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

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A B S T R A C T
Soil matric potential ($\psi_{\text{matric}}$) was modeled for two years at four sites with different soil profile characteristics. Canopy volumes and foliar $\delta^{15}$N ratios ($\delta^{15}$N) of Larrea tridentata were related to average soil water availability ($\psi_{\text{matric}}$) and the modeled duration of available soil water (consecutive days $\psi_{\text{matric}} > -6.0$ MPa). Weakly developed soils on young (Holocene) alluvial deposits had the longest duration (129 d) and highest $\psi_{\text{matric}}$ (-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 ($2.23 \text{ m}^3 \pm 0.342 \text{ SE}$) than in moderately or strongly developed older soils ($0.57 \text{ m}^3 \pm 0.082 \text{ SE}$; $0.56 \text{ m}^3 \pm 0.123 \text{ SE}$, respectively). The fourth site possessed a soil with a silty- 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 ($0.46 \text{ m}^3 \pm 0.073 \text{ SE}$). Foliar $\delta^{15}$N variation was better explained by average $\psi_{\text{matric}}$ ($R^2 = 0.69$; $p < 0.001$) than duration of available soil water ($R^2 = 0.46$; $p < 0.001$). 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-source soils (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 $\delta^{15}$N isotopic ratios ($\delta^{15}$N) in the evergreen shrub, Larrea tridentata (creosotebush) as a function of soil matric potential ($\psi_{\text{matric}}$) modeled over two years for four hydrologically distinct Mojave Desert soils. $\psi_{\text{matric}}$ 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). $\delta^{15}$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 $\delta^{15}$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 $\delta^{15}$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...
Young Alluvial exhibit only weak B-horizon development (Table 1). Beneath this stone pavement, and the underlying sandy soils, pebbles cover the surface; a silt-rich Av horizon is located directly beneath the pavements, and clay-enriched argillic (Btk) horizons (Table 1). Calcium carbonate occurs throughout these horizons (Table 1); it seems the primary effect of the argillic horizon is limiting the depth of available water, due to the manner in which these horizons impede surface infiltration. The range of high to low values of \( \psi_{\text{matric}} \) was from Young Alluvial, Old Alluvial, Intermediate Alluvial to Pavement site (Table 1), with all pooled \( \psi_{\text{matric}} \) significantly different from each other (One-way ANOVA, \( F_{\text{1,242}} = 141.00; p < 0.001 \)). 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 \( \psi_{\text{matric}} \) 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 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 \( L. \ tridentata \) were estimated for the mean of 31–131 individual canopy volume observations and 13–129 \( \psi_{\text{matric}} \) estimations at each site; letters differ at \( p < 0.05 \) (a-adjusted LSD).

### Table 1

Soil horizon depths, horizon soil fine fraction composition, seasonal duration of soil matric potential (\( \psi_{\text{matric}} \)) > –6.0 MPa, average \( \psi_{\text{matric}} \), and \( L. \ tridentata \) 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 31–131 individual canopy volume observations and 13–129 \( \psi_{\text{matric}} \) estimations at each site; letters differ at \( p < 0.05 \) (a-adjusted LSD).

<table>
<thead>
<tr>
<th>Site</th>
<th>Horizon</th>
<th>Depth (cm)</th>
<th>Silt (%)</th>
<th>Clay (%)</th>
<th>Dur. (d)</th>
<th>( \psi_{\text{matric}} ) (MPa)</th>
<th>Vol. (m³)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Y.A.</td>
<td>Av</td>
<td>0–2</td>
<td>22.8%</td>
<td>5.2%</td>
<td>120</td>
<td>–1.8 ± 0.89³</td>
<td>2.23 ± 0.342³</td>
</tr>
<tr>
<td></td>
<td>Ac</td>
<td>2–6</td>
<td>16.9%</td>
<td>5.1%</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Ck1</td>
<td>6–35</td>
<td>9.8%</td>
<td>5.0%</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>I.A.</td>
<td>Av</td>
<td>0–5</td>
<td>29.0%</td>
<td>23.2%</td>
<td>80</td>
<td>–4.5 ± 0.11⁴</td>
<td>0.57 ± 0.082⁵</td>
</tr>
<tr>
<td></td>
<td>Bwk</td>
<td>5–9</td>
<td>15.0%</td>
<td>17.4%</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Btk1</td>
<td>9–20</td>
<td>15.0%</td>
<td>13.1%</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Btk2</td>
<td>20–35</td>
<td>10.9%</td>
<td>4.1%</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>O.A.</td>
<td>Av</td>
<td>0–4</td>
<td>28.5%</td>
<td>31.0%</td>
<td>30</td>
<td>–3.2 ± 0.22⁶</td>
<td>0.56 ± 0.123⁷</td>
</tr>
<tr>
<td></td>
<td>Abv/k</td>
<td>4–6</td>
<td>18.8%</td>
<td>21.9%</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Btk1</td>
<td>6–25</td>
<td>10.0%</td>
<td>20.0%</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Btk2</td>
<td>25–35</td>
<td>13.7%</td>
<td>19.9%</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pavement</td>
<td>Av</td>
<td>0–4</td>
<td>22.0%</td>
<td>9.8%</td>
<td>13</td>
<td>–5.5 ± 0.27⁸</td>
<td>0.46 ± 0.073⁹</td>
</tr>
<tr>
<td></td>
<td>Bwk</td>
<td>4–32</td>
<td>15.7%</td>
<td>4.9%</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Btk1</td>
<td>32–35</td>
<td>9.8%</td>
<td>3.1%</td>
<td></td>
<td></td>
<td></td>
</tr>
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</table>

Fig. 1. Foliage \( ^{15} \text{N} \) ratios of \( L. \ tridentata \) (creosotebush) as a function of consecutive days with soil matric potential (\( \psi_{\text{matric}} \)) exceeding –6.0 MPa, and the average \( \psi_{\text{matric}} \). Over that time period in four distinct Mojave Desert soils. Horizontal standard error bars (S.E.) are for the mean of 31–131 individual canopy volume observations and 13–129 \( \psi_{\text{matric}} \) estimations at each site; letters show significant differences in \( ^{15} \text{N} \) at \( p < 0.05 \) (a-adjusted LSD); linear regressions are fit to all individual \( ^{15} \text{N} \) 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 15N composition ratio (δ15N) 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 F3,139 = 14.70; p ≤ 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 d at −1.8 MPa was accompanied by 4x greater plant volumes (Table 1). However, in soils of the Young Alluvial site, where 120 d at −4.5 MPa (Intermediate Alluvial) and 13 d at −5.6 MPa (Pavement) had equivalent plant sizes. It may be the case, poorly developed soils allow L. tridentata at the Young Alluvial site to more readily occupy larger soil volumes with more frequent favorable ψmatric compared to the older, more well-developed soils, where stronger argillic horizon development may limit rooting depth (Gile et al., 1998), and low ψmatric may limit plant water relations and growth. In contrast, the strong stone pavement and silt-rich Ah horizon at the Pavement site may limit infiltration and facilitate surface run-off, resulting in very low ψmatric, 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 δ15N differed across the four soils (arc sine transformed data, one-way ANOVA F3,16 = 54.10, p ≤ 0.001), with highest δ15N in plants from the Alluvial site (6.18±0.316 SE), significantly higher than δ15N at the Intermediate Alluvial (3.87±0.438 SE) and Old Alluvial sites (4.17±0.2495SE), 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 ψmatric had significant, negative linear relationships with δ15N (F1,38 = 84.56 and F1,38 = 36.62; p ≤ 0.001 for average ψmatric and duration of water availability, respectively). However, average ψmatric had a much stronger relationship to foliar 15N ratios, explaining ca. 20% more variation in δ15N 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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References