

## The effect of water and nitrogen amendments on photosynthesis, leaf demography, and resource-use efficiency in *Larrea tridentata*, a desert evergreen shrub

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**Summary.** In the Chihuahuan Desert of southern New Mexico, both water and nitrogen limit the primary productivity of *Larrea tridentata*, a xerophytic evergreen shrub. Net photosynthesis was positively correlated to leaf N, but only in plants that received supplemental water. Nutrient-use efficiency, defined as photosynthetic carbon gain per unit N invested in leaf tissue, declined with increasing leaf N. However, water-use efficiency, defined as the ratio of photosynthesis to transpiration, increased with increasing leaf N, and thus these two measures of resource-use efficiency were inversely correlated. Resorption efficiency was not significantly altered over the nutrient gradient, nor was it affected by irrigation treatments. Leaf longevity decreased significantly with fertilization although the absolute magnitude of this decrease was fairly small, in part due to a large background of insect-induced mortality. Age-specific gas exchange measurements support the hypothesis that leaf aging represents a redistribution of resources, rather than actual deterioration or declining resource-use efficiency.

**Key words:** *Larrea tridentata* – Leaf demography – Nutrient resorption – Nutrient-use efficiency – Photosynthesis – Water-use efficiency

The physiological performance of individual leaves varies with both leaf age and plant nutrient status (Mooney et al. 1978; Reader 1978; Gulmon and Chu 1981; Field and Mooney 1981, 1983). Similarly, leaf longevity both in individual species and in plant communities varies with nutrient availability (Monk 1966; Schlesinger and Chabot 1977; Shaver 1981, 1983; Bloom et al. 1985). The physiological performance of a whole plant can be considered to be the result of the interaction between the age structure of the leaf population and age-specific leaf physiology (Nilsen et al. 1987), yet both of these factors may be controlled by the availability of various soil resources.

Recent authors (Shaver 1981; Chabot and Hicks 1982) have pointed out that changes in leaf longevity in response to environmental conditions can be expected to affect such plant-specific processes as: 1) nutrient use efficiency (defined as total C fixed per unit nutrient over the lifetime

of a leaf; Small 1972), 2) the ability of old leaves to act as a source of nutrients for new leaf production (Turner and Olsen 1976; Jonasson and Chapin 1985), and 3) the ability of overwintering leaves to serve as nutrient storage organs (Hadley and Bliss 1964; Mooney and Rundel 1978). In addition, changes in leaf longevity in the dominant species of a community may also affect nutrient turnover rates and nutrient cycling processes at the ecosystem level. However, the responses of leaf longevity to increased nutrient availability have differed among species of study.

In contrast to the well-documented pattern of an increase in proportion of evergreen species relative to deciduous species as habitat fertility decreases (Monk 1966; Bloom et al. 1985), several studies have found that leaf longevity decreases under nutrient stress as nutrients from old leaves are preferentially translocated to support new growth (Osman and Milthorpe 1971; Turner and Olsen 1976; Bazzaz and Harper 1977; Reader 1980; Tolley-Henry and Raper 1986). Perhaps part of this discrepancy can be explained by the results of Shaver (1983), who found that while fertilization decreased overall leaf survivorship in *Leidum palustre* through a sharp increase in winter leaf mortality (thus agreeing with observed community-level evergreen/deciduous changes), fertilization actually decreased leaf losses during the growing season (consistent with the cited empirical studies).

Alternatively, effects on leaf longevity may depend on the degree of nutrient stress. While experiments that specifically reduced nutrient availability to plants have tended to show reduced longevity, milder conditions that reduced relative growth rates or leaf production, such as reduced light or increased crowding, have tended to show increased longevity (Bazzaz and Harper 1977; Abul-Fatih and Bazzaz 1980; Nilsen 1986).

The effects of other resources on leaf demography have not been as well examined. For example, studies of the effects of water availability on leaf turnover have been limited primarily to either drought-deciduous or determinately seasonally-deciduous species (Nilsen and Muller 1981; Sharifi et al. 1983; Nilsen et al. 1986).

*Larrea tridentata* (DC.) Cov., an evergreen xerophytic shrub, is one of the most widespread perennial species of southwestern U.S. deserts (Shreve 1942). *Larrea* remains metabolically active throughout the year, and will grow and flower opportunistically whenever environmental con-

study of each age class. All other leaf age classes on twigs were removed, and scars were coated with Vaseline jelly to prevent desiccation. In several preliminary studies it was found that gas exchange rates stabilized within one day of manipulations; two days were allowed to elapse between twig manipulations and measurements to avoid any short-term wound response.

Leaves were harvested immediately after gas exchange measurements and were analyzed for leaf weight and N concentration as above. Gas exchange data were expressed per unit leaf weight, rather than per unit leaf area, as this allows the assessment of carbon gain as a return on an investment in leaf biomass or unit N taken up (Field and Mooney 1983).

### Statistical analyses

Data were analyzed using the General Linear Models procedure of SAS (SAS Institute Inc. 1982). The Univariate procedure of SAS was used to verify the normality of all data. Comparisons among plots were made following methods of Fisher et al. (1988) for a strip-plot design (Damon and Harvey 1987). The error term used to test the irrigation effects was modified to reflect the randomized, rather than blocked, arrangement of irrigation treatments. When the analysis of variance indicated that there were no significant differences among whole-plot (irrigation treatment) means, values were combined and used to analyze differences among sub-plot (N treatment) means. All linear and multiple linear regressions between variables were similarly performed using the GLM procedure of SAS.

## Results

### Growth and tissue nutrients

Both water and nitrogen additions to *Larrea* resulted in significant increases in the number of live leaves on marked twigs (Fig. 1). The total net number of live leaves was significantly greater in irrigated than in unirrigated plots ( $P < 0.03$ ), although responses to the two irrigation treatments were not significantly different. There were no statistically significant differences among treatments for branch elongation, although branch lengths demonstrated the same trend as leaves in response to both N and irrigation.

The N concentration of live leaves increased significantly in response to N fertilization by the spring after the first application ( $P < 0.05$  across all irrigation treatments). Irrigation had no effect on leaf N in fertilized shrubs, yet had an unpredictable effect on leaf N in unfertilized shrubs (Fig. 2). Leaf N was significantly lower in unfertilized shrubs that received 6 mm water/wk in 1986, but this difference disappeared during the 1987 growing season. There were no differences in leaf N concentrations between unwatered shrubs and shrubs receiving 25 mm water/mo during the experiment.

Leaf N was highest in January and lowest in June for all plots in both years. All plots had significant increases in leaf N between September and January (Fig. 2).

### Gas exchange measurements

Net photosynthetic rates of *Larrea* in March, 1987 were very low, and averaged less than 30% of the rates measured in June, presumably due to low daytime and near-freezing

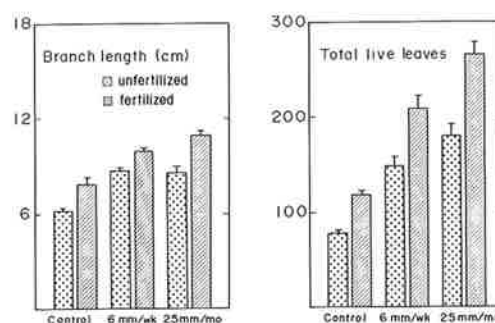


Fig. 1. Annual branch elongation and total annual leaf production in each irrigation (0, 6 mm added precipitation  $\cdot$  week $^{-1}$ , or 25 mm precipitation  $\cdot$  month $^{-1}$ )  $\times$  N (0 or 10 g N  $\cdot$  m $^{-2}$ ) treatment,  $\pm$  1 SE

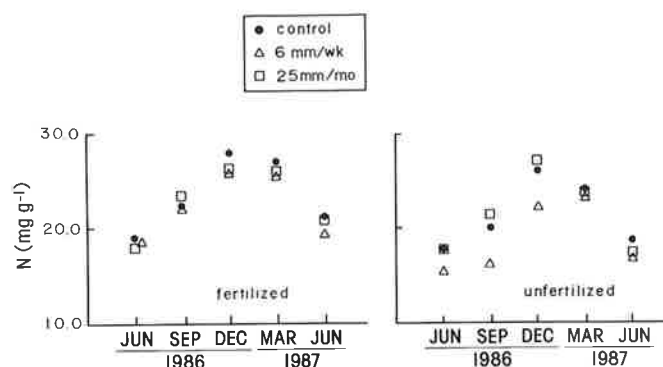


Fig. 2. Seasonal changes in leaf N concentration for fertilized and unfertilized plots

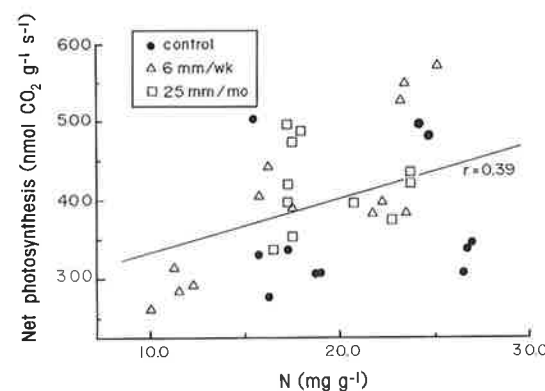


Fig. 3. Relationship between net photosynthesis and leaf N in *Larrea tridentata*. Regression line is for all irrigation treatments combined

nighttime temperatures during the early spring. Multiple regressions of net photosynthesis against leaf N and specific leaf mass indicated only a slight negative correlation with specific leaf mass ( $r = -0.44$ ,  $P < 0.04$ ). There were no differences among irrigation or fertilization treatments for any gas exchange parameters.

In June, net photosynthesis was significantly positively correlated to leaf N ( $r = 0.39$ ,  $P < 0.02$ ; Fig. 3). Both the correlation and the slope of the regression were significantly greater if only plots receiving supplemental water were considered ( $r = 0.64$ ,  $P < 0.005$ ). Although there was no significant difference between slopes for plots receiving 6 mm/wk versus plots receiving 25 mm/mo supplemental water, when

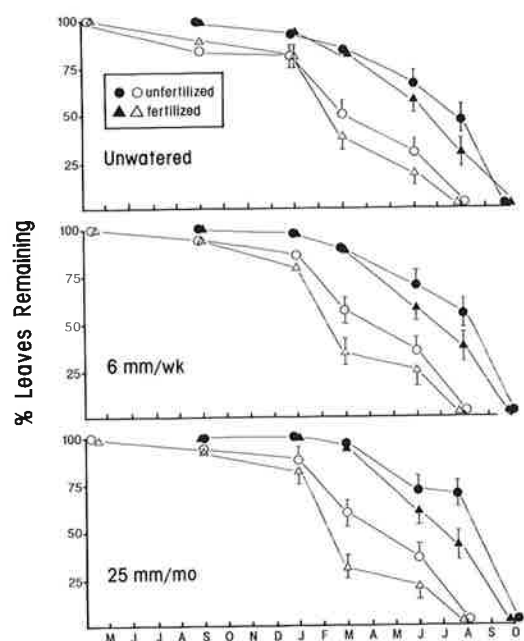


Fig. 8. Patterns of leaf survivorship in spring (open symbols) and fall (closed symbols) leaf cohorts with fertilization in *Larrea tridentata*

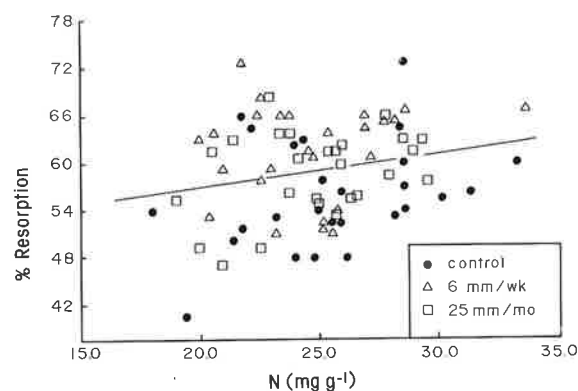


Fig. 9. Relationship between resorption efficiency, defined as percent of maximum live leaf N withdrawn prior to abscission, and leaf N in *Larrea tridentata*

than 13 months due to a sharp increase in senescence the following fall. Although there were no significant differences in leaf survivorship among irrigation treatments at any sampling date, leaf survivorship was significantly lower in fertilized plots by June of 1987 ( $P < 0.05$ ). Because leaf survivorship differences with fertilization did not appear until after at least 8 months for both cohorts, differences in either mean or median leaf longevity between fertilized and unfertilized plots were slight.

There were no differences between estimates of insect damage for fertilized and unfertilized plots. In many cases it was difficult to determine if insect damage was the ultimate cause of leaf abscission. The most conservative estimate of insect-induced mortality was 13% over all treatments, while the least conservative estimate was 28% of total leaf mortality.

### Nutrient use efficiency

During all seasons, absolute amounts of nutrient resorption increased with increasing leaf N. Although mean nutrient resorption efficiency was significantly greater in spring than in fall or winter, nutrient resorption efficiency did not vary significantly with increasing N (Fig. 9). There were no significant differences in mean resorption efficiency among irrigation treatments.

### Discussion

Water and nitrogen amendments, both individually and interactively, increased leaf production in *Larrea*, consistent with results found both in this species and in other semi-arid species (Lauenroth et al. 1978; Romney et al. 1978; Fisher et al. 1988). In a similar study, Fisher et al. (1988) found that small, frequent precipitation events had a greater effect on plant growth than larger, less frequent events. In the current study, however, the pattern of added water did not affect either branch elongation or total leaf production. Neither irrigation treatment affected leaf N concentration, a result also found by Lightfoot and Whitford (1987).

Many studies have reported strong correlations between either net photosynthesis (A) or photosynthetic capacity ( $A_{max}$ ) and total leaf nitrogen (reviews in Natr 1975; Field and Mooney 1986), both within single species and across species types. In this study, realized, rather than potential photosynthesis was measured at field humidities and temperatures and at high natural irradiances. Realized photosynthetic rates showed a positive relationship with leaf N in June, although there was a great deal of variability encountered in individual plant responses, and this relationship was not significant in unwatered plots. Other studies have noted a high variability in the response of *Larrea* to experimentally altered environmental conditions (Lajtha 1987; Lightfoot and Whitford 1987; Fisher et al. 1988). As individual *Larrea* shrubs represent a conglomerate of mixed-age, often physiologically-isolated stems that grow and die at different rates, part of this variability can be attributed to differential responses of different ages of branches.

The lack of a relationship between net photosynthesis and leaf N in March can possibly be explained by an overwhelming temperature limitation, although growth increments were significantly greater in fertilized plots during this time interval. A lack of photosynthetic response in plants where absolute growth responded to increased N availability was also noted by Oechel et al. (1981) and Bigger and Oechel (1982).

During the early summer, there was an increase in WUE and a decrease in NUE with increasing leaf N, and thus NUE and WUE were inversely correlated. One possible explanation for a relationship between NUE and plant nutrient content (Fig. 5) and between NUE and WUE (Fig. 6) is autocorrelation of axes, a problem discussed also by Vitousek (1982) for ecosystem-level measures of nutrient use and ecosystem fertility. In the case of Fig. 5 the relationship could emerge because the Y axis reduces to  $CO_2$  uptake divided by the X axis. However, the relationship between  $CO_2$  gain and plant N (Fig. 3) argues against autocorrelation as being the only explanation for the relationship in Fig. 5, because the axes cannot then be algebraically reduced. Simulation trials show that the slope of Fig. 5 is

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