



Short-term patterns in water and nitrogen acquisition by two desert shrubs following a simulated summer rain

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Abstract

A field experiment was conducted at the Jornada Long-Term Ecological Research (LTER) site in the Chihuahuan Desert of New Mexico to compare the rapidity with which the shrubs *Larrea tridentata* and *Prosopis glandulosa* utilized water, CO_2 and nitrogen (N) following a simulated summer rainfall event. Selected plants growing in a roughly 50-m² area were assigned to treatment and control groups. Treatment plants received the equivalent of 3 cm of rain, while no supplemental water was added to the control plants. Xylem water potential (Ψ_x) and net assimilation rate (A_{net}) were evaluated one day before and one and three days after watering. To monitor short-term N uptake, soils around each plant were labeled with eight equally distant patches of enriched ^{15}N before watering. Each tracer patch contained 20 ml of 20 mM $^{15}\text{NH}_4^{15}\text{NO}_3$ (99 atom%) solution applied to the soil at 20 cm from the center of the plant at soil depths of 10 and 20 cm. Nitrogen uptake, measured as leaf $\delta^{15}\text{N}$, was evaluated at smaller time intervals and for a longer period than those used for Ψ_x and A_{net} . Both A_{net} and Ψ_x exhibited a significant recovery in watered vs. control *Larrea* plants within 3 days after the imposition of treatment, but no such recovery was observed in *Prosopis* in that period. *Larrea* also exhibited a greater capacity for N uptake following the rain. Leaf $\delta^{15}\text{N}$ was five-fold greater in watered compared to unwatered *Larrea* plants within 2 days after watering, while foliar $\delta^{15}\text{N}$ was not significantly different between the watered and unwatered *Prosopis* plants during the same period. Lack of a significant change in root $^{15}\text{NO}_3^-$ uptake kinetics of *Larrea*, even three days after watering, indicated that the response of *Larrea* to a wetting pulse may have been due to a greater capacity to produce new roots. The differential ability of these potential competitors in rapidly acquiring pulses of improved soil resources following individual summer rainfall events may have significant implications for the dynamic nature of resource use in desert ecosystems.

Introduction

Water is the primary environmental factor that limits plant growth and development in desert ecosystems (Noy-Meir 1973). In many deserts of the southwestern United States, summer precipitation is a substantial proportion of the annual water budget. In the Chihuahuan desert for example, summer precipitation (July to September) accounts for more than half of the annual rainfall (Conley et al. 1992). Summer rains in these ecosystems are, however, highly erratic in tim-

ing, duration and intensity. Also, they rarely recharge soil water below 30 cm and due to high potential evapotranspiration even the recharge of the upper soil is short-lived (Schlesinger et al. 1987). Therefore, an important characteristic of desert plants is to tolerate long periods of limited water and N availabilities yet be able to quickly respond to short term improvement of those resources.

Though much is known about how plants cope with drought, the extent and significance of plant

responses to transient periods of improved soil resources, particularly N, following summer rainfall events are relatively unknown. Such responses may provide important mechanistic insights into (1) the dynamic nature of resource use and species composition in desert ecosystems, and (2) how those ecosystem characteristics may respond to predicted changes in summer precipitation particularly in aridlands of the southwestern United States (Mitchell et al. 1990).

It has been shown that summer rains as small as 5 to 10 mm can trigger temporary recovery in plant water relations (Sala & Lauenroth 1982; Sala et al. 1982). However, during these brief intervals of improved soil moisture, the availability of other soil resources such as N may also temporarily improve (Birch 1960; Davidson et al. 1990; Cabrera 1993; Cui & Caldwell 1997). If the recovery of N uptake lags significantly behind water uptake then the potential carbon gain may not be fully realized. This is perhaps why water availability alone is an insufficient predictor of the productivity of *Larrea tridentata* when soil moisture is high for extended periods (Cunningham et al. 1979). Therefore, in examining the relative sensitivity of dominant desert species to summer precipitation it is important to consider rapid uptake recovery of not only water but also other growth limiting resources such as N.

The few available studies indicate that desert perennials differ in their ability to rapidly respond to summer precipitation. Using largely seasonal data and variation in stable isotope signature, Ehleringer and colleagues have suggested that desert perennials vary significantly in their ability to acquire water (Donavan & Ehleringer 1994; Lin et al. 1996; Ehleringer et al. 1991). In contrast our previous work (Bassiri-Rad & Caldwell 1992a,b) showed that in potted plants water uptake was equally rapid in three dominant perennials of the Great Basin (*Agropyron desertorum*, *Pseudoregneria spicata* and *Artemisia tridentata*) after relief from a period of drought, but recovery of N uptake was significantly different among these species.

Here, in a field experiment, we compared the short term recovery of water, N and carbon (C) uptake in two dominant shrubs of the Chihuahuan desert, USA, for several days following a simulated summer rain. The species studied were: creosotebush (*Larrea tridentata*) and mesquite (*Prosopis glandulosa*). During the last 100 years these species have increasingly replaced the original grassland species in large areas of the Sonoran and Chihuahuan deserts (Buffington

& Herbel 1965; Gibbens & Beck 1988). *Larrea* and *Prosopis* differ in key functional traits such as mode of N uptake, rooting depth and distribution, structure, phenology and physiology (Reynolds et al. 1997). *Larrea* is a shallow rooted, drought adapted evergreen, whereas *Prosopis* is a deep rooted, N₂-fixing deciduous shrub, yet it is unclear if such differences result in a differential capacity to utilize pulses of improved soil resources following summer rainfall events. We hypothesized that functional differences in structure and physiology of these species may result in a differential capacity for rapid uptake of resources (e.g., water, C and N) following a summer rain.

Methods

Site description

This study was conducted in June 1994 at the Jornada Experiment Range in the Jornada basin of the Chihuahuan Desert, 40 km NNE of Las Cruces, New Mexico, USA. The study site is an extensive stand of mixed creosote-bush and mesquite on the eastern side of the Doña Ana mountain range. The soil, a Typic Haplargid, has a coarse-loamy texture with a characteristic calcic horizon within the upper two meters (Nash & Dougherty 1990). Annual precipitation is about 230 mm, of which 52% occurs between July and September (Conley et al. 1992). However, this period is also accompanied by high potential evapotranspirational losses due to high vapor pressure deficit and air temperatures.

Water relations and gas exchange

We selected eight reproductively mature individuals each of *Larrea* and *Prosopis*, all approximately equal in size within an area of ca. 50 m². For each species, we randomly assigned five plants to receive a one-time treatment of water equivalent to 3 cm of rain applied in a 0.5 m radius from the center of the plant and three control plants to receive no supplemental water. To reduce runoff and maximize percolation into the rooting zone, berms were erected around each plant by using soil from beyond the canopy to avoid disruption of surface roots near the canopy. Net photosynthetic rates (A_{net}) were measured one day before, and one and three days after the simulated rain. Measurements were made using a portable photosynthesis system (Model 6200, LI-COR Inc., Lincoln, NE) on two terminal, sunlit branches per plant. Measurements

were made three times per day at ca. 07:00, 10:00 and 14:00 h. Two Ψ_x measurements were taken per plant using a model 13005-1442 plant water status console (Soil Moisture Corp., Santa Barbara, CA). The predawn xylem water potentials were measured each day shortly after 5 am. Changes in soil water content were determined gravimetrically within a 50-cm radius of each plant at a depth of 15 cm.

^{15}N uptake

Nitrogen uptake was assessed using ^{15}N . One day before the simulation of a rainfall event, patches of 20 mm $^{15}\text{NH}_4$ $^{15}\text{NO}_3$ (99 atom% enriched) solution were applied to eight microsites around each plant. Using long-needle syringes, 20 ml patches of ^{15}N tracer were applied at 20 cm from the center of each plant both at 10 and 20 cm depths. Nitrogen uptake was determined by monitoring the appearance of ^{15}N in the leaf tissues at 0, 12, 28, 48, 72, 144, 480 and 720 h after the watering treatment. To account for the potential ^{15}N signal variability within a single plant, at least six leaves were composited from several locations within the canopy in both the vertical and horizontal axis.

A separate group of 15 *Larrea* plants at a nearby site was used to evaluate changes in root NO_3^- uptake kinetics using an excised root technique (Epstein 1972). These plants were watered as described above. Root samples from five randomly selected plants were collected at one day before, and one and three days after, the simulated rain for NO_3^- uptake kinetics. Root segments were obtained by excavating plants to a depth of 30 cm. Intact roots were placed in plastic bags containing moist paper towels and were quickly transferred to a laboratory at New Mexico State University where the uptake study was performed on excised root segments. To exclude non-active tissues, only white or light brown roots <1 mm in diameter were used. Nitrate uptake from a series of 99 atom% K^{15}NO_3 solutions (5, 50, 150, 250, 500, 1000 μM) was determined using these excised root segments. A detailed description of this procedure is given in BassiriRad et al. (1993). Root NO_3^- uptake rates are expressed in $\mu\text{mol} (\text{gdw root})^{-1} \text{h}^{-1}$.

Leaf and root samples were oven dried at 75 °C for several days and then ground in a Wiley Mill to a fine mesh. The ^{15}N determination was done at the Duke University Phytotron by combustion in an element analyzer linked on line with a stable isotope ratio mass spectrometer (SIRA series II VG Isotech, Middlewich,

UK). Leaf enrichment of ^{15}N is expressed in δ notation relative to an atmospheric-air standard (Mariotti 1984) as:

$$\delta^{15}\text{N} = ((R_{\text{sample}}/R_{\text{standard}}) - 1) \times 1000\text{‰}$$

where R_{sample} and R_{standard} are the molar ratios of $^{15}\text{N}/^{14}\text{N}$ of the sample and standard, respectively.

Statistical methods

For each species, data for leaf $\delta^{15}\text{N}$, NO_3^- uptake kinetics, xylem water potential and assimilation rate were analyzed using one-way repeated measures analyses of variance (ANOVAs), using watering treatment as the independent variable and time (days after watering, or hour within a single day) as the repeated factor (Sokal & Rohlf 1981). Mean values for watered and unwatered plants of each species at individual times were compared with a student *t*-tests and differences were considered significant at $P < 0.05$ (Sokal & Rohlf 1981).

Results

Water relations and gas exchange

Although our site received a total of 20 mm of rain within a 10 day period prior to the start of our experiments, both initial soil and plant water status indicated very dry conditions (Figures 1, 2). Twenty-four hours after watering, gravimetric soil water content under the watered canopies was more than four fold higher than that obtained prior to watering and declined gradually thereafter (Figure 1). There was no immediate plant response to this increase in soil moisture as values of Ψ_x were not significantly different between the watered and unwatered plants for either species one day after watering (Figure 2). Although we had intended to take diurnal measurements of xylem water potential, instrument failure resulted in only one (predawn) reading on the day before watering and three readings on the day after watering. Water status in *Larrea* was significantly improved ($P = 0.004$ from ANOVA) after three days in watered compared to unwatered plants. In contrast, during the same period, there was no significant recovery of the leaf water status in *Prosopis* plants.

In both species the highest A_{net} occurred during early morning followed by a relatively sharp decline

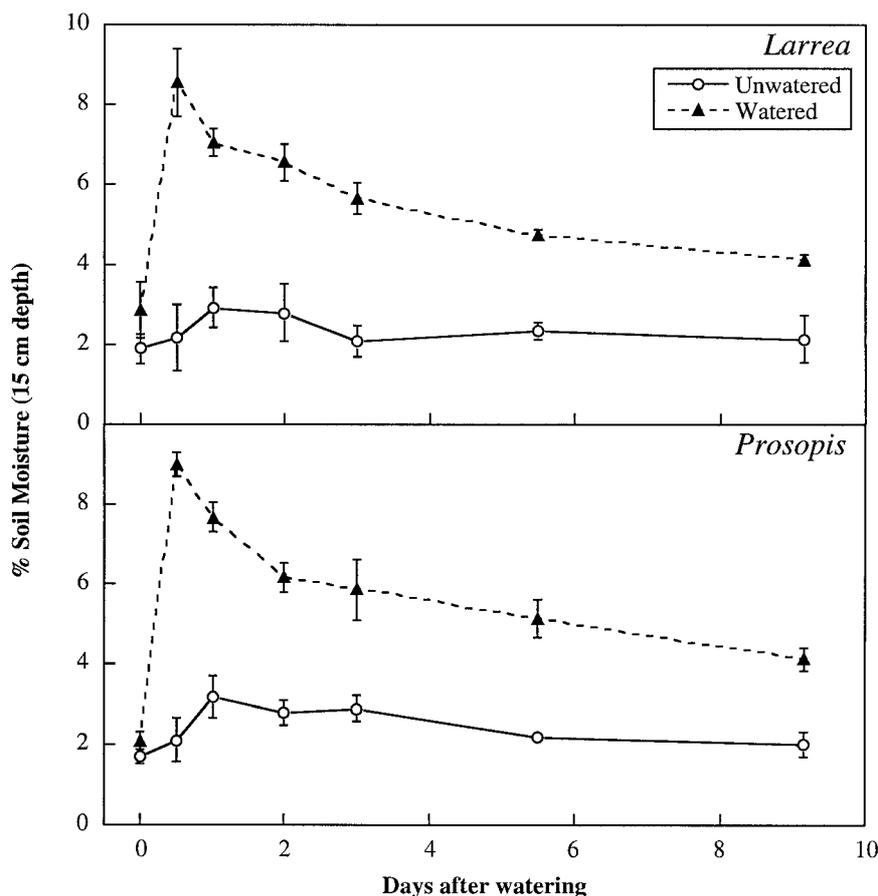


Figure 1. Gravimetric soil moisture content at various times before and after the simulated rain. Each point is the mean ± 1 se from 5 watered and 3 unwatered plants of *Larrea* and *Prosopis*. Soil samples were taken from the depth of 15 cm below the surface within a 30 cm radius from the center of the canopy. Time zero represents soil moisture content prior to watering.

throughout the day (Figure 3). The short-term pattern of C uptake following the simulated rain was similar to that of the water uptake. Rates of photosynthesis between watered and unwatered plants of both species were not significantly different at any time during the experiment except for *Larrea* plants after three days. On this date, A_{net} was significantly higher for watered as opposed to unwatered *Larrea* plants. These differences were statistically significant for 13:00 h ($P = 0.037$ by t -test) and marginally significant for all the other readings on that date ($P = 0.09$ from repeated ANOVA).

^{15}N uptake

The watered *Larrea* plants showed a marked increase in foliar ^{15}N . Twenty-eight hours after the simulated rain, foliar $\delta^{15}\text{N}$ in watered *Larrea* plants increased from ca. 9 ± 0.4 to $48 \pm 14\%$ (mean ± 1 se), but only

to $14 \pm 5\%$ in unwatered plants (Figure 4 insert). Three days after the simulated rain, leaf $\delta^{15}\text{N}$ in watered *Larrea* plants increased more than eleven fold while the increase in control plants was only two fold. This increase in foliar ^{15}N was not related to specific root activity since root physiological uptake capacity for NO_3^- , particularly in the range of 5–500 μM NO_3^- concentration in the external solution, was virtually identical for *Larrea* roots collected before and up to three days after watering (Figure 5). During the same period, both watered and unwatered *Prosopis* plants showed very little uptake of ^{15}N following the simulated rain (Figure 4 insert).

Between 15 and 22 days after watering, six natural rain events occurred in amounts ranging from 2–8 mm (Figure 4). These small events apparently triggered substantial N uptake in the unwatered *Larrea* plants by twenty days after initial watering (Figure 4) and may

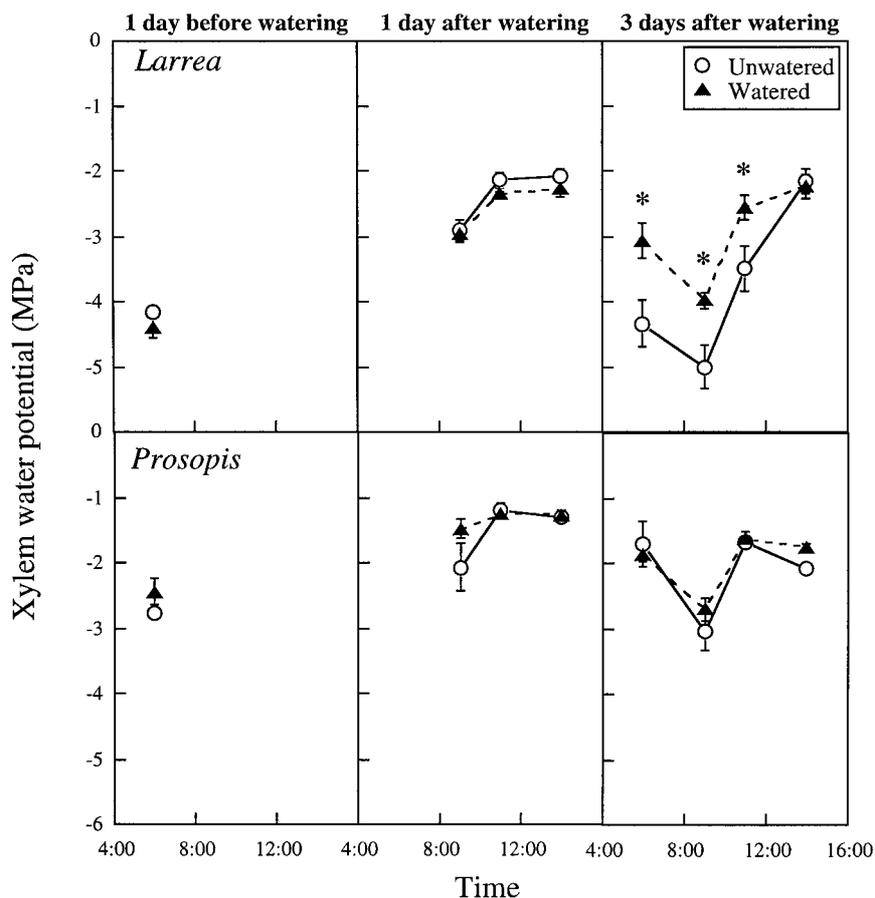


Figure 2. Daily changes in xylem water potentials of watered and unwatered (control) plants of *Larrea* and *Prosopis* one and three days after the simulated rain. The day before the simulated rain, only predawn xylem water is shown. Each point is the mean ± 1 se from 3 control and 5 watered plants. * denotes statistically significant ($P \leq 0.05$) differences between watered and control treatments.

have extended the period of favorable soil moisture content long enough to result in significant N uptake by both watered and unwatered *Prosopis* plants (Figure 4). While unwatered *Larrea* plants were quicker than unwatered *Prosopis* plants in acquiring soil N after the natural rains, unwatered *Prosopis* plants also accumulated a significant leaf $\delta^{15}\text{N}$ by 30 days after the imposition of the treatments. Nevertheless, at this date leaf $\delta^{15}\text{N}$ was not significantly different between watered and unwatered *Prosopis* plants, while significant differences in leaf ^{15}N content were maintained between treatments in *Larrea* plants (Figure 4).

Discussion

Studies of water uptake, growth and physiological responses of desert shrubs to summer precipitation have

often used temporal scales of weeks or months (Branson et al. 1976; Brown & Archer 1990; Davis & Mooney 1985; Donovan & Ehleringer 1994). Rewetting of desert soils and the corresponding increase in plant activity following a summer rain (even after a major summer storm) is often very short-lived (Nobel 1988). Therefore it is crucial to evaluate the dynamics of resource acquisition and physiological responses to individual rain events on a scale of hours and days. The few studies that have examined these aspects on scales of hours and days have been primarily conducted on shallow rooted species of desert and tropical succulents (North & Nobel 1994; Huang & Nobel 1992; Nobel & Huang 1992) and perennial grasses (Sala & Lauenroth 1982; Lauenroth et al. 1987) and have mainly considered responses in water uptake. We are not aware of any study that has evaluated hourly and/or daily time course of N uptake of intact roots un-

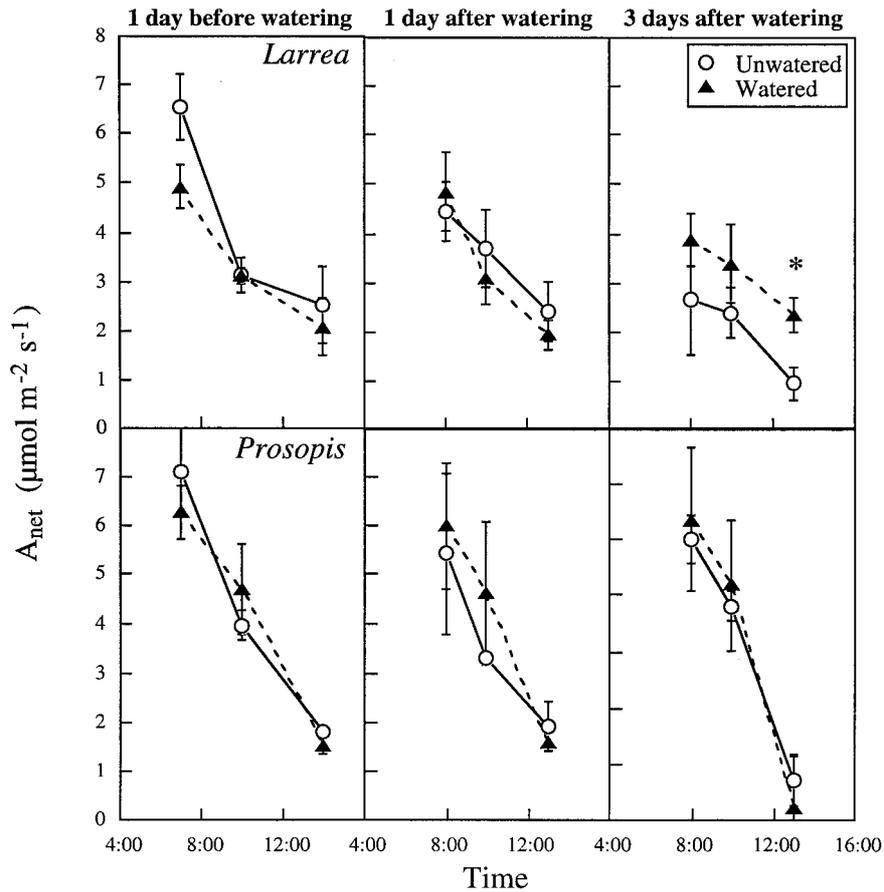


Figure 3. Diurnal changes in A_{net} of watered and unwatered (control) plants of *Larrea* and *Prosopis* at one day before and one and three days after the simulated rain. Each point is the mean ± 1 se from 3 control and 5 watered plants. * denotes statistically significant ($P \leq 0.05$) differences between watered and control treatments.

der field conditions. Although BassiriRad & Caldwell (1992a,b) examined daily responses of water status and N uptake during a period of release from drought, those studies were conducted on pot grown plants.

Larrea and *Prosopis* differed significantly in the timing and magnitude of water, C and N uptake. The daily pattern of xylem water potential indicated that in both species tested here, predawn xylem water potential was not the highest value of the day. However, it is not uncommon for desert shrubs to exhibit a maximum xylem water potential in mid-day rather than predawn (Halvorson & Patten 1974). In *Larrea*, Syvertsen et al. (1975) referred to this behavior as 'anomalous diurnal pattern of water potentials'. Following the simulated rainfall event *Larrea* acquired both water and nitrogen more rapidly than *Prosopis*. By the third day following rain, Ψ_x in watered *Larrea* plants was consistently (except for the last daily reading) 1 MPa higher than in

the unwatered plants while no recovery was observed in *Prosopis* plants (Figure 2). This recovery is as rapid as that observed for some cold desert species of the Great Basin region (BassiriRad & Caldwell 1992a,b) but is much slower than that found for the perennial grass *Bouteloua* (Lauenroth et al. 1987).

The recovery of leaf water status in *Larrea* was accompanied by a recovery in A_{net} (Figure 3) and stomatal conductance (data not shown). This indicates that stomatal limitation of photosynthesis during drought can be partially reversed following a rainfall event more rapidly in *Larrea* than *Prosopis*. Relatively small *Larrea* shrubs, much like those used in this study, have been shown to exhibit a strong stomatal control of A_{net} in response to summer rains (Franco et al. 1994). Figure 3 shows the first reading of the day, at 7 AM, represented the highest A_{net} (A_{max}). Franco et al., (1994) working at a nearby site, also showed

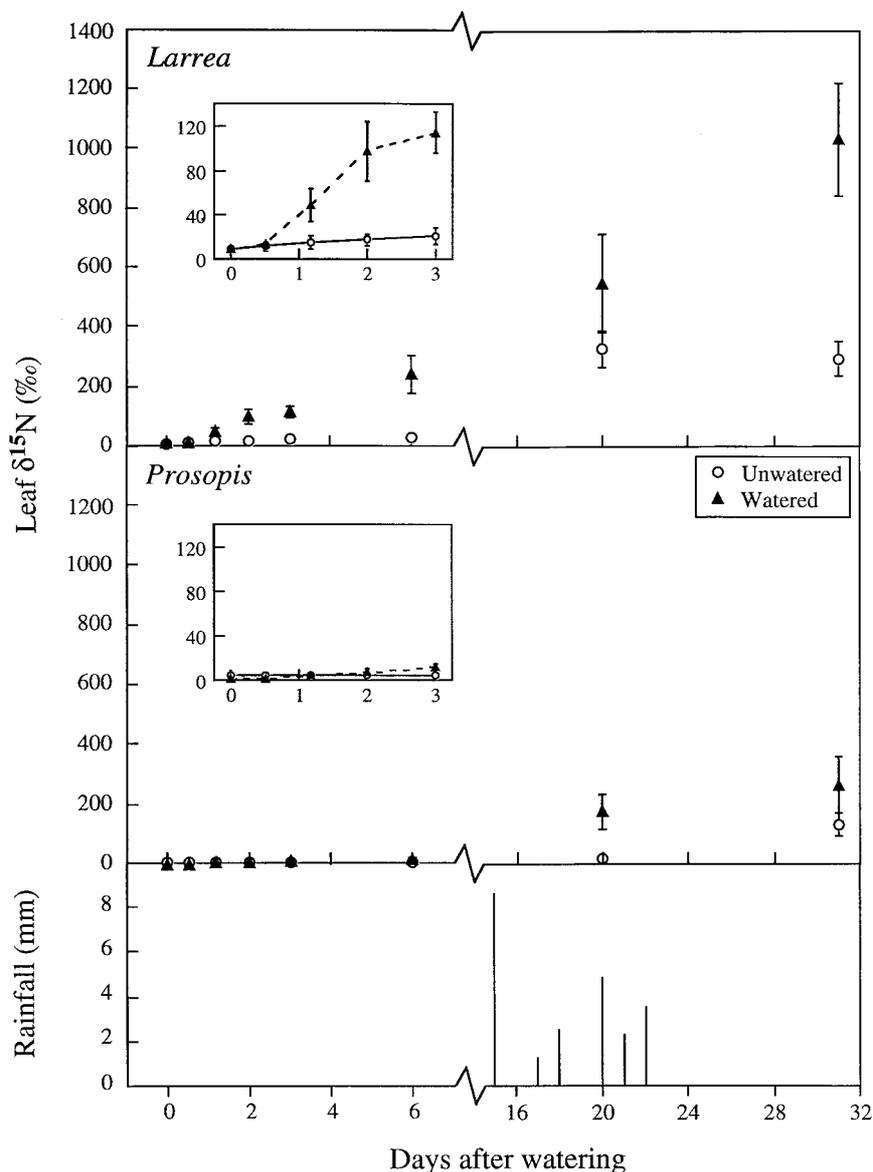


Figure 4. Time course changes in leaf $\delta^{15}\text{N}$ uptake before and after simulated rainfall event for watered and unwatered *Larrea* and *Prosopis* plants. Insets show leaf $\delta^{15}\text{N}$ accumulation for the first three days following the watering treatment. Each point is the mean of 3 control and 5 watered plants ± 1 se. Bottom panel shows actual precipitation at the site during the study period.

that A_{\max} in *Larrea* occurred relatively early in the morning i.e., at 8 AM. However, it must be pointed out that because an insufficient number of data points are presented for each day, we are unable to accurately pinpoint the time of the day when A_{\max} occurred. In fact, it is entirely possible that for both species A_{\max} occurred at any time between 7 and 10 AM, but was not apparent in Figure 3 because of the infrequent number of observations.

Nitrogen uptake also occurred more quickly in *Larrea* than *Prosopis* following the simulated rainfall (Figure 4). The differences in rapidity of water and N uptake between the species tested here may in part be attributed to a greater rooting density in *Larrea* than *Prosopis* in the surface soil (Freckman & Virginia 1989). On the other hand, the fact that throughout the study xylem water potential was substantially higher in *Prosopis* than *Larrea* (Figure 2)

indicates that *Prosopis* may have access to deeper soil water sources and hence it is relatively unresponsive to changes in soil water content in the upper layers. Deep rooted species often experience less water stress during a drying period than the shallow rooted ones, but respond less quickly to new input of moisture (Davis & Mooney 1985). The presence of substantial viable shallow roots in *Prosopis*, as observed by us during the application of tracer and by Freckman & Virginia (1989) in a nearby site, however, raises the possibility that mechanisms other than rooting depth may be involved in the differential responses of these species.

There are two major mechanisms that may account for the faster recovery of water status and N uptake in *Larrea* than in *Prosopis*: higher growth of new roots and/or increased root specific activity. In some desert species, new roots, with significantly higher hydraulic conductances than the established roots, can be produced within a few hours following a summer shower (Hunt et al. 1987; Lauenroth et al. 1987; Nobel & Sanderson 1984). Rapid development of new roots during a drought recovery period was also a major mechanism regulating the uptake of Ca^{2+} and PO_4^{3-} uptake in barley seedlings (Shone & Flood 1983) and NO_3^- uptake in wheat seedlings (Brady et al. 1995). Although BassiriRad & Caldwell (1992a,b) suggested that resumption of NO_3^- uptake during a period of drought recovery was primarily due to increased unit absorption rate of roots, in the present study, root NO_3^- uptake kinetics of *Larrea* was virtually unchanged up to three days after watering (Figure 5). This indicates that root proliferation rather than changes in root activity may have been a major factor affecting resource acquisition in *Larrea*. By three days after the simulated summer rain, unwatered *Larrea* plants showed a small yet detectable rise in $\delta^{15}\text{N}$. N uptake in unwatered plants is perhaps in response to N-enriched microsites. Nutrient-enriched microsites, such as those applied in our tracer patches, have been shown to cause rapid root proliferation and enhanced root uptake kinetics (Jackson & Caldwell 1989; Caldwell et al. 1991) and may thereby cause this apparent N uptake in unwatered plants.

The slower rate of N uptake from the soil exhibited by *Prosopis* may reflect this species capacity for symbiotic N_2 -fixation thus lessening its reliance on soil N. However, it is commonly observed that as available soil N, particularly NO_3^- , increases root uptake rather than symbiotic fixation becomes the dominant mode of N acquisition in legumes (Becana & Sprent 1987; Streeter 1985). Furthermore, several studies

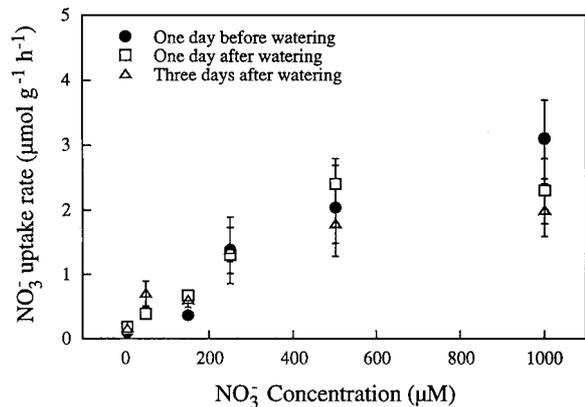


Figure 5. Net NO_3^- uptake rates of excised *Larrea* roots as a function of external NO_3^- concentration. The assay solution concentrations were 5, 50, 150, 250, 500 and 1000 μM $^{15}\text{NO}_3^-$ (99 atom% enriched). Each point represents an average of 5 replicates ± 1 se. Temperature of the assay solutions were $25^\circ\text{C} \pm 1$.

conducted at different desert sites have shown that a substantial proportion of N uptake in *Prosopis* is soil driven. For example, *Prosopis* plants from both the Sonoran and Chihuahuan desert, acquired more than half of their N supply from the soil N pool (Shearer et al. 1983; Lajtha & Schlesinger 1986). The soil pool was also the main source of N uptake in our *Prosopis*. Assuming a value of -1.3‰ for ^{15}N abundance of purely fixed N in *Prosopis* and that the ^{15}N value of untreated *Larrea* leaves represented the abundance of soil ^{15}N (Shearer et al. 1983), we estimated that during the period of ^{15}N accumulation, only 45% of the N uptake in *Prosopis* was derived from atmospheric N_2 -fixation.

It is unclear why *Prosopis* does not quickly respond to summer precipitation despite having viable shallow roots. One possible explanation may involve a greater sensitivity of *Prosopis* than *Larrea* roots to high soil temperature. At this site, soil temperature at the depth of 5 cm for late June and July is often greater than 40°C (Kemp et al. 1992). The possibility exists that at such high temperatures root water and N uptake in *Prosopis* are heat inactivated. Fernandez & Caldwell (1975) speculated that in a number of desert shrubs root growth during mid summer is progressively shifted deeper in the soil profile in order to avoid the excess thermal load in the upper soil layers. Recently, Lin et al. (1996) invoked heat inactivation as a possible mechanism explaining why roots of a number of dominant cold desert shrubs were unable to utilize a simulated summer rain. Further evidence of temper-

ature sensitivity in *Prosopis* roots may be drawn from the work of Jenkins et al. (1988) who concluded that only the deep roots are the probable site of N₂-fixation.

In conclusion, *Larrea* was much more effective than *Prosopis* in water, N and C uptake following a simulated summer rainfall event. Studies of plant and community dynamics in desert systems almost universally invoke various modes of drought tolerance as key mechanisms to niche differentiation, competition, individual survival and succession. Here we suggest that knowledge of the mechanisms of plant 'recovery' from drought and the relative differences among the dominant species may provide a complementary perspective in better understanding these systems. Further studies are needed to assess the relative importance of these pulses of resource uptake to the overall annual water, C and N budget of these and other desert species. However, because summer rains often lead to a very brief period of improved resources and because plants are faced with a 'use it rapidly or lose it' proposition, such studies must employ temporal scales of hours and days rather than weeks and months. Finally, in addition to providing insight into the dynamic nature of resource use in desert ecosystems, the approaches used here can be used in conjunction with the projected seasonal shifts in regional precipitation to evaluate the potential changes in vegetation composition of the system. The data presented here indicate that resource use in *Larrea* is more closely associated with summer precipitation than *Prosopis*. Consequently, we cautiously suggest that the future success of *Larrea* in the Chihuahuan desert will be more responsive than its deep-rooted counterpart to changes in summer precipitation.

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