root length RGR increased RLD. This is consistent with the model simulations of Barber (1995), which predicted that both NO_3^- and NH_4^+ uptake would increase linearly with root length growth rate and be affected minimally as a result of inter-root competition at high RLD. Sensitivity analysis of this same model also predicted that increased N uptake rates would be most important for NO_3^- capture but less important for NH_4^+ because of low soil diffusion rates. This, coupled with the rapid decline in soil NH_4^+ in our study (Fig. 7), suggests that the increased plant N capture with higher inflow rates was mainly due to increased NO_3^- inflow rate.

Whereas N inflow rate always had the strongest path to plant N capture, variation in N capture appeared to be influenced more by variation in N flow rates than by variation in RLD over the short term than the long term, partly supporting our initial hypothesis. Similar patterns were observed in simulation models by Jackson & Caldwell (1996) using a modification of the Barber (1995) model so that soil heterogeneity and root plasticity could be assessed. In these simulations, when roots encountered a previously unexplored patch of NO_3^-, elevated root N inflow rates contributed most to N capture within 2 days but proportionately less over 10 days, whereas increased root growth was unimportant for N capture during the first 2 days but more important over 10 days. Our experimental results are consistent with the model results.

Although the total soil inorganic N pool declined by approximately 60% across both pulses (Fig. 7), our path analysis indicated that soil ^{15}N concentration had a limited direct effect on ^{15}N inflow rate (Fig. 8a,b). Thus, our prediction that N inflow rates would decline with soil N through a pulse was not supported. One reason that soil N concentration had a minimal effect on N inflow rate may be because much of the NH_4^+ was nitrified through the pulse (West 1991; Schaffer & Evans 2005), resulting in only moderate declines in the soil NO_3^- pool. Nitrate is highly mobile in the soil, and most species have a high affinity (low K_m) relative to soil solution NO_3^- (where K_m equals the solution NO_3^- concentration equal to half I_{max}) (Barber 1995). As a result, when NO_3^- dominates the soil inorganic N pool as in our experiment, N inflow rates should remain close to I_{max} until soil NO_3^- is largely depleted. With the assumption of Michaelis–Menten kinetics and our experimental conditions, factors controlling I_{max}, and not soil N concentration, should be the major determinant of N inflow rate.

A significant amount of variation in N inflow rate was attributed to variation in root RGR both in the short and long term (Fig. 8a,b). During the mid spring pulse, when root length RGR were highest for both species (Fig. 5), *A. confertifolia* and *A. parryi* N inflow rates were 5- and 22-fold greater, respectively, immediately following the mid spring pulse relative to the early spring pulse (Fig. 6c,d). In cropping systems, I_{max} has been shown to increase substantially as plant growth rate and N demand increase (Siddiqi *et al*. 1990; Mattson *et al*. 1991; Steingrobe & Schenk 1994). Although low soil temperatures could also contribute to low N inflow rates in early spring by slowing the rate of biochemical processes, previous work has shown that the degree to which low temperature affects I_{max} is mainly determined by the degree to which low temperature affects growth rate and plant demand (White *et al*. 1988; Engels *et al*. 1992). It appears therefore that low root length RGR and low plant N demand decrease I_{max} in these *Atriplex* species and are therefore the major factors limiting N inflow rates in these species in early spring.

Although simulation models and our results suggest an important role for both root growth rate and root N inflow rate for N capture from pulses, not all studies in arid systems have found such a relationship. For example, root growth rate was the major mechanism by which the shrub *Larrea tridentata* captured N from late-season N pulses, while uptake rates remained unchanged (BassiriRad *et al*. 1999). By contrast, the major mechanism of N capture by the tussock grass *Agropyron desertorum* and the shrub *Artemisia tridentata* following simulated summer rain events was increased N diffusion to the root surface as a result of increased soil moisture; following the pulse, N inflow rates increased minimally and root growth did not increase (Ivans *et al*. 2003). Our results suggest that the specific timing of the experimental pulse could contribute to differences in responses among these studies. That is, root growth and N uptake rates may not necessarily be expected to increase following late-season N pulses when plant relative growth rates and N demand are low.

Consistent with our prediction, a decline in soil water content following a pulse had a significant indirect effect on plant N capture over the long term (8–28 days) through a direct effect on N inflow rate (Fig. 8b). This could be due to a number of mechanisms. Models of nutrient flow to the root show that declines in soil water content decrease both nutrient mass flow and diffusion (Nye & Tinker 1977). Decreased soil volumetric water content following a pulse would have reduced effective diffusivity and increased the potential for development of depletion zones around roots even though average soil NO_3^- levels were relatively high (Fig. 7). In addition, even moderate water deficits can reduce the I_{max} of arid land plants (BassiriRad &

Caldwell 1992; Matzner & Richards 1996). Thus, the effect of low soil water content on N inflow rate is probably due to a combination of both reduced I_{max} and reduced soil supply rate.

Although microbial biomass ^{15}N was a significant pool of N following a pulse relative to plant N pools (Table 1), the path coefficient from microbial immobilization to soil N was weak and the indirect path from microbial immobilization to plant N capture was not significant (Fig. 8a,b), contrary to our prediction. It is possible that we underestimated microbial biomass N as microbial biomass is generally concentrated in the upper soil layers but our soil sampling included the entire 0–30-cm layer pooled together. Additionally, because we did not know the efficiency of extracting ^{15}N from microbial biomass in these desert soils, we did not apply a conversion factor (Brookes *et al*. 1985), as is typically used in forested and agricultural systems to account for ^{15}N not readily extractable by the chloroform fumigation method. These factors combined may have resulted in underestimates of microbial biomass N, and thus contributed to lower total ^{15}N recovery during a pulse (Table 1). Nevertheless, even if the total amount of microbial biomass was underestimated we expected that this underestimate would be similar across species and treatments. Consequently, the interrelationships between microbial biomass N and the other variables in the model would not be expected to change.

The high proportion of unexplained variance (*U*, Fig. 8a,b) in microbial biomass ^{15}N suggests that we did not include some important factors influencing microbial biomass N in our model. When we constrained our path model to include only root responses the fit of our model improved significantly. This suggests that a better understanding of the factors influencing mineralization and immobilization rates is necessary to predict more accurately plant response to N pulses in these systems. Although we predicted soil water content would influence microbial biomass, this factor explained essentially none of the variance in microbial biomass ^{15}N for the range of water content encountered in this study. Other studies have demonstrated a limited effect of moderate changes in soil water on microbial biomass in arid systems (Mazzarino *et al*. 1998; Zhang & Zak 1998), and it is possible that microbial biomass N is more related to specific patterns of wet–dry cycles rather than simply to soil water content (Austin *et al*. 2004). Although we expected that microbes would be N limited and therefore immobilize a large amount of N, poor litter quality in arid systems can result in N or carbon limitations (Aerts & Chapin 2000). It is possible that in our system microbial biomass is more limited by labile carbon substrates than N, as has been demonstrated in a number of other arid systems (Gallardo & Schlesinger 1995; Núñez *et al*. 2001; Schaffer & Evans 2005).

Taken together, these results demonstrate that interactions among a number of root responses and soil processes influence the amount of N captured during a pulse. When N pulses occur during periods of high relative growth rate, N capture was greater owing to increased RLD and higher N inflow rates related to greater plant N demand. The rapid loss of NH_4^+ from the system compared with NO_3^-, potentially due to high nitrification rates, combined with low immobilization rates during the pulses allowed adequate soil NO_3^- supply during a pulse. As a result, soil N supply rates did not initially limit plant N capture from a pulse. Instead, factors reducing I_{max}, such as low soil water content and low plant N demand, appear to reduce N inflow rate and limit N capture.

Physiological traits allowing rapid capture of a limiting resource or depletion of a limiting resource to low levels are expected to be important determinants of competitive ability (Grime 1977; Tilman 1988). Our results suggest, however, that 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 depend strongly on the seasonal timing of a pulse. If such environmental variation impacts on the competitive ability of a species, then competitive hierarchies in any given year could change based on the temporal N dynamics. Thus, by altering competitive advantages over time, seasonal variation in timing of an N pulse may also facilitate species coexistence in these pulse-driven systems (Chesson *et al*. 2004). Further experiments with plants in competitive environments, however, are needed to assess fully the ecological consequences of this heterogeneity for survival, competitive ability and diversity maintenance.

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