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Source: *The New Phytologist*, Vol. 169, No. 4, Pollination Mutualism in Caryophyllaceae (2006), pp. 799-808

Published by: Wiley on behalf of the New Phytologist Trust

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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

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Received: 4 August 2005

Accepted: 24 October 2005

- Leaf-level CO₂ assimilation (A_{area}) can largely be predicted from stomatal conductance (g_s), leaf morphology (SLA) and nitrogen (N) content (N_{area}) 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 A_{area} and g_s , but similar shoot water potential (Ψ_{shoot}) compared with control and +N plants; differences in A_{area} were attributed to lower leaf N_{area} and g_s . During the summer, +H₂O and +H₂O +N plants displayed higher A_{area} than control and +N plants, which was attributed to higher Ψ_{shoot} , g_s and SLA. Throughout the year, A_{area} was strongly correlated with g_s but weakly correlated with leaf N_{area} 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 A_{area} in summer, but also with low leaf N_{area} and lower A_{area} in the long term the following spring.

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

New Phytologist (2006) **169**: 799–808

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doi: 10.1111/j.1469-8137.2005.01628.x

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; Weltzin *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_{area}) or leaf mass basis can largely be described by leaf traits such as N-content per leaf area (N_{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_{area} , but low SLA and g_s for a given A_{area} , presumably to increase water conservation (Wright *et al.*, 2001, 2003). For *Larrea*, A_{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_{area} may be less dependent on changes in leaf N_{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 H₂O.

The aim of the current study on *Larrea* was to: (1) determine how increased N deposition and simulated summer monsoon precipitation would affect A_{area} and the leaf traits that generally influence A_{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 H₂O and N colimited: (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_{area} , leading to increased A_{area} ; (2) during the hot and dry early summer there would be differences in leaf N_{area} caused by to N deposition, but no difference in A_{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_{area} would greatly increase and be associated with increased Ψ and g_s , and N deposition would be associated with both increased leaf N_{area} and A_{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_{area} at different times of the year. It was also assumed that variation in A_{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 CaNO₃ 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 $\delta^{15}\text{N}$ analyses, that the added N is indeed being taken up by *Larrea* plants – the $\delta^{15}\text{N}$ of the CaNO_3 fertilizer was *c.* +1.5‰, which resulted in a *c.* 1‰ lower $\delta^{15}\text{N}$ value of *Larrea* leaves in +N plots (+3‰ vs +4‰ in controls). Given the high N volatilization rates in desert soils, this decreased $\delta^{15}\text{N}$ (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 during the first measurement to minimize *T* effects on the leaf-air vapor pressure deficit (VPD) and *A*; average block *T* and leaf VPD were, respectively: 14.0°C and 1.46 kPa on 3 April; 22°C and 2.3 kPa on 6 May; 30°C and 4.5 kPa on 1 July; 27°C and 2.9 kPa on 30 July; 29°C and 4.0 kPa on 13 August; and 25°C and 2 kPa on 10 September. All measurements were made under saturating photosynthetic photon fluence rate (PPFR = 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$), that had been previously determined as saturating by light response curves, using a red/blue LED (LI 6400–02B).

The *A/C_i* curves (assimilation rate/internal CO_2 concentration) were generated *in situ* during the spring (28 March) and summer (14 and 15 August) on *Larrea* shoots using the gas exchange system detailed earlier. Shoots were exposed for 5 min at each CO_2 concentration in the following sequence –360 $\mu\text{mol CO}_2 \text{ mol}^{-1}$, then 80, 120, 200, 280, 450, 550, 800, 1100 and 1600 $\mu\text{mol CO}_2 \text{ mol}^{-1}$. The value of *C_i* at each *C_a* was calculated using the equations of von Caemmerer & Farquhar (1981). The *A/C_i* curves were analysed with an Excel (Microsoft, Redmond, WA, USA) macro using methods described by Harley *et al.* (1992) with temperature constants as described in Bernacchi *et al.* (2001, 2003). For a detailed description of the methodology see Appendix A in Ellsworth *et al.* (2004). Electron transport

rate (*J_{max}*) and maximum carboxylation velocity of Rubisco (*V_{cmx}*) were temperature corrected for 25°C using the macro. Relative stomatal vs nonstomatal limitation was estimated for both the spring and summer measurements as described by Farquhar and Sharkey (1982).

Plant water status was measured using a plant water console (Model 3000 pressure chamber; Soil Moisture Equipment Corp., Santa Barbara, CA, USA) during predawn hours (*c.* 03 : 00–05 : 00 h). Shoot samples were collected from the same shrubs from which photosynthesis was measured later in the morning.

Leaf samples were scanned using an HP Scanjet 3500c flatbed scanner (Hewlett-Packard Co., Palo Alto, CA, USA), and leaf area (LA) was calculated using SCION IMAGE (version 4.0.2; Scion Corp., Frederick, MD, USA; see O'Neal *et al.*, 2002). Gas exchange parameters were computed using the scanned LA values with LI-6400 simulator software (ver 5.1, LICOR Inc.). Leaves were subsequently dried at 60°C for 2 d and weighed to determine SLA. After determining SLA, dried leaf samples were ground and analysed 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 avoid pseudo-replication. The three-way 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_{area}* and *N_{area}*, *A_{area}* and *g_s*, and *A_{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_{area}*, *g_s* 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_{area}*, *g_s* and SLA to *A_{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_{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_{area} , g_s , SLA and N_{area} . Two components were retained and analysed using ANOVA with H_2O , 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 MGCFC 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_2O 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_{area} , g_s , predawn Ψ_{shoot} , N_{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 Ψ_{shoot} ($P < 0.05$). We observed a synergistic effect of N and H_2O in only one instance, for A_{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 $+H_2O$ and $+H_2O + N$ the previous year had a mean A_{area} c. 30% lower than control and +N-treated plants (Table 1). For $+H_2O$ and $+H_2O + N$ plants, lower A_{area} was accompanied by c. 27% lower

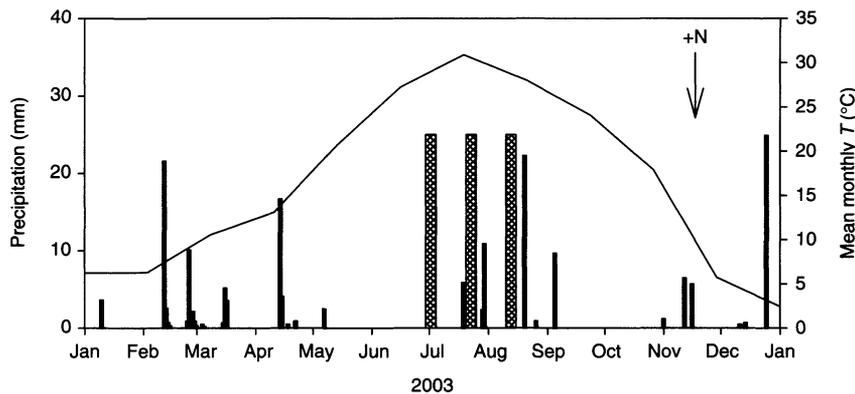


Fig. 1 Natural and artificial precipitation (mm), and mean monthly temperature ($^{\circ}C$) at the Mojave Global Change Facility in 2003. Three simulated monsoon events on 1 July, 22 July and 13 August (hatched bars) delivered a total of 75 mm of H_2O during the summer, the third year in which monsoonal precipitation had been applied. Natural precipitation for 2003 is depicted with thin, closed bars. (Note: the arrow indicates nitrogen (N) deposition in November 2003, which was also applied in November 2001 and November 2002).

Table 1 Results of ANOVA for effects of simulated summer monsoon precipitation (H_2O), nitrogen deposition (N), and date on physiological parameters for *Larrea tridentata*

	H_2O	N	Date	$H_2O \times N$	$H_2O \times \text{Date}$	$N \times \text{Date}$	<i>n</i>
A_{area}	2.82*	0.13	26.70***	3.04*	22.57***	0.92	119
g_s	4.26**	0.55	32.71***	1.57	23.57***	1.33	119
N_{area}	65.93***	0.15	7.65***	0.43	7.59***	1.02	127
Ψ_{shoot}	63.91***	6.67**	155.66***	0.29	26.20***	1.46	103
SLA	65.93***	2.08	5.21***	0.51	7.59***	1.02	130
df	1	1	5	1	5	5	
	H_2O	N	S	$H_2O \times N$	$H_2O \times S$	$N \times S$	<i>n</i>
V_{cmax}	5.42**	0.43	3.40*	0.96	3.50*	0.00	21
J_{max}	5.97**	2.64	6.17**	2.44	6.95**	4.04*	21
df	1	1	1	1	1	1	

Parameters included: assimilation of CO_2 per unit leaf area (A_{area}), stomatal conductance (g_s), leaf N content (N_{area}), predawn shoot water potential (Ψ_{shoot}), specific leaf area (SLA), maximum carboxylation capacity (V_{cmax}), and maximum electron transport rate (J_{max}). V_{cmax} and J_{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 (***, $P < 0.01$; **, $0.01 < P < 0.05$; *, $0.05 < P < 0.10$).

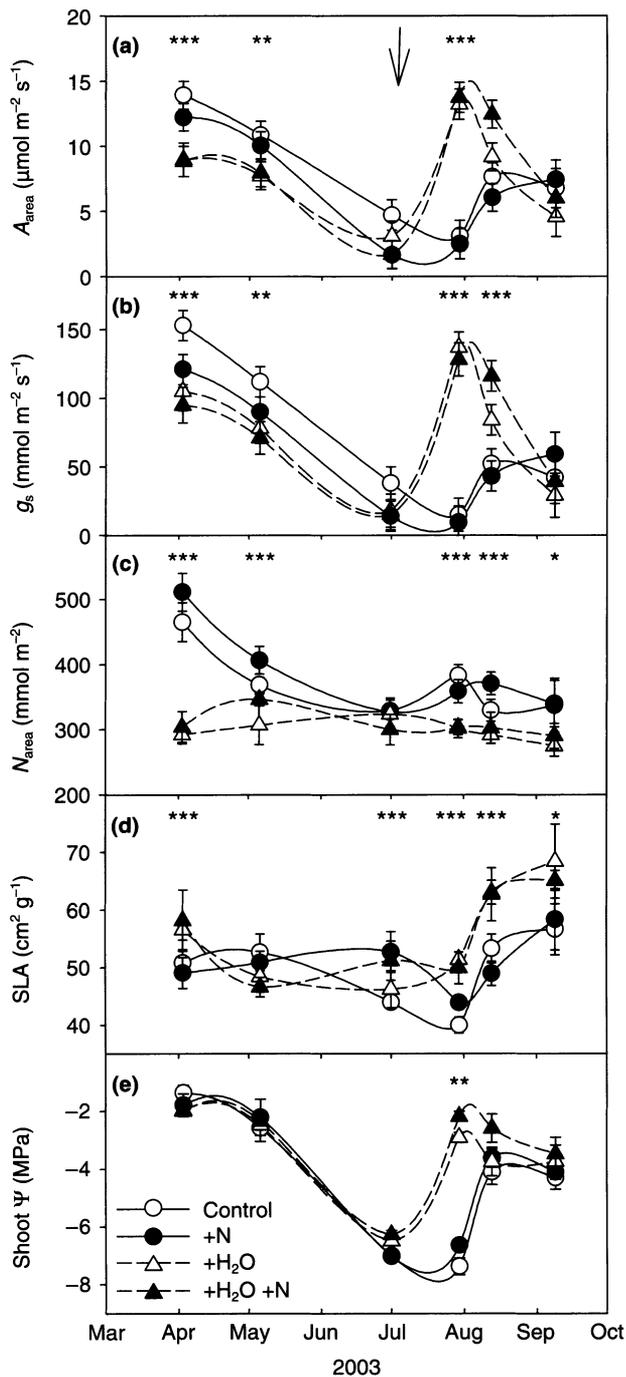


Fig. 2 Gas exchange parameters, leaf nitrogen (N) content and shoot water potential over the course of the 2003 growing season for *Larrea tridentate*. (a) Area-based net photosynthetic rate (A_{area}); (b) stomatal conductance to water vapor (g_s); (c) area-based leaf N content (N_{area}); (d) specific leaf area (SLA); (e) predawn shoot water potential (Ψ_{shoot}). Treatment designations are shown in (e) for the entire panel, control (open circles), +N (closed circles), +H₂O (open triangles), +H₂O+N (closed triangles). All points are mean \pm 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.

g_s and c . 39% lower N_{area} , whereas SLA was c . 10% higher than in controls and +N plants (Fig. 2). Differences in A_{area} could not be attributed to treatment differences affecting Ψ_{shoot} , which was indistinguishable during spring (mean Ψ_{shoot} for all treatments = -2.1 MPa). A similar but weaker pattern was also seen in late May under drying conditions (Figs 1 and 2), when all plant responses decreased from those recorded in March. June was the driest month in 2003 (Fig. 1), with all plant responses very low; with the exception of SLA no response differed significantly by treatment during this period (Fig. 2). After initiation of the summer monsoon treatment in July, +H₂O and +H₂O+N plants had at least fourfold higher rates of A_{area} , nearly sixfold higher g_s , c . 20% higher SLA, but almost 20% less leaf N_{area} than control and +N plants. By September, 4 wk after the last monsoon treatment event, but only days after receiving over 20 mm of natural precipitation (Fig. 1), control and +N plants had increased Ψ_{shoot} , A_{area} and g_s similar to values for +H₂O and +H₂O+N plants, although N_{area} remained lower and SLA higher in the latter treatments.

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_{area} . Subsequent ANOVA on PC1 revealed a strong H₂O-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_{area} and an equally high negative loading for SLA. ANOVA on PC2 also showed a significant H₂O-by-season interaction ($F_{1,90} = 7.53$;

High g_s and A_{area}

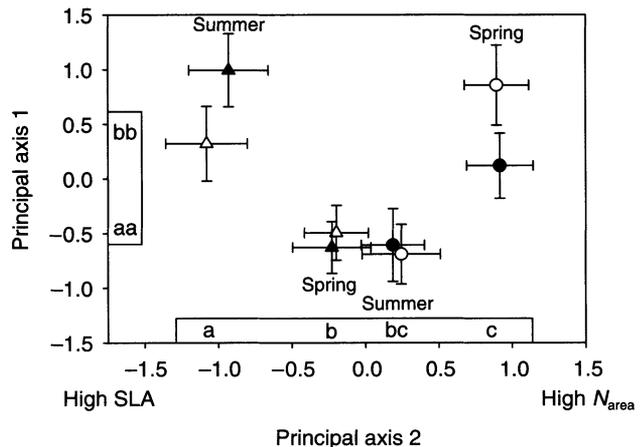


Fig. 3 Mean principal component (PC) scores for all treatments (symbols same as in 2e) pooled into seasons (summer and spring). Loadings associated with the PCs are indicated on the x and y axes. Mean \pm SE ($n = 12-18$) from the first two PCs are shown; significant differences ($\alpha = 0.10$ from *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.

$P < 0.01$). In the spring, control and +N plants were characterized by high N_{area} , A_{area} and g_s but low SLA, whereas +H₂O and +H₂O +N plants had significantly lower means for both principal components. During the summer, +H₂O and +H₂O +N plants had higher mean values of A_{area} , g_s and SLA and lower mean values of N_{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_{area} , g_s , N_{area} and SLA

Few effects of N deposition were observed in any measured parameter, therefore treatments were collapsed into +Monsoon (i.e. +H₂O and +H₂O +N) and –Monsoon (control and +N) groups, the latter functioning as the control henceforth (Figs 4 and 5). Simple linear regressions of leaf N_{area} , g_s and SLA demonstrated significant relationships with A_{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_{area} when regressed alone (Fig. 4a,b). Much of this variation was independent of covariation with N_{area} and SLA (partial r^2 from multiple regression with g_s , N_{area} and SLA was between 29% and 71%). The slope describing the strong relationship between A_{area} and g_s did not vary significantly by monsoon treatment or season combinations.

N_{area} had a significant relationship with A_{area} for –Monsoon plants in the spring and for +Monsoon plants during the summer, explaining 34% and 37% of the variance in A_{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_{area} and N_{area} for +Monsoon plants in the summer compared with –Monsoon plants (Fig. 4c,d). The significant relationships between A_{area} and N_{area} were caused by covariation between N_{area} and g_s , as the multiple regression revealed weak partial relationships between

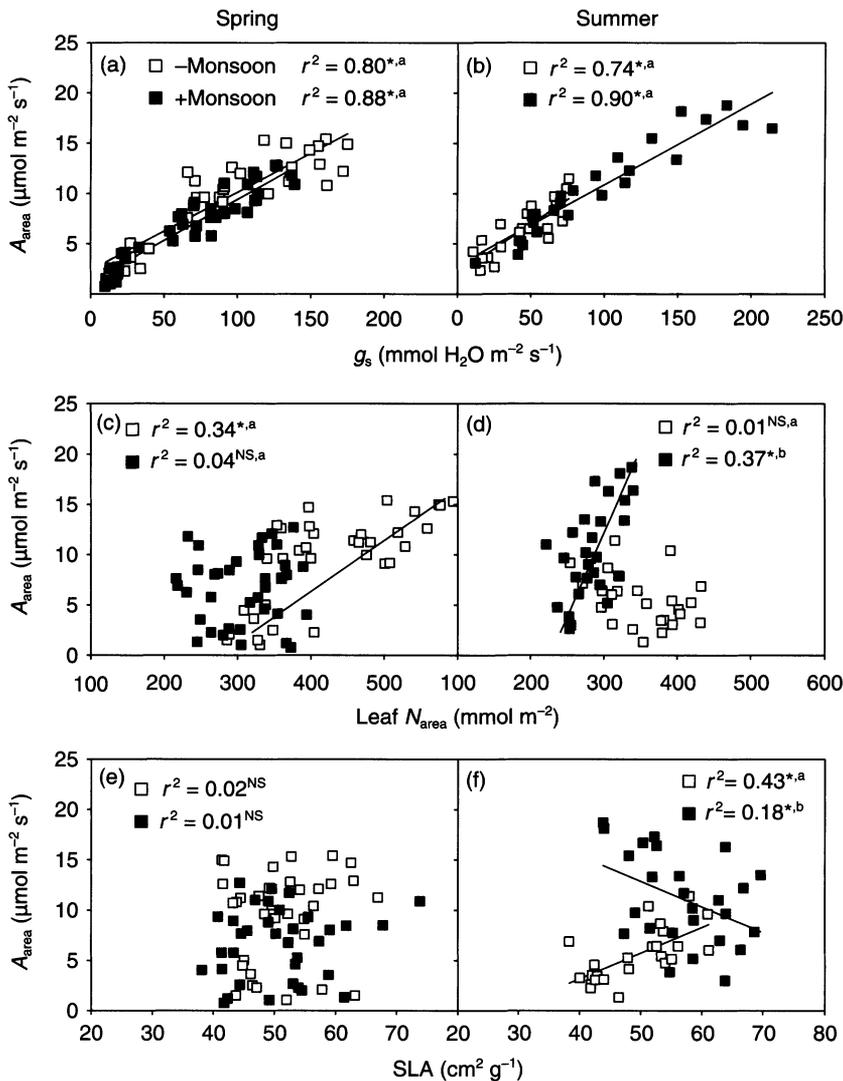


Fig. 4 Relationships derived from linear regressions between area-based net photosynthetic rate (A_{area}) with stomatal conductance to water vapor (g_s), area-based leaf N content (N_{area}) and specific leaf area (SLA). Data were pooled into spring (a,c,e) and summer (b,d,f) seasons, and collapsed into two treatments, +Monsoon (+H₂O and +H₂O +N) and –Monsoon (control and +N). (a) A_{area} by g_s in spring; (b) A_{area} by g_s in summer; (c) A_{area} by N_{area} in spring; (d) A_{area} by N_{area} in summer (e) A_{area} by SLA in spring; (f) A_{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.

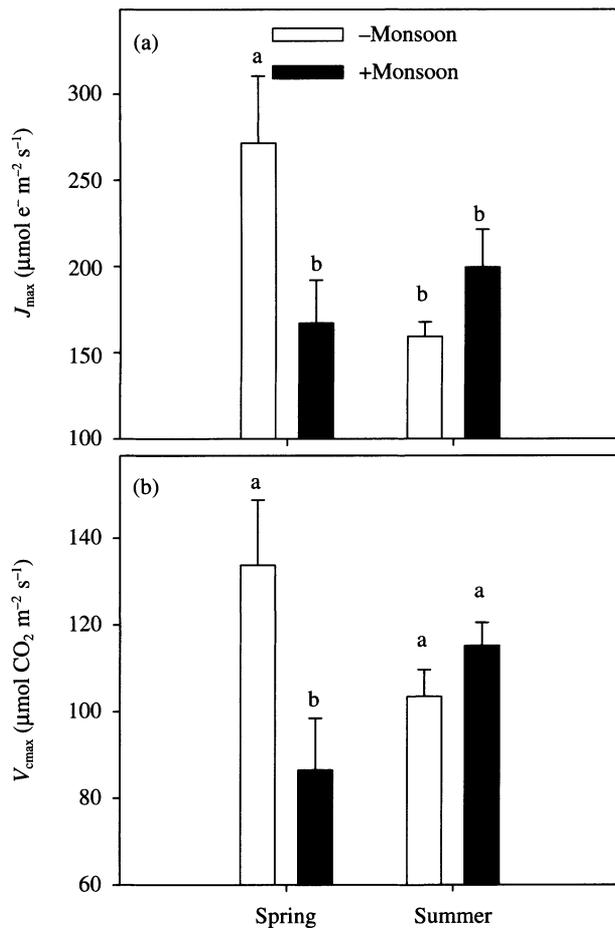


Fig. 5 Photosynthetic parameters derived from A/C_i (assimilation rate/internal CO_2 concentration) curves during the spring and summer, and collapsed into two treatments; +Monsoon and (+ H_2O and + H_2O +nitrogen (N) and -Monsoon (control and +N). (a) Maximum rate of electron transport (J_{\max}); (b) maximum velocity of carboxylation (V_{cmax}). Means did not differ between N deposition treatments and were pooled into irrigated and nonirrigated treatments. Mean \pm SE are depicted ($n = 4-6$), and significant differences ($P < 0.05$) are indicated by different letters.

N_{area} and A_{area} (partial r^2 from multiple regression of A_{area} with g_s , N_{area} and SLA was between 0.003 and 0.025%). A moderate, significant correlation between N_{area} and g_s was demonstrated in -Monsoon plants in the spring ($r = 0.66$, $P < 0.0001$) and for +Monsoon plants in the summer ($r = 0.65$, $P < 0.0001$; data not shown). There was no evidence that the relationship between N_{area} and A_{area} was predicated on covariation between N_{area} and SLA. We observed no relationship between SLA and A_{area} for either +Monsoon or -Monsoon plants in the spring; however, during summer the slopes varied significantly by monsoon treatment (Fig. 4e,f).

A/C_i curves

The A/C_i curves were generated in early spring and after the second simulated monsoon event in summer. Significant

treatment effects on the maximum rate of carboxylation (V_{cmax}) and the rate of electron transport (J_{\max}) were limited to the + H_2O treatment, season, and their interaction, as N deposition had little effect (Table 1). Therefore, data were collapsed as in Fig. 4 into +Monsoon and -Monsoon groups irrespective of N treatment. During the spring, +Monsoon plants, subjected to treatments the previous summer, had significantly lower rates of J_{\max} and V_{cmax} than -Monsoon plants (Fig. 5). During the summer, both J_{\max} and V_{cmax} decreased from spring values in -Monsoon plants, becoming lower than +Monsoon plants which had increased values from the spring. However, summer differences between treatments were not significant ($P > 0.05$). An analysis of the relative stomatal limitation to photosynthesis, to distinguish between stomatal and nonstomatal limitations, revealed no difference between treatments in the spring, but c. 10% greater stomatal limitation in the summer for -Monsoon plants (data not shown).

Discussion

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_{area} , most likely increasing NPP in *Larrea tridentata* irrespective of increased N deposition. However, the positive effect of increased summer monsoon precipitation on A_{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_{area} the following spring – dilution of leaf N_{area} leading to lower rates of g_s and A_{area} . During either spring or summer, A_{area} was strongly associated with high rates of g_s , but whether N_{area} was also positively associated with A_{area} , albeit more weakly, was dependent on the season. Although N deposition did not significantly alter leaf N_{area} , N_{area} varied throughout the growing season and was positively associated with A_{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_{area} .

In the spring, the highest rates of A_{area} , g_s , V_{cmax} and J_{\max} were observed in -Monsoon plants (i.e. control and +N plants). There was no difference in plant Ψ_{shoot} between -Monsoon and +Monsoon plants (i.e. + H_2O and + H_2O +N plants). Therefore, differences in plant water status do not explain differences observed in gas exchange parameters. High leaf N_{area} was weakly but positively correlated with A_{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_{cmax} and N_{area} , lower values of V_{cmax} in +Monsoon plants can be explained by the lower leaf N_{area} (Wullschleger, 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_{area} and N_{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_{area} and g_s were associated with +Monsoon plants, and differed from spring responses as there were also large differences in Ψ_{shoot} and only small differences in leaf N_{area} between –Monsoon and +Monsoon plants. Alleviation of summer drought conditions and increasing Ψ were most likely responsible for increasing A_{area} and g_s in the +Monsoon plants, as has been reported for this species (Meinzer *et al.*, 1988; Franco *et al.*, 1994). V_{cmax} and J_{max} did not differ significantly between treatments, even though A_{area} was lower in –Monsoon plants at ambient CO_2 levels. In this case, the reduction in A_{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_{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_{area}) the following spring.

Seasonal changes in leaf N_{area}

Contrary to our original hypothesis, N deposition did not lead to significantly higher leaf N_{area} or higher A_{area} , although leaves with higher N_{area} did realize a higher A_{area} in the spring. Water input during the previous summer determined whether leaves possessed high N_{area} . Presumably, rapid growth and high A_{area} in response to the +Monsoon treatment during the summer (2002) resulted in the dilution of leaf N_{area} in the following spring (2003) in these long-lived, evergreen leaves. Lajtha & Whitford (1989) found a twofold increase in N_{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_{area} did not occur in plants receiving +Monsoon treatments because added summer rain may have counteracted the natural accumulation of leaf N_{area} through enhanced growth (B. Newingham & S. Smith, unpubl.) and subsequent N dilution, thereby reducing the maximum potential rate of A_{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_{area} , although leaf $\delta^{15}\text{N}$ 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 $^{15}\text{NO}_3^-$ enrichment and required proliferation of new roots to increase foliar $\delta^{15}\text{N}$. That N deposition did not increase leaf N_{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_2O and NO_3^- , requiring sufficient H_2O 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_{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_{area} and SLA, combined with lower N_{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_{area} may be part of an arid-land plant strategy employed to maximize photosynthesis while maintaining relatively low g_s , thereby minimizing water loss (Wright *et al.*, 2001). However, plants exposed to a simulated summer monsoon had generally lower leaf N_{area} , which in turn resulted in lower A_{area} when compared with controls at similar water potentials (i.e. the next spring growing season). When analysed across the entire year, the A_{area} –SLA relationship was poor and the A_{area} – N_{area} 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_{area} – N_{area} relationship and other leaf trait relationships, shown to have strong predictive value in interspecific comparisons across biomes (Reich *et al.*, 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_{area} –leaf trait relationships on plant water status.

Acknowledgements

This work was supported by the US Department of Energy, Office of Science (BER), Program for Ecosystem Research (ER DE-FG02ER63361). We also acknowledge Cara Evangelista, Ranna Nash and Nicole Sikula.

References

- BassiriRad H, Tremmel DC, Virginia RA, Reynolds JF, de Soyza AG, Brunell MH. 1999. Short-term patterns in water and nitrogen acquisition by two desert shrubs following a simulated summer rain. *Plant Ecology* 145: 27–36.
- Bernacchi CJ, Pimentel C, Long SP. 2003. *In vivo* temperature response functions of parameters required to model RuBP-limited photosynthesis. *Plant, Cell & Environment* 26: 1419–1430.
- Bernacchi CJ, Singsaas EL, Pimentel C, Portis AR, Long SP. 2001. Improved temperature response functions for models of Rubisco-limited photosynthesis. *Plant, Cell & Environment* 24: 253–259.
- Billings S, Schaeffer S, Zitzer S, Charlet T, Smith S, Evans R. 2002. Alterations of nitrogen dynamics under elevated carbon dioxide in an intact Mojave Desert ecosystem: evidence from nitrogen-15 natural abundance. *Oecologia* 131: 463–467.
- Bloom AJ, Chapin FS III, Mooney HA. 1985. Resource limitation in plants – an economic analogy. *Annual Review of Ecology and Systematics* 16: 363–392.
- von Caemmerer S, Farquhar GD. 1981. Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. *Planta* 153: 376–387.
- Centritto M, Loreto F, Chartzoulakis K. 2003. The use of low $[CO_2]$ to estimate diffusional and non-diffusional limitations of photosynthetic capacity of salt-stressed saplings. *Plant, Cell & Environment* 26: 585–594.
- Chapin FS III. 1980. The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics* 11: 233–260.
- Ellsworth DS. 2000. Seasonal CO_2 assimilation and stomatal limitations in a *Pinus taeda* canopy. *Tree Physiology* 20: 435–445.
- Ellsworth DS, Reich PB, Naumburg ES, Koch GW, Kubiske ME, Smith SD. 2004. Photosynthesis, carboxylation and leaf nitrogen responses of 16 species to elevated pCO_2 across four free-air CO_2 enrichment experiments in forest, grassland and desert. *Global Change Biology* 10: 2121–2138.
- Evans JR. 1989. Photosynthesis and nitrogen relationship in leaves of C_3 plants. *Oecologia* 78: 9–19.
- Evans JR, Seemann JR. 1989. The allocation of protein nitrogen in the photosynthetic apparatus: cost, consequences and control. In: Briggs WR, ed. *Photosynthesis*. New York, NY, USA: Liss, 183–205.
- Farquhar GD, Sharkey TD. 1982. Stomatal conductance and photosynthesis. *Annual Review of Plant Physiology* 33: 317–345.
- Farquhar GD, von Caemmerer S, Berry JA. 2001. Models of photosynthesis. *Plant Physiology* 125: 42–45.
- Fenn ME, Haeuber Royal, Tonnesen GS, Baron JS, Grossman-Clarke S, Hope D, Jaffe DA, Copeland S, Geiser L, Rueth HM, Sickman JO. 2003. Nitrogen emissions, deposition, and monitoring in the western United States. *Bioscience* 53: 391–403.
- Field C, Mooney HA. 1986. The photosynthesis–nitrogen relationship in wild plants. In: Givnish TJ, ed. *On the economy of plant form and function*. Cambridge, UK: Cambridge University Press, 25–55.
- Flexas J, Medrano H. 2002. Drought-inhibition of photosynthesis in C_3 plants. Stomatal and non-stomatal limitations revisited. *Annals of Botany* 89: 183–189.
- Franco AC, de Soyza AG, Virginia RA, Reynolds JF, Whitford WG. 1994. Effects of plant size and water relations on gas exchange and growth of the desert shrub *Larrea tridentata*. *Oecologia* 97: 171–178.
- Galloway JN. 1998. The global nitrogen cycle: changes and consequences. *Environmental Pollution* 102: 15–24.
- Galloway JN, Dentener FJ, Capone DG, Boyer EW, Howarth RW, Seitzinger SP, Asner GP, Cleveland CC, Green PA, Holland EA, Karl DM, Michaels AF, Porter JH, Townsend AR, Vörösmarty CJ. 2004. Nitrogen cycles: past, present, and future. *Biogeochemistry* 70: 153–226.
- Grassi G, Magnani F. 2005. Stomatal, mesophyll conductance and biochemical limitations to photosynthesis as affected by drought and leaf ontogeny in ash and oak trees. *Plant, Cell & Environment* 28: 834–849.
- Grime JP. 1994. The role of plasticity in exploiting environmental heterogeneity. In: Caldwell MM, Pearcy Royal, eds. *Exploitation of environmental heterogeneity in plants*. San Diego, CA, USA: Academic Press, 1–18.
- Harley P, Thomas R, Reynolds J, Strain BR. 1992. Modeling photosynthesis of cotton grown in elevated CO_2 . *Plant, Cell & Environment* 15: 271–282.
- Higgins RW, Shi W. 2001. Intercomparison of the principal modes of interannual and intraseasonal variability of the North American Monsoon System. *Journal of Climate* 14: 403–417.
- Hooper DU, Johnson L. 1999. Nitrogen limitation in dryland ecosystems: responses to geographical and temporal variation in precipitation. *Biogeochemistry* 46: 247–293.
- Houghton JT, Ding Y, Griggs DJ, Noguer M, van der Linder PJ, Dai X, Maskell K, Johnson CA. 2001. *Climate change 2001: the scientific basis. Contribution of Working Group 1 to the Third Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, UK: Cambridge University Press.
- Hunter RB. 1994. *Status of flora and fauna on the Nevada test site, 1994. DOE/INV/11432-195 UC-721. National Technical Information Service*, 89. Springfield, VA, USA: US Department Commerce, 590–596.

- Huxman TE, Snyder KA, Tissue D, Leffler AJ, Ogle K, Pockman WT, Sandquist DR, Potts DL, Schwinning S. 2004. Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. *Oecologia* 141: 254–268.
- Jordan DN, Zitzer SF, Hendrey GR, Lewin KF, Nagy J, Nowak RS, Smith SD, Coleman JS, Seemann JR. 1999. Biotic, abiotic and performance aspects of the Nevada desert free-air CO₂ enrichment (FACE) facility. *Global Change Biology* 5: 659–668.
- Killingbeck KT, Whitford WG. 1996. High foliar nitrogen in desert shrubs: an important ecosystem trait or defective desert doctrine? *Ecology* 77: 1728–1737.
- Lajtha K, Whitford WG. 1989. The effect of water and nitrogen amendments on photosynthesis, leaf demography, and resource-use efficiency in *Larrea tridentata*, a desert evergreen shrub. *Oecologia* 80: 341–348.
- Lal R. 2004. Carbon sequestration in dryland ecosystems. *Environmental Management* 33: 528–544.
- Lawlor DW, Cornic G. 2002. Photosynthetic carbon assimilation and associated metabolism in relation to water deficits in higher plants. *Plant, Cell & Environment* 25: 275–294.
- Medlyn BE, Badeck F-W, De Pury DG, Barton CVM, Broadmeadow M, Ceulemans R, Angelis P De, Forstreuther M, Jach ME, Kellomäki S, Laitat E, Marek M, Philippot S, Rey A, Strassmeyer J, Laitinen K, Liozon R, Portier R, Roberntz P, Wang K, Jstbid PG. 1999. Effects of elevated [CO₂] on photosynthesis in European forest species: a meta-analysis of model parameters. *Plant, Cell & Environment* 22: 1475–1496.
- Medrano H, Escalona JM, Bota J, Gulías J, Flexas J. 2002. Regulation of photosynthesis of C₃ plants in response to progressive drought: stomatal conductance as a reference parameter. *Annals of Botany* 89: 895–905.
- Meinzer FC, Sharifi MR, Nilsen ET, Rundel PW. 1988. Effects of manipulations of water and nitrogen regime on the water relations of the desert shrub *Larrea tridentata*. *Oecologia* 77: 480–486.
- Mooney HA, Rundel PW. 1979. Nutrient relations of the evergreen shrub *Adenostoma fasciculatum* in the California chaparral. *Botanical Gazette* 140: 109–113.
- Naumburg E, Housman DC, Huxman TE, Charlet TN, Loik ME, Smith SD. 2003. Photosynthetic responses of Mojave desert shrubs to free air CO₂ enrichment are greatest during wet years. *Global Change Biology* 9: 276–285.
- Naumburg E, Loik ME, Smith SD. 2004. Photosynthetic responses of *Larrea tridentata* to seasonal temperature extremes under elevated CO₂. *New Phytologist* 162: 323–330.
- Nemani RR, Keeling CD, Hashimoto H, Jolly WM, Piper SC, Tucker CJ, Myrneni RB, Running SW. 2003. Climate-driven increases in global terrestrial production from 1982 to 1999. *Science* 300: 1560–1563.
- Noy-Meir I. 1973. Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* 4: 23–51.
- O'Neal ME, Landis DA, Isaacs R. 2002. An inexpensive, accurate method for measuring leaf area and defoliation through digital analysis. *Journal of Economic Entomology* 95: 1190–1194.
- Ogle K, Reynolds JF. 2002. Desert dogma revisited: coupling of stomatal conductance and photosynthesis in the desert shrub, *Larrea tridentata*. *Plant, Cell & Environment* 25: 909–921.
- Reich PB, Ellsworth DS, Walters MB. 1997. From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences, USA* 94: 13730–13734.
- Reich PB, Ellsworth DS, Walters MB. 1998. Leaf structure (specific leaf area) modulates photosynthesis-nitrogen relations: evidence from within and across species and functional groups. *Functional Ecology* 12: 948–958.
- Reich PB, Ellsworth DS, Walters MB, Vose JM, Gresham C, Volin JC, Bowman WD. 1999. Generality of leaf trait relationships: a test across six biomes. *Ecology* 80: 1955–1969.
- Romney EM, Wallace A. 1980. Ecotonal distribution of salt-tolerant shrubs in the northern Mojave Desert. *Great Basin Naturalist Memoirs* 4: 134–139.
- Rothstein DE, Zak D. 2001. Relationships between plant nitrogen economy and life history in three deciduous-forest herbs. *Journal of Ecology* 89: 385–394.
- Schulze E-D, Kelliher FM, Körner C, Lloyd J, Leuning R. 1994. Relationships among maximal stomatal conductance, ecosystem surface conductance, carbon assimilation rate, and plant nitrogen nutrition: a global ecology scaling exercise. *Annual Review of Ecology and Systematics* 25: 629–660.
- Smil V. 1990. Nitrogen and phosphorus. In: Turner BL, Clark WC, Kaes RW, Richards JF, Mathews JT, Meyer WB, eds. *The Earth as transformed by human action*. Cambridge, UK: Cambridge University Press, 423–436.
- Smith SD, Nowak RS. 1990. Ecophysiology of plants in the Intermountain lowlands. In: Osmond CB, Pitelka LF, Hidy GM, eds. *Plant biology of the basin and range. Ecological studies*, Vol. 80. Berlin, Germany: Springer, 179–241.
- Smith SD, Monson RK, Anderson JE. 1997. *Physiological ecology of North American desert plants*. Berlin, Germany: Springer.
- Vitousek PM. 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. *Oikos* 57: 7–13.
- Vitousek PM, Aber JA, Howarth RW. 1997. Human alteration of the global nitrogen cycle: sources and consequences. *Ecological Applications* 7: 737–750.
- Weltzin JF, Loik ME, Schwinning S, Williams D, Fay P, Haddad B, Harte J, Huxman T, Knapp A, Lin G, Pockman W, Shaw R, Small E, Smith M, Smith S, Tissue D, Zak J. 2003. Assessing the response of terrestrial ecosystems to potential changes in precipitation. *Bioscience* 53: 941–952.
- West NE, Skujins JJ. 1978. *Nitrogen in desert ecosystems*. Stroudsburg, PA, USA: Dowden, Hutchinson & Ross.
- Wong SC, Cowan IR, Farquhar GD. 1979. Stomatal conductance correlates with photosynthetic capacity. *Nature* 282: 424–426.
- Wong SC, Cowan IR, Farquhar GD. 1985. Leaf conductance in relation to rate of CO₂ assimilation. I. Influence of nitrogen nutrition, phosphorus nutrition, photon flux density, and ambient partial pressure of CO₂ during ontogeny. *Plant Physiology* 78: 821–825.
- Wright IJ, Reich PB, Westoby M. 2001. Strategy shifts in leaf physiology, structure and nutrient content between species of high- and low-rainfall and high- and low-nutrient habitats. *Functional Ecology* 15: 423–434.
- Wright IJ, Reich PB, Westoby M. 2003. Least-cost input mixtures of water and nitrogen for photosynthesis. *American Naturalist* 161: 98–111.
- Wullschlegel SD. 1993. Biochemical limitations to carbon assimilation in C₃ plants – a retrospective analysis of the A/G curves from 109 species. *Journal of Experimental Botany* 44: 907–920.
- Yan S, Wan C, Sosebee RE, Wester DB, Fish EB, Zartman RE. 2000. Responses of photosynthesis and water relations to rainfall in the desert shrub creosote bush (*Larrea tridentata*) as influenced by municipal biosolids. *Journal of Arid Environments* 46: 397–412.