Short Communication

Growth and foliar δ^{15}N of a Mojave desert shrub in relation to soil hydrological dynamics

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ABSTRACT

Soil matric potential (ψ_{matric}) was modeled for two years at four sites with different soil profile characteristics. Canopy volumes and foliar ^{15}N ratios (δ^{15}N) of Larrea tridentata were related to average soil water availability (ψ_{matric}) and the modeled duration of available soil water (consecutive days ψ_{matric} > −6.0 MPa). Weakly developed soils on young (Holocene) alluvial deposits had the longest duration (129 d) and highest ψ_{matric} (−1.8 MPa), compared to soils with moderate horizon development in intermediate-aged (late Pleistocene) deposits (80 d, −4.3 MPa) and in soils with strong horizons on old (mid-late Pleistocene) deposits (20 d, −3.2 MPa). Plant canopy volume was highest in weakly developed soils (2.23 m^3 ± 0.342 SE) than in moderately or strongly developed older soils (0.57 m^3 ± 0.082 SE; 0.56 m^3 ± 0.123 SE, respectively). The fourth site possessed a soil with a silt- and clay-rich horizon beneath a strong stone pavement, and had the shortest, most water-limited regime (13 d; −5.5 MPa) and smallest plant canopies (0.46 m^3 ± 0.073 SE). Foliar δ^{15}N variation was better explained by average ψ_{matric} ($R^2 = 0.69$; $p \leq 0.001$) than duration of available soil water ($R^2 = 0.49$; $p \leq 0.001$). Together, these findings suggest soil hydrological regimes establish thresholds for plant growth, and plant N-dynamics are tightly coupled to desert soil hydrological characteristics.

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Water and nitrogen are considered as co-limiting factors of arid-land ecosystem processes (Evans and Ehleringer, 1994; Hamerlynck et al., 2004). Desert soils are chronically low in organic matter, and plant N-limitation is directly affected by microbial immobilization and C-limitation, and disturbance to N-fixing soil crusts (Billings et al., 2002; Evans and Belnap, 1999; Titus et al., 2002). In deserts, plant growth is tightly linked to ultimately a function of soil physical features that affect precipitation infiltration, percolation, and temporal persistence of soil water (Hamerlynck et al., 2002; McAuliffe, 1994; McAuliffe, 2003). However, few studies have sought to discriminate between the relative importance of the temporal persistence of soil water to that of soil water availability. To do so, we measured plant size and foliar ^{15}N isotopic ratios (δ^{15}N) in the evergreen shrub, Larrea tridentata (creosotebush) as a function of soil matric potential (ψ_{matric}) modeled over two years for four hydrologically distinct Mojave Desert soils. ψ_{matric} varies as a function of soil texture, and is the dominant feature of soil water potential, and thus is the primary determinant of plant available water and plant water potential (Campbell and Norman, 1998). δ^{15}N

ratios provide a powerful indicator of integrated N-dynamics (Billings et al., 2002; Evans, 2001). It should be stressed that we did not use foliar δ^{15}N to establish how soil characteristics affect plant N-acquisition, assimilation or variation in N-sources (Billings et al., 2002; Evans, 2001; Evans and Belnap, 1999; Evans and Ehleringer, 1994; Heaton, 1987; Shearer et al., 1983). Rather, we sought to establish how soil characteristics influenced soil water persistence and availability, and determine which of these better explained variation in leaf δ^{15}N, giving us better insight on the coupling between desert ecosystem and hydrological processes.

Fieldwork was conducted on an alluvial fan complex ("bajada") flanking the western slopes of the Providence Mountains in the Mojave National Preserve, California, USA (34°54–58′N, 115°36–39′W). Sites were located on four different alluvial fan deposits differing in age (Holocene to late Pleistocene) and soil characteristics. Three of the sites were on alluvial fan deposits composed of coarse-grained, mixed plutonic (syenogranite and syenite) parent materials. The Young Alluvial site is a late Holocene (∼ 4000 YBP) gravelly deposit, while the Intermediate and Old Alluvial sites are located on two different late Pleistocene deposits (∼12,000 and ∼50,000 YBP, respectively) of cobbly to bouldery alluvium. Young Alluvial site soils lack significant horizon development, but those of the two older deposits contain increasingly

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Table 1
Soil horizon depths, horizon soil fine fraction composition, seasonal duration of soil matric potential (ψ_{matric}) > −6.0 MPa, average ψ_{matric}, and *Larrea tridentata* canopy volumes across four Mojave Desert soils. Site names, horizon depths and fine soil data are from Hamerlynck et al. (2002); horizon designations follow McDonald et al. (1996). Standard error bars (S.E.) are for the mean of 31−311 individual canopy volume observations and 13−129 ψ_{matric} estimations at each site; letters differ at $p \le 0.05$ (α-adjusted LSD).

Site	Horizon	Depth (cm)	silt	clay	Dur. (d)	ψ_{matric} (MPa)	Vol. (m^3)
Y.A.	Av	0−2	22.8%	5.2%	120	−1.8 ± 0.89[a]	2.23 ± 0.342[a]
	AC	2−6	16.9%	5.1%			
	Ck1	6−35	9.8%	5.0%			
I.A.	Av	0−5	29.0%	23.2%	80	−4.5 ± 0.11[c]	0.57 ± 0.082[b]
	Bwk	5−9	15.0%	17.4%			
	Btk1	9−20	15.0%	13.1%			
	Btk2	20−35	10.9%	4.1%			
O.A.	Av	0−4	28.5%	31.0%	30	−3.2 ± 0.22[b]	0.56 ± 0.123[b]
	ABvk	4−6	18.8%	21.9%			
	Btk1	6−25	10.0%	20.0%			
	Btk2	25−35	13.7%	19.9%			
Pave.	Av	0−4	22.0%	9.8%	13	−5.5 ± 0.27[d]	0.46 ± 0.073[b]
	Bwk	4−32	15.7%	4.9%			
	Bk1	32−35	9.8%	3.1%			

strong surface stone pavements, fine-grained Av horizons located directly beneath the pavements, and clay-enriched argillic (Btk) horizons (Table 1). Calcium carbonate occurs throughout these soils, but strongly cemented calcic horizons ("caliche") are absent. A fourth site, the *Pavement* site, consists of deposits derived from fluvially reworked dune deposits mixed with pebble-sized clasts. A continuous stone pavement of a single tightly-packed layer of pebbles covers the surface; a silt-rich Av horizon is located directly beneath this stone pavement, and the underlying sandy soils exhibit only weak B-horizon development (Table 1).

Soil matric potential (ψ_{matric}), was estimated using the one-dimensional, process-based Simultaneous Heat and Water (SHAW) model, which calculates ψ_{matric} from changes in saturated and unsaturated volumetric soil water content resulting from transfers of heat and infiltration of water between soil layers, each having distinct texture, porosity, and saturated hydraulic conductivity (Flerchinger and Saxton, 1989) as determined for our soils by McDonald et al. (1996). SHAW simulations were run using precipitation and climate data for the Jan. 1, 1995 to Dec. 30, 1996 period, which encompass our plant measurements (for more detail, see Hamerlynck et al., 2002). From these, we determined the number of days that ψ_{matric} ranged from 0 to −6 MPa, which represents the range of xylem water potentials over which *L. tridentata* sustains positive photosynthetic rates (Hamerlynck et al., 2000; Oechel et al., 1972). These data were averaged across 5, 25, and 35 cm depths, representing the bulk of *L. tridentata*'s rooting zone (Gile et al., 1998). These analyses showed that fine-grained Av horizons

had the greatest effect on temporal persistence and ψ_{matric} of plant available water, due to the manner in which these horizons impede surface infiltration. The range of high to low values of ψ_{matric} was Young Alluvial, Old Alluvial, Intermediate Alluvial to Pavement site (Table 1), with all pooled ψ_{matric} significantly different from each other (One-way ANOVA $F_{3,242} = 141.0$; $p \le 0.001$). Young and Intermediate Alluvial soils, which had weakly developed Av horizons (Hamerlynck et al., 2002; McDonald et al., 1996) had much longer 0 to −6.0 MPa ψ_{matric} periods (129 and 80 days, respectively) compared to Old Alluvial and Desert Pavement site soils (20 and 13 days, respectively) which have much stronger Av development (Fig. 1). Dramatic decreases in soil water persistence were not associated with the degree of argillic horizon (Btk) development. This is evidenced by a difference of only 7 d in the duration of available soil moisture in the Old Alluvial site containing the strongest argillic horizon and the Pavement site that lacked an argillic horizon (Table 1). Thus, it seems the primary effect of the argillic horizon is limiting the depth of infiltration (McDonald et al., 1996; Nimmo et al., 2009).

At each site, volumes of individual plants were estimated using mensuration formulae used previously (Hamerlynck et al., 2002; McAuliffe et al., 2007). Basal diameter, canopy diameters (major and minor perpendicular axes) and plant heights of individual *L. tridentata* plants were measured. Volumes of *L. tridentata* were estimated as frustum of inverted right-angle circular cone ($V = 1/3\pi(R_1^2 + R_2^2 + R_1 R_2)$, where R_1 = canopy radius and R_2 = basal radius. Plant tissue from these individuals was gathered from April
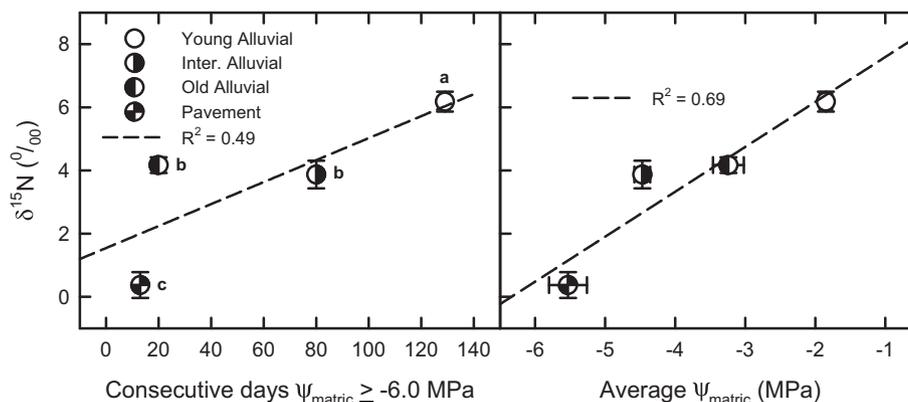
Fig. 1. Foliar δ^{15}N ratios of *Larrea tridentata* (creosotebush) as a function of consecutive days with soil matric potential (ψ_{matric}) exceeding −6.0 MPa, and the average ψ_{matric} over that time period in four distinct Mojave Desert soils. Horizontal standard error bars (S.E.) are for the mean of 31-13-129 ψ_{matric} estimations, vertical standard error bars are for the mean of 10 δ^{15}N measurements. Letters show significant differences in δ^{15}N at $p \le 0.05$ (α-adjusted LSD); linear regressions are fit to all individual δ^{15}N observations at each site.

to May 3, 1996 growing season. Leaves were placed in a cooler, transported back to the lab, dried at 80 °C for 48 h and analyzed for ^{15}N composition ratio ($\delta^{15}N$) on a mass spectrophotometer (Finnegan Delta C, Finnegan Instruments, Bremen, Germany) at the Institute of Ecology's Stable Isotope/Soil Biology Laboratory at the University of Georgia, Athens, GA. Significant site-specific differences were apparent (log$_{10}$-transformed data, one-way ANOVA $F_{3,139} = 14.70$; $p \leq 0.0001$), with plants at the Young Alluvial site significantly larger than smaller, similar sized plants at the Intermediate Alluvial, Old Alluvial and Pavement sites (Table 1). Hydrological limitations to plant size were more relaxed in soils of the Young Alluvial site, where 120 + days at −1.8 MPa was accompanied by 4x greater plant volumes (Table 1). However, soil characteristics that yielded hydrological regimes as divergent as 20 d at −3.2 MPa (Old Alluvial), 80 d at −4.5 MPa (Intermediate Alluvial) and 13 d at −5.6 MPa (Pavement) had equivalent plant sizes. It may be the coarse, poorly developed soils allow *L. tridentata* at the Young Alluvial site to more readily occupy larger soil volumes with more frequent favorable ψ_{matric} compared to the older, more well-developed soils, where stronger argillic horizon development may limit rooting depth (Gile et al., 1998), and low ψ_{matric} may limit plant water relations and growth. In contrast, the strong stone pavement and silt-rich Av horizon at the Pavement site may limit infiltration and facilitate surface run-off, resulting in very low ψ_{matric}, limiting growth at this site. Hamerlynck et al. (2002) conjectured the small plant sizes at these sites may reflect effects of more frequent mortality and recruitment, and that size differences may have been due to differences in age structure. However, subsequent work quantifying drought-induced mortality and canopy die-back showed *L. tridentata* at these sites was less severe than at the Young Alluvial site (Hamerlynck and McAuliffe, 2008), which suggests differences in size likely reflect hydrological limitations to growth across the sites.

Larrea tridentata $\delta^{15}N$ differed across the four soils (arcsine transformed data, one-way ANOVA $F_{3,16} = 54.10$, $p \leq 0.001$), with highest $\delta^{15}N$ in plants from the Alluvial site (6.18‰ ± 0.316 SE), significantly higher than $\delta^{15}N$ at the Intermediate Alluvial (3.87‰ ± 0.438 SE) and Old Alluvial sites (4.17‰ ± 0.249SE), which in turn were significantly greater than in Pavement site plants (0.37‰ ± 0.409 SE; Fig. 1). Both duration of plant available soil water and average ψ_{matric} had significant, negative linear relationships with $\delta^{15}N$ ($F_{1,38} = 84.56$ and $F_{1,38} = 36.62$; $p \leq 0.001$ for average ψ_{matric} and duration of water availability, respectively). However, average ψ_{matric} had a much stronger relationship to foliar ^{15}N ratios, explaining ca. 20% more variation in $\delta^{15}N$ than did the duration of available water (Fig. 1), clearly showing soil water availability, not temporal persistence, more strongly influenced nitrogen dynamics. These findings indicate that Mojave Desert ecosystems are closed, source-limited systems, where plant activity utilizes all available nutrient sources (Evans, 2001), the availability of which are strongly affected by landform-related soil hydrological characteristics.

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