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Enhanced monsoon precipitation and nitrogen deposition affect leaf traits and photosynthesis differently in spring and summer in the desert shrub Larrea tridentata

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Summary

- Leaf-level CO₂ assimilation (Aₘ) can largely be predicted from stomatal conductance (gₛ), leaf morphology (SLA) and nitrogen (N) content (Nₘ) in species across biomes and functional groups.
- The effects of simulated global change scenarios, increased summer monsoon rain (+H₂O), N deposition (+N) and the combination (+H₂O +N), were hypothesized to affect leaf trait-photosynthesis relationships differently in the short- and long-term for the desert shrub Larrea tridentata.
- During the spring, +H₂O and +H₂O +N plants had lower Aₘ and gₛ, but similar shoot water potential (Ψₛ) compared with control and +N plants; differences in Aₘ were attributed to lower leaf Nₘ and gₛ. During the summer, +H₂O and +H₂O +N plants displayed higher Aₘ than control and +N plants, which was attributed to higher Ψₛ, gₛ and SLA. Throughout the year, Aₘ was strongly correlated with gₛ but weakly correlated with leaf Nₘ and SLA.
- We concluded that increased summer monsoon had a stronger effect on the performance of Larrea than increased N deposition. In the short term, the +H₂O and +H₂O +N treatments were associated with increasing Aₘ in summer, but also with low leaf Nₘ and lower Aₘ in the long term the following spring.

Key words: global change, Larrea tridentata, nitrogen, photosynthesis, water relations.

Introduction

Changes in global and regional precipitation patterns are likely to have consequences on growth and photosynthesis for plants of arid ecosystems in the south-western USA (Higgins & Shi, 2001; Houghton et al., 2001; Welzien et al., 2003; Huxman et al., 2004). In addition, creation of reactive nitrogen (N) species has increased 10-fold since the late nineteenth century, nearly doubling the total N input into terrestrial ecosystems, with current deposition estimates of 29–45 kg N ha⁻¹ yr⁻¹ for deserts downwind of major south-western cities in the USA (Smil, 1990; Vitousek et al., 1997; Galloway, 1998; Fenn et al., 2003; Galloway et al., 2004). A concurrence of these two global change phenomena, increased precipitation and N deposition, may greatly impact arid-land plants that exhibit low annual net primary production (NPP) and photosynthesis rates as a consequence of both low mean annual precipitation (MAP) and soil N content (Noy-Meir, 1973; Smith et al., 1997). To anticipate the ecological effects of these global change scenarios, an intact Mojave Desert ecosystem was subjected to fertilization and summer irrigation, simulating increased N deposition and monsoon activity. Changes in plant water potential, CO₂ assimilation and leaf traits that have been correlated with CO₂ assimilation are reported in the short- and long-term for the dominant Mojave Desert perennial, Larrea tridentata.
The rate of CO₂ assimilation on a leaf area \( (A_{\text{area}}) \) or leaf mass basis can largely be described by leaf traits such as N-content per leaf area \( (N_{\text{area}}) \), stomatal conductance \( (g_s) \), and specific leaf area or specific leaf area (SLA) (Field & Mooney, 1986; Reich et al., 1997, 1999). For interspecific comparisons, photosynthetic leaf-trait relationships have revealed common slopes for species from different functional groups and biomes, but different intercepts as arid-land perennial species generally construct leaves of high \( N_{\text{area}} \) but low SLA and \( g_s \) for a given \( A_{\text{area}} \) presumably to increase water conservation (Wright et al., 2001, 2003). For Larrea, \( A_{\text{area}} \) can largely be modeled as a function of \( g_s \), where \( g_s \) is a function of plant water potential (Ψ) and leaf-air vapor pressure deficit (Yan et al., 2000; Ogle & Reynolds, 2002; Naumburg et al., 2003, 2004). This suggests that for Larrea, and perhaps intraspecific comparisons in general, variation in \( A_{\text{area}} \) may be less dependent on changes in leaf \( N_{\text{area}} \) or SLA.

Nitrogen commonly limits plant growth in terrestrial and aquatic ecosystems (Vitousek, 1990). This has been shown in desert environments, where low N levels exist within the biologically active soil zone (West & Skujins, 1978; Smith et al., 1997). The presence of abundant N-fixing organisms in undisturbed desert soils can result in high pulses of N availability and therefore moderately high leaf N content in desert perennials (Killingbeck & Whitford, 1996; Billings et al., 2002). However, for slow-growing plants native to relatively infertile soils, root uptake of N may not increase in response to N pulses (Chapin, 1980). Therefore, increased N deposition may not be associated with increased uptake of N (BassiriRad et al., 1999), increased leaf N content, increased rates of photosynthesis (Lajtha & Whitford, 1989) or growth (Hooper & Johnson, 1999) in arid-land plants. Given the very low MAP and unpredictability of precipitation events in the Mojave Desert, greater N availability may have little impact on desert plant photosynthesis in the absence of sufficient \( \text{H}_2\text{O} \).

The aim of the current study on Larrea was to: (1) determine how increased N deposition and simulated summer monsoon precipitation would affect \( A_{\text{area}} \) and the leaf traits that generally influence \( A_{\text{area}} \); and (2) determine how these relationships vary outside of the monsoon period during the spring primary growing season, and the early summer dry season (June). We hypothesized that because deserts are \( \text{H}_2\text{O} \) and N colimiting: (1) during the cool and moist early spring there would be no difference in Ψ or \( g_s \) between treatments, and N deposition would be associated with increased leaf \( N_{\text{area}} \); leading to increased \( A_{\text{area}} \); (2) during the hot and dry early summer there would be differences in leaf \( N_{\text{area}} \) caused by N deposition, but no difference in \( A_{\text{area}} \) or \( g_s \) because of the overriding effects of low Ψ on all plants; and (3) during and immediately after the added summer monsoon events, \( A_{\text{area}} \) would greatly increase and be associated with increased Ψ and \( g_s \) and N deposition would be associated with both increased leaf \( N_{\text{area}} \) and \( A_{\text{area}} \) for treatments combining N deposition with monsoon events. It was explicitly assumed that water availability would dictate the photosynthesis-leaf trait relationship, and that different leaf traits would be associated with increased \( A_{\text{area}} \) at different times of the year. It was also assumed that variation in \( A_{\text{area}} \) would have no relationship to changes in SLA in this intraspecific comparison.

### Methods and Materials

#### Study site and sampling dates

The Mojave Global Change Facility (MGCF) is located on the Nevada Test Site (36°49' N, 115°55' W; altitude 970 m) as part of the US Department of Energy's National Environmental Research Park Network. This area of the northern Mojave Desert has been closed to the public and livestock grazing for over 50 yr, and therefore provides a relatively undisturbed ecosystem. Vegetation at the MGCF is typical of the Mojave Desert, consisting of perennial shrubs and grasses (< 20% perennial plant cover), as well as annual forbs and grasses (Jordan et al., 1999). The dominant shrub, Larrea tridentata (DC) Cov. (Zygophyllaceae), is a C₃ evergreen (Smith et al., 1997). MAP at the MGCF is 138 ± 62 mm, falling mostly during winter months (Hunter, 1994), with highly episodic summer precipitation and a low relative frequency of large rainfall events that are effective in stimulating woody plant activity (Huxman et al., 2004).

Individual study plots were 14 × 14 m (196 m²). For each plot, a 16 × 16 m area was subjected to the treatment (or treatment combination), which allows for a 1-m buffer area so that the entire 14 × 14 m plot could be used for measurements. Overall, the experiment involved three factors arranged in a factorial design involving 96 plots with two monsoon treatments (+ and 0), three N treatments (0, 10, and 40 kg N ha⁻¹ yr⁻¹) and two biological soil disturbance regimes (+ and 0), with a sample size of eight plots per cell. In this paper, we focused on results from treatments imposing summer monsoons (+H₂O), N deposition at 40 kg N ha⁻¹ yr⁻¹ (+N), and the combination of summer monsoon and N deposition (+H₂O +N) compared with control plots receiving ambient water and N. In 2003, as in 2001 and 2002, H₂O was applied in three 25 mm events every 3 wk from early July to mid-August. The total supplemental 75 mm H₂O represents a threefold increase in mean annual summer precipitation, but only a 50% increase in MAP.

Supplemental N was added in November each year as Ca(NO₃)₂ in solution via sprinklers, approximating the range of N deposition in the Las Vegas, NV, USA (10 kg N ha⁻¹ year⁻¹) and Los Angeles, CA, USA (40 kg N ha⁻¹ year⁻¹) areas. This resulted in a total application of no more than 5 mm of water, which was also added to all non-+N plots to ensure equal watering among treatments (this level of added water results in a shallow wetting front that is insufficient to stimulate perennial plant activity or germination of annual plants; Huxman et al., 2004). Adding N in the autumn occurs before natural winter precipitation, which moves the N down into the soil profile to make it available to plants (Smith & Nowak, 1990), and also at a time when microbial activity is low due to cold soils. We
have confirmed, using $^{15}\text{N}$ analyses, that the added N is indeed being taken up by Larrea plants – the $^{15}\text{N}$ of the Ca(NO$_3$)$_2$ fertilizer was c. +1.5%, which resulted in a c. 1% lower $^{15}\text{N}$ value of Larrea leaves in +N plots (+3% vs +4% in controls). Given the high N volatilization rates in desert soils, this decreased $^{15}\text{N}$ (toward the fertilizer value) suggests that at least a modest proportion of the applied N was available for perennial plant uptake. Larrea plants were sampled throughout the 2003 growing season, including the relatively wet spring period (3 April and 6 May), at the end of the dry period before the simulated monsoon events (1 July), 1 wk after the second (30 July) and third (13 August) monsoon events, and a month after the third monsoon event (10 September).

Gas exchange and plant water status

Shoots selected for gas exchange were located on the outside of the canopy, and characterized by a newly emerged leaf pair and at least four additional pairs of oppositely attached leaves, ensuring a heterogeneous mix of leaf ages. Because leaves are flushed in distinct cohorts following rainfall events and then retained for a year or more (Smith et al., 1997), leaf age remained relatively constant throughout each seasonal measurement period. Photosynthesis was measured using a portable open-flow gas exchange system (LI-6400; LICOR, Inc., Lincoln, NE, USA). Measurements were taken under ambient environmental conditions between 07:30 and 10:30 h to avoid potential midday stomatal closure. Previous studies at our site have determined that maximum assimilation for Larrea occurs during these hours, and that mid-morning $A$ can be used to accurately predict daily net $A$ (Naumburg et al., 2003). Block temperature ($T$) was set at the ambient $T$ recorded on Larrea shoots located on the outside of the canopy and analyzed for N content at the Stable Isotope Facility, University of California, Davis, CA, USA.

Statistical analyses

Differences in physiological parameter means among monsoon treatments, N treatments, and date were tested using mixed model analysis of variance (ANOVA; PROC MIXED; SAS V.8; SAS Institute, Cary, NC, USA). Water, N, date, and their interactions were modeled as fixed effects, while plot and individual plant within-plot were modeled as random effects to account for spatial variability and repeated measurements. A date-within-season interaction was dropped in cases where it was not significant because of the large numbers of parameters in the model relative to the sample size. Post-hoc linear contrasts were used to determine a seasonal effect in cases where 'date' was significant because of the limited df. We adopted a statistical cut-off value (alpha) of 0.10 because of the low statistical power associated with small sample size and high variability in the context of the natural environment. For significant overall effects ($\alpha = 0.10$), pairwise differences were examined using the Tukey post-hoc test.

We tested for treatment differences in slopes between $A_{\text{area}}$, $N_{\text{area}}$, $A_{\text{rea}}$, and $g_{\text{rea}}$ and $A_{\text{area}}$ and SLA using an analysis of covariance (ANCOVA). The model included $H_2O$, N and season, with all appropriate interactions with and without the covariate ($N_{\text{area}}$, $g_{\text{rea}}$ and SLA, respectively) as fixed effects, and plot and individual plant within-plot as random effects to account for spatial variability and repeated measurements. A date-within-season effect tended to reduce much of the variability caused by treatment that we desired to explore in the model (since different dates had different ambient conditions), so it was not included in the final model. Significant differences among slopes were further explored using pairwise tests.

A multiple linear regression was used to study the respective contributions of $N_{\text{area}}$, $g_{\text{rea}}$ and SLA to $A_{\text{area}}$. Partial $r^2$ values were obtained for each effect by fitting the model with and without
the effect of interest. A separate model was fitted for each irrigation and season combination, irrespective of N, because the ANCOVA above indicated no heterogeneity of slopes in response to the +N treatment. The effect of individual or date was not included in this model because most of the variation in \( A_{\text{area}} \) was apparently environmentally, not genetically, induced (data not shown). Insufficient data were available to look at multivariate relationships within each date.

Multivariate relationships were further explored using a principal components analysis (PCA), which included \( A_{\text{area}}, g_s, \) SLA and \( N_{\text{area}} \). Two components were retained and analysed using ANOVA with H\(_2\)O, N, season and their interactions as fixed effects, and plot and individual within-plot as random effects for Tukey post-hoc tests.

**Results**

**Precipitation and overall treatment effects**

Natural precipitation at the MGCF in the 2003 hydrologic year (1 October 2002–30 September 2003) totaled 149 mm (c. 8% higher than MAP), with three monsoon events adding 25 mm of H\(_2\)O every 3 wk (Fig. 1). We use hydrologic-year precipitation for Mojave Desert functional studies, as autumn rains tend to be stored in the soil and not used by plants until the following spring growing season. \( A_{\text{area}}, g_s, \) predawn \( \Psi_{\text{shoot}}, N_{\text{area}} \) and SLA all responded significantly to the monsoon treatment, date, and their interaction, reflecting the primary importance of seasonal water availability (Table 1). Few effects of N deposition were observed in any measured parameter, with the significant exception of predawn \( \Psi_{\text{shoot}} \) (\( P < 0.05 \)). We observed a synergistic effect of N and H\(_2\)O in only one instance, for \( A_{\text{area}} \) (Table 1), and this effect was weakly significant (0.05 < \( P < 0.10 \)).

**Gas exchange, leaf N content, SLA and shoot water potential**

During early spring, Larrea plants treated with +H\(_2\)O and +H\(_2\)O +N the previous year had a mean \( A_{\text{area}} \) c. 30% lower than control and +N-treated plants (Table 1). For +H\(_2\)O and +H\(_2\)O +N plants, lower \( A_{\text{area}} \) was accompanied by c. 27% lower

**Table 1** Results of ANOVA for effects of simulated summer monsoon precipitation (H\(_2\)O), nitrogen deposition (N), and date on physiological parameters for Larrea tridentata

<table>
<thead>
<tr>
<th>Parameter</th>
<th>H(_2)O</th>
<th>N</th>
<th>Date</th>
<th>H(_2)O x N</th>
<th>H(_2)O x Date</th>
<th>N x Date</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>( A_{\text{area}} )</td>
<td>2.82*</td>
<td>0.13</td>
<td>26.70***</td>
<td>3.04*</td>
<td>22.57***</td>
<td>0.92</td>
<td>119</td>
</tr>
<tr>
<td>( g_s )</td>
<td>4.26**</td>
<td>0.55</td>
<td>32.71***</td>
<td>1.57</td>
<td>23.57***</td>
<td>1.33</td>
<td>119</td>
</tr>
<tr>
<td>( N_{\text{area}} )</td>
<td>65.93***</td>
<td>0.15</td>
<td>7.65***</td>
<td>0.43</td>
<td>7.59***</td>
<td>1.02</td>
<td>127</td>
</tr>
<tr>
<td>( \Psi_{\text{shoot}} )</td>
<td>63.91***</td>
<td>6.67**</td>
<td>155.66***</td>
<td>0.29</td>
<td>26.20***</td>
<td>1.46</td>
<td>103</td>
</tr>
<tr>
<td>SLA</td>
<td>65.93***</td>
<td>2.08</td>
<td>5.21***</td>
<td>0.51</td>
<td>7.59***</td>
<td>1.02</td>
<td>130</td>
</tr>
<tr>
<td>( V_{\text{max}} )</td>
<td>5.42**</td>
<td>0.43</td>
<td>3.40*</td>
<td>0.96</td>
<td>3.50*</td>
<td>0.00</td>
<td>21</td>
</tr>
<tr>
<td>( I_{\text{max}} )</td>
<td>5.97**</td>
<td>2.64</td>
<td>6.17**</td>
<td>2.44</td>
<td>6.95**</td>
<td>4.04*</td>
<td>21</td>
</tr>
<tr>
<td>df</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
</tbody>
</table>

Parameters included: assimilation of CO\(_2\) per unit leaf area (\( A_{\text{area}} \)), stomatal conductance (\( g_s \)), leaf N content (\( N_{\text{area}} \)), predawn shoot water potential (\( \Psi_{\text{shoot}} \)), specific leaf area (SLA), maximum carboxylation capacity (\( V_{\text{max}} \)), and maximum electron transport rate (\( I_{\text{max}} \)). \( V_{\text{max}} \) and \( I_{\text{max}} \) measurements were restricted to one date each in spring and autumn seasons (S) and were analysed accordingly. F-statistics are reported, accompanied by significance levels (***, \( P < 0.01 \); **, 0.01 < \( P < 0.05 \); *, 0.05 < \( P < 0.10 \)).
Fig. 2 Gas exchange parameters, leaf nitrogen (N) content and shoot water potential over the course of the 2003 growing season for *Larrea tridentate*. (a) Area-based net photosynthetic rate ($A_{\text{area}}$); (b) stomatal conductance to water vapor ($g_s$); (c) area-based leaf N content ($N_{\text{area}}$); (d) specific leaf area (SLA); (e) predawn shoot water potential ($\psi_{\text{shoot}}$). Treatment designations are shown in (e) for the entire panel, control (open circles), +N (closed circles), +H$_2$O (open triangles), +H$_2$O+N (closed triangles). All points are mean ± SE ($n = 4–6$); ***, $P < 0.01$; **, $0.01 < P < 0.05$; *, $0.05 < P < 0.10$. The arrow indicates the beginning of the monsoon treatments.

Fig. 3 Mean principal component (PC) scores for all treatments (symbols same as in 2e) pooled into seasons (summer and spring). Loadings associated with the PCs are indicated on the x and y axes. Mean ± SE ($n = 12–18$) from the first two PCs are shown; significant differences ($\alpha = 0.10$ from post-hoc tests following ANOVA with independent variables as in Table 1) for PC1 are on the left; significant differences for PC2 are shown along the bottom.

Principal components analysis

Principal components analysis was used to elucidate season-by-treatment effects on leaf characteristics (Fig. 3). The first principal component (PC1) explained c. 50% of total variance, with high positive loadings for $g_s$ and $A_{\text{area}}$. Subsequent ANOVA on PC1 revealed a strong H$_2$O-by-season interaction ($F_{1,90} = 27.1; P < 0.0001$). The second principal component (PC2) explained c. 38% of the variance, with a high positive loading for $N_{\text{area}}$ and an equally high negative loading for SLA. ANOVA on PC2 also showed a significant H$_2$O-by-season interaction ($F_{1,90} = 7.53; P < 0.005$).

In the spring, control and +N plants were characterized by high \( N_{\text{area}} \), \( A_{\text{area}} \) and \( g_s \) but low SLA, whereas +H\(_2\)O and +H\(_2\)O +N plants had significantly lower means for both principal components. During the summer, +H\(_2\)O and +H\(_2\)O +N plants had higher mean values of \( A_{\text{area}} \), \( g_s \) and SLA and lower mean values of \( N_{\text{area}} \) than did control and +N plants. The +N treatment did not significantly impact principal component scores in any instance (data not shown).

Seasonal effects on the relationships between \( A_{\text{area}} \), \( g_s \), \( N_{\text{area}} \) and SLA

Few effects of N deposition were observed in any measured parameter, therefore treatments were collapsed into +Monsoon (i.e. +H\(_2\)O and +H\(_2\)O +N) and –Monsoon (control and +N) groups, the latter functioning as the control henceforth (Figs 4 and 5). Simple linear regressions of leaf \( N_{\text{area}} \), \( g_s \) and SLA demonstrated significant relationships with \( A_{\text{area}} \) that differed between seasons and monsoon treatment (Fig. 4). ANCOVA results suggested there was no heterogeneity of slopes associated with +N or its interactions (data not shown). For all season and treatment combinations, \( g_s \) explained between 74% and 90% of the variation in \( A_{\text{area}} \) when regressed alone (Fig. 4a,b). Much of this variation was independent of covariation with \( N_{\text{area}} \) and SLA (partial \( r^2 \) from multiple regression with \( g_s \), \( N_{\text{area}} \) and SLA was between 29% and 71%). The slope describing the strong relationship between \( A_{\text{area}} \) and \( g_s \) did not vary significantly by monsoon treatment or season combinations.

\( N_{\text{area}} \) had a significant relationship with \( A_{\text{area}} \) for –Monsoon plants in the spring and for +Monsoon plants during the summer, explaining 34% and 37% of the variance in \( A_{\text{area}} \), respectively (Fig. 4c,d). ANCOVA revealed significant heterogeneity of slopes by monsoon treatment and season (data not shown), driven by a significantly steeper slope between \( A_{\text{area}} \) and \( N_{\text{area}} \) for +Monsoon plants in the summer compared with –Monsoon plants (Fig. 4c,d). The significant relationships between \( A_{\text{area}} \) and \( N_{\text{area}} \) were caused by covariation between \( N_{\text{area}} \) and \( g_s \), as the multiple regression revealed weak partial relationships between

Fig. 4 Relationships derived from linear regressions between area-based net photosynthetic rate (\( A_{\text{area}} \)) with stomatal conductance to water vapor (\( g_s \)), area-based leaf N content (\( N_{\text{area}} \)) and specific leaf area (SLA). Data were pooled into spring (a,c,e) and summer (b,d,f) seasons, and collapsed into two treatments, +Monsoon (+H\(_2\)O and +H\(_2\)O +N) and –Monsoon (control and +N). (a) \( A_{\text{area}} \) by \( g_s \) in spring; (b) \( A_{\text{area}} \) by \( g_s \) in summer; (c) \( A_{\text{area}} \) by \( N_{\text{area}} \) in spring; (d) \( A_{\text{area}} \) by \( N_{\text{area}} \) in summer; (e) \( A_{\text{area}} \) by SLA in spring; (f) \( A_{\text{area}} \) by SLA in summer. Individual treatment regressions are noted by asterisks for significant and NS for nonsignificant relationships. Different superscript letters indicate a significant difference in pairwise comparisons of slopes of relationships between treatments within a season.
Seasonal changes in photosynthesis and leaf traits

Water availability is the most important environmental factor limiting NPP for over 40% of the earth's vegetated surface (Lal, 2004), and changing monsoon dynamics increase NPP in arid ecosystems (Nemani et al., 2003). Our data suggest that an increase in summer monsoon precipitation in the south-western USA will lead to increased $A_{\text{area}}$, most likely increasing NPP in Larrea tridentata irrespective of increased N deposition. However, the positive effect of increased summer monsoon precipitation on $A_{\text{area}}$ will be limited to a potentially short duration after precipitation events as a result of rapid rates of evapotranspiration leading to soil moisture depletion (Smith et al., 1997). What we found surprising was the apparent indirect effect of summer precipitation on $A_{\text{area}}$ the following spring – dilution of leaf $N_{\text{area}}$ leading to lower rates of $g_s$ and $A_{\text{area}}$. During either spring or summer, $A_{\text{area}}$ was strongly associated with high rates of $g_s$, but whether $N_{\text{area}}$ was also positively associated with $A_{\text{area}}$, albeit more weakly, was dependent on the season. Although N deposition did not significantly alter leaf $N_{\text{area}}$, $N_{\text{area}}$ varied throughout the growing season and was positively associated with $A_{\text{area}}$ only when $g_s$ was sufficiently high in the early spring, and during monsoon treatment in the summer. SLA was affected by monsoon precipitation, but for the most part was not correlated with variation in $A_{\text{area}}$.

In the spring, the highest rates of $A_{\text{area}}$, $g_s$, $V_{\text{cmax}}$ and $J_{\text{max}}$ were observed in $-$Monsoon plants (i.e. control and $+$N plants). There was no difference in plant $W_{\text{shoot}}$ between $-$Monsoon and $+$Monsoon plants (i.e. $+$H$_2$O and $+$H$_2$O $+$N plants). Therefore, differences in plant water status do not explain differences observed in gas exchange parameters. High leaf $N_{\text{area}}$ was weakly but positively correlated with $A_{\text{area}}$ in $-$Monsoon plants, and may have positively affected photosynthetic
capacity by increasing the content of proteins associated with carbon fixation and electron transport (Wong et al., 1979, 1985; Evans & Seemann, 1989; Evans, 1989). Given the reported linear relationship between $V_{\text{cm}}$ and $N_{\text{area}}$, lower values of $V_{\text{cm}}$ in +Monsoon plants can be explained by the lower leaf $N_{\text{area}}$ (Wullschlegel, 1993; Medlyn et al., 1999). Analysis of relative stomatal limitation (RSL) revealed no difference in stomatal (i.e. diffusional) limitation between +Monsoon and -Monsoon plants during the spring, further implying N-dependent biochemical limitations were operating in +Monsoon plants to a greater extent than in -Monsoon plants. Although the relationship of $A_{\text{area}}$ and $N_{\text{area}}$ has been demonstrated in many previous studies (Field & Mooney, 1986; Evans, 1989; Schulze et al., 1994; Reich et al., 1999), here the relationship was seasonally dependent, disappearing as summer drought commenced.

During the summer, high rates of $A_{\text{area}}$ and $g_{s}$ were associated with +Monsoon plants, and differed from spring responses as there were also large differences in $\Psi_{\text{boot}}$ and only small differences in leaf $N_{\text{area}}$ between -Monsoon and +Monsoon plants. Alleviation of summer drought conditions and increasing $\Psi_{\text{boot}}$ were most likely responsible for increasing $A_{\text{area}}$ and $g_{s}$ in the +Monsoon plants, as has been reported for this species (Meinzer et al., 1998; Franco et al., 1994), $V_{\text{max}}$ and $J_{\text{max}}$ did not differ significantly between treatments, even though $A_{\text{area}}$ was lower in -Monsoon plants at ambient CO$_2$ levels. In this case, the reduction in $A_{\text{area}}$ at ambient CO$_2$ was partly compensated for at higher CO$_2$ concentrations, although our analysis of RSL revealed only c. 10% higher stomatal limitation in -Monsoon plants. Stomatal limitations to photosynthesis can account for up to a 65% reduction in $A_{\text{area}}$ in exposed canopy leaves experiencing summer drought, and are undoubtedly significant for drought-adapted species (Ellsworth, 2000; Flexas & Medrano, 2002; Lawlor & Cornic, 2002; Medrano et al., 2002; Centritto et al., 2003; Grassi & Magnani, 2005). Here, we have demonstrated that relief of stomatal limitation to photosynthesis by +Monsoon treatment may have led to increased nonstomatal limitation (via lower leaf $N_{\text{area}}$) the following spring.

Seasonal changes in leaf $N_{\text{area}}$

Contrary to our original hypothesis, N deposition did not lead to significantly higher leaf $N_{\text{area}}$ or higher $A_{\text{area}}$, although leaves with higher $N_{\text{area}}$ did realize a higher $A_{\text{area}}$ in the spring. Water input during the previous summer determined whether leaves possessed high $N_{\text{area}}$. Presumably, rapid growth and high $A_{\text{area}}$ in response to the +Monsoon treatment during the summer (2002) resulted in the dilution of leaf $N_{\text{area}}$ in the following spring (2003) in these long-lived, evergreen leaves. Lajtha & Whitford (1989) found a twofold increase in $N_{\text{area}}$ in Larrea leaves during the winter, followed by a gradual reduction during the spring/summer growing season. Perennials may accumulate N in older leaves and stems (Mooney & Rundel, 1979; Romney & Wallace, 1980; but see Killingbeck & Whitford, 1996) during nongrowing periods, and then use this N source during the growing season when there is greater competition for nutrients. This may be a strategy employed by Larrea in the Mojave Desert, where it does not exhibit active growth in the winter (owing to nightly freeze events) during a time when soils tend to be moist and microbial activity is mineralizing soil N. However, in this study, the accumulation of high leaf $N_{\text{area}}$ did not occur in plants receiving +Monsoon treatments because added summer rain may have counteracted the natural accumulation of leaf $N_{\text{area}}$ through enhanced growth (B. Newingham & S. Smith, unpubl.) and subsequent N dilution, thereby reducing the maximum potential rate of $A_{\text{area}}$ in the spring. This implies that C uptake rates during and after the +Monsoon treatments may not have been balanced with increased N uptake rates — two processes thought to be interdependent (Bloom et al., 1985; Grime, 1994; Rothstein & Zak, 2001).

Nitrogen deposition did not increase leaf $N_{\text{area}}$, although leaf $^{15}$N signature indicated that the added N was taken up by Larrea plants. This implies that when presented with a pulse of N, Larrea may have limited N-uptake capacity. This was suggested by BassiriRad et al. (1999), as root uptake kinetics were not upregulated in response to $^{15}$NO$_3^-$ enrichment and required proliferation of new roots to increase foliar $^{15}$N. That N deposition did not increase leaf $N_{\text{area}}$ implies: (1) Larrea may not have the capacity to increase NO$_3^-$ uptake when NO$_3^-$ becomes abundant owing to adaptive constraints to infertile soil (Chapin, 1980); (2) Larrea is colimited by H$_2$O and NO$_3^-$, requiring sufficient H$_2$O availability to stimulate new root growth to increase NO$_3^-$ uptake (BassiriRad et al., 1999); or (3) the lack of an effect from N deposition may be an artifact of our autumn application of N, with spring application or natural N deposition occurring over the whole year potentially giving a different result. Although we cannot completely rule out the latter, the second possibility is most likely the case as we have demonstrated no effect from N deposition in the absence of additional summer monsoon precipitation in 2003.

Finally, although they are beyond the scope of this work, there are important ecosystem-scale processes that may affect the leaf-level responses that we have observed here, and vice versa. Obviously, a significant increase in summer rain in an environment with a long-term history of winter precipitation and low, highly episodic summer rainfall may change plant growth, allocation between shoots and roots, rooting distributions and the biogeochemical cycling of N. Long-term increases in N deposition could similarly affect these important parameters. Of particular relevance to our results, the spring decline in $N_{\text{area}}$ following enhanced summer rainfall may have been caused by changes in whole-plant allocation patterns, or possibly by increased soil N losses through volatilization in the summer, which in turn would lower leaf N in the +Monsoon treatment plots and subsequently lower photosynthesis in the spring growing season. In turn, long-term increases in $A_{\text{area}}$ and SLA, combined with lower $N_{\text{area}}$, would have potentially important feedback on primary production, herbivory and
decomposition processes. Our research team is currently investigating these ecosystem-level responses at the MGCF.

Conclusions

High leaf $N_{\text{are}}$ may be part of an arid-land plant strategy employed to maximize photosynthesis while maintaining relatively low $g_{\text{s}}$ thereby minimizing water loss (Wright et al., 2001). However, plants exposed to a simulated summer monsoon had generally lower leaf $N_{\text{are}}$, which in turn resulted in lower $A_{\text{are}}$ when compared with controls at similar water potentials (i.e. the next spring growing season). When analysed across the entire year, the $A_{\text{are}}$--SLA relationship was poor and the $A_{\text{are}}$--$N_{\text{are}}$ relationship weak, at best, with the only significant correlation for the latter during times of high plant water potential in concert with seasonal water pulses. Therefore, the $A_{\text{are}}$--$N_{\text{are}}$ relationship and other leaf trait relationships, shown to have strong predictive value in interspecific comparisons across biomes (Reich et al., 1999, 1997, 1998, 1999), may be functionally of poor predictive value for intraspecific comparisons and in the absence of plant water status data. In order to anticipate global change scenarios on plant performance in water-limited systems, models incorporating plant or soil water status (Ogle & Reynolds, 2002) with biochemistry and gas exchange (Farquhar et al., 2001) will need to be developed to accurately predict responses for photosynthesis from leaf traits (Reich et al., 1999). The underlying reason for seasonal responses shown here for a desert evergreen xerophyte, L. tridentata, most likely originates from this dependence of the $A_{\text{are}}$--leaf trait relationships on plant water status.

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References


