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The effect of varying nitrogen and phosphorus availability on nutrient use by *Larrea tridentata,* a desert evergreen shrub

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Summary. In a phytotron study of the effects of nitrogen and phosphorus supply ratio on nutrient uptake and use by *Larrea tridentata,* seedlings responded to increases in *N* and *P* availability with increases in leaf size, total biomass, and leaf nutrient concentration, and with decreases in root: shoot ratio. *N* and *P* use efficiency decreased with increasing *N* and *P* availability, respectively, but increased with increasing availability of the other nutrient, suggesting that *Larrea* responds both to the absolute and to the relative availability of limiting nutrients. Absolute amounts of *N* and *P* resorption, as well as *N* and *P* resorption efficiencies did not demonstrate a significant trend with nutrient availability, and there was no evidence of significant interactions between the two nutrients. More studies of the effects of nutrient interactions in the cycling and use of nutrients by different plant species are needed before more general conclusions can be drawn.

Key words: *N:P* ratio – Nutrient use efficiency – Nutrient resorption efficiency – *Larrea tridentata*

Larrea tridentata (DC). Cov. (creosotebush) is a dominant shrub throughout the warm deserts of the United States. Productivity in many desert ecosystems is limited primarily by water, but during the wet seasons nutrient availability, particularly nitrogen availability, may determine the growth and carbon allocation of desert shrubs (Fisher et al. 1988). Nutrient use efficiency, defined as biomass produced per unit nutrient taken up from the soil, is relatively high in desert shrubs (Lajtha 1987). High nutrient use efficiency can reduce the dependence of plant growth on soil nutrient availability (Gray 1983), and minimize losses from the ecosystem by maintaining nutrients in organic form (Gosz 1981). Nutrient losses from individual plants may be reduced by lower leaf turnover (Shaver 1981) or higher resorption of nutrients before leaf abscission (Lajtha and Schlesinger 1986).

Interactions between the global biogeochemical cycles of major plant nutrients have received considerable interest in recent years (Bolin and Cook 1983; McGill and Cole 1981; Likens et al. 1981). However, less attention has been given to nutrient interactions during the uptake and use of nutrients by plants. Shaver and Melillo (1984) found that the efficiency of *N* and *P* uptake by four freshwater marsh species was affected by the supply of the other nutrient. Similarly, in a field study of a *Larrea tridentata* community Lajtha (1987) found that *N* and *P* resorption efficiencies were significantly positively correlated.

A greenhouse fertilization experiment was conducted to examine the effects of varying *N* and *P* supply as well as *N:P* ratio on nutrient uptake and nutrient use in *Larrea.* We initially hypothesized that:
1) Plants would respond to more favorable nutrient regimes (increased levels of *N* and/or *P* and/or more favorable *N:P* ratios) with increases in leaf area, leaf weight, and total biomass.
2) Root:shoot ratio would increase with less favorable nutrient regimes (Chapin 1980).
3) Nutrient use efficiency would increase for plants with less favorable nutrient regimes. Nutrient use efficiency was defined as:

$$E_{\text{use}} = \frac{\text{plant biomass}}{\text{plant } N \text{ or } P \text{ mass}}$$

4) Efficiency of *N* and *P* resorption from senescing leaves prior to abscission would increase with less favorable nutrient regimes, although absolute amounts of nutrient recovery would decrease (Lajtha 1987). Nutrient resorption efficiency was defined as:

$$E_{\text{res}} = \frac{(\text{mass } N \text{ or } P \text{ per unit area live leaves}) - (\text{mass } N \text{ or } P \text{ per unit area dead leaves})}{\text{mass } N \text{ or } P \text{ per unit area live leaves}}$$

5) *N* and *P* resorption from senescing leaves would be independent of each other, and would be dependent only on the availability of each nutrient in the supply solution.

Methods

Seeds were collected from shrubs of *Larrea tridentata* on an east-facing alluvial piedmont slope of the Dona Ana Mountains on the New Mexico State University Experimental Ranch about 40 km NNE of Las Cruces, New Mexico, in the Chihuahuan Desert. Fruits from over 30 shrubs were mixed and stored in paper bags at room temperature prior to the greenhouse experiment. Seeds were extracted from mericarps and planted in sterile sand in March 1986. Germinated seedlings were misted with deionized water for

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Table 1. Nutrient treatment solutions

In 1 l deionized water:

4 ml A stock solution
2 ml B stock solution
HCl to adjust pH to 6.5

A stock solution

Nutrient	Concentration (g/l)
Sequestrene (330 Fe DTPA)	38.44
$MgSo_4 \cdot 7H_2O$	126.65
$ZnSO_4 \cdot 7H_2O$	0.056
$MnSO_4 \cdot H_2O$	0.195
$CuSO_4 \cdot 5Fl_2$	0.021
H_3BO_3	0.725
$MoO_3 \cdot 2H_2O$	0.005
MoO_3-anhydrous	0.004
NaCl	5.85
$CaCl_2 \cdot 2H_2O$	73.1
$CaSO_4 \cdot 2H_2O$	86.0
$KHCO_3$	154.0

B stock solution

Treatment	NH_4NO_3 (g/l)	$NaH_2PO_4 \cdot H_2O$ (g/l)
1N1P	40.0	6.24
5N1P	200.0	6.24
25N1P	1000.0	6.24
1N5P	40.0	31.2
5N5P	200.0	31.2
25N5P	1000.0	31.2
1N25P	40.0	156.0
5N25P	200.0	156.0
25N25P	1000.0	156.0

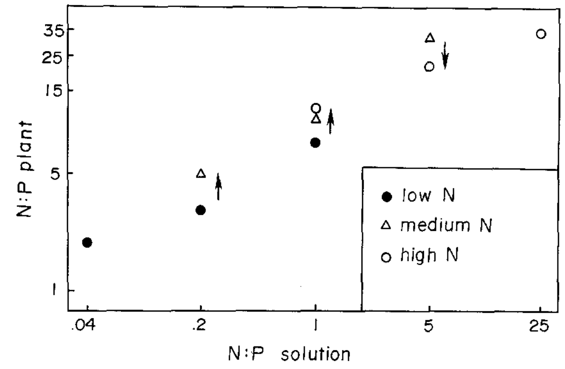

Fig. 1. *N:P* ratio of *Larrea* seedlings as a function of the *N:P* ratio of nutrient solutions, both plotted on a log scale. Arrows depict the trend in the *N:P* ratio of plants with increasing absolute nutrient supply concentrations within each nutrient ratio treatment

2 s/min, 8 h/day in the Duke University Phytotron Greenhouse with a 16/8 h photoperiod and a 26/20° C temperature regime. After 2 months, seedlings were transplanted into 8-cm pots containing a mixture of sand and vermiculite (4:1 sand:coarse vermiculite by volume). Seedlings were sorted into 3 size classes, and plants from each size class were distributed equally among the 9 treatments with 10 plants/treatment.

Treatments consisted of both an *N* and *P* gradient in a 2-way factorial design. Nine nutrient treatments were used, differing in the amount and concentration of *N* and *P* in the nutrient solution (Table 1). An excess of treatment solution (30 ml) or deionized water was supplied by completely saturating and flushing the soil. This method was selected because it could accomodate increased demands for water and nutrients as the plants grew. Plants were watered by hand at the soil surface to minimize foliar leaching. The nutrient solution for each treatment was applied 3 times a week, with waterings of deionized water following days of nutrient treatments.

Dead abscised leaves were collected throughout the growth experiment. All seedlings were harvested after 3 months and separated into the following components:

1) live leaves
2) dead leaves (both attached and fully abscised)
3) stems
4) roots

Leaf area of live and dead leaves was measured using a LI-COR 3000 Leaf Area Meter. Plant components were dried at 70° C for 48 h prior to weighing, and were ground in a Wiley Mill to pass a 20-mesh screen. Samples were digested using a sulfuric acid-hydrogen peroxide flux (Lowther 1980) and analyzed for total *N* and *P* using standard Technicon Auto Analyzer methods (Technicon 1977).

The General Linear Models Procedure of SAS (SAS Institute, Inc., 1982) was used to perform both the one-way and two-way analysis of variance in order to accomodate the unbalanced nature of the final design that resulted from slight mortality following transplanting. When the GLM procedure indicated statistical significance, Tukey's Studentized Range Test was used to distinguish differences among treatments. The GLM procedure was also used to perform all multiple regressions.

Results

N:P ratios in plant tissues

The *N:P* ratio in leaves, roots, and whole plants varied significantly ($P < 0.0001$) among treatments, and was positively correlated with the *N:P* ratio of the treatment solutions (Fig. 1). The mean *N:P* ratio in whole plants was 12.1 for the highest (25N25P) nutrient treatment, which also had the maximum growth. Within any given nutrient supply ratio, increasing the absolute concentrations of *N* and *P* (for example, from the 1:1 to the 5:5 to the 25:25 treatment) caused the ratio in seedlings to either increase or decrease in the direction of that value (see arrows, Fig. 1).

Nutrient concentrations in plant tissues

Concentrations of *N* in live leaves and roots increased with increasing levels of *N* ($P < 0.0001$) but were not affected by *P* supply (Table 2, Fig. 2). Concentrations of *P* in live leaves and roots increased significantly ($P < 0.0001$) with increasing levels of *P*, presumably due to luxury uptake of *P* at low *N* levels but dilution of *P* concentrations by plant growth at higher levels of *N* (Table 2, Fig. 2). The interaction of *N* and *P* was also significant ($P < 0.0001$), perhaps because the effect of increased plant growth, and thus dilution of *P* concentrations, with increasing *N* occurred only at medium and high levels of *P* supply.

Table 2. Concentrations of N and P in live leaves and roots, and leaf area and leaf weight per leaf at each nutrient supply treatment [mean (SE)]. Values within each column with the same superscript are not significantly different at $P < 0.005$

Treatment	% N		% P		Leaf area per leaf (cm^2)	Leaf weight per leaf (mg)
	live leaves	roots	live leaves	roots		
1N1P	1.85^{d} (0.09)	1.48^{d} (0.08)	0.199^{d} (0.029)	0.181^{e} (0.015)	0.19^{ab} (0.02)	1.96^{ab} (0.32)
5N1P	3.23^{abcd} (0.38)	3.04^{abc} (0.26)	0.101^{d} (0.011)	0.121^{e} (0.018)	0.15^{ab} (0.02)	1.94^{ab} (0.16)
25N1P	4.39^{a} (0.36)	3.34^{abc} (0.35)	0.120^{d} (0.003)	0.114^{e} (0.006)	0.15^{ab} (0.02)	1.82^{ab} (0.20)
1N5P	2.28^{cd} (0.15)	1.37^{d} (0.16)	0.779^{b} (0.156)	0.518^{b} (0.069)	0.12^{ab} (0.04)	1.21^{ab} (0.36)
5N5P	3.19^{abcd} (0.33)	2.42^{cd} (0.22)	0.304^{cd} (0.069)	0.294^{cd} (0.048)	0.22^{a} (0.02)	2.34^{a} (0.20)
25N5P	3.95^{ab} (0.37)	4.25^{a} (0.30)	0.155^{d} (0.018)	0.225^{de} (0.022)	0.21^{a} (0.03)	2.55^{a} (0.43)
1N25P	2.47^{bcd} (0.01)	1.43^{d} (0.05)	1.083^{a} (0.000)	0.960^{a} (0.039)	0.07^{b} (0.02)	0.82^{b} (0.25)
5N25P	2.39^{cd} (0.22)	2.65^{bcd} (0.56)	0.499^{bc} (0.034)	0.416^{bc} (0.035)	0.22^{a} (0.04)	2.24^{ab} (0.42)
25N25P	3.61^{abc} (0.29)	4.00^{ab} (0.55)	0.280^{cd} (0.019)	0.324^{cd} (0.012)	0.24^{a} (0.04)	2.40^{a} (0.35)

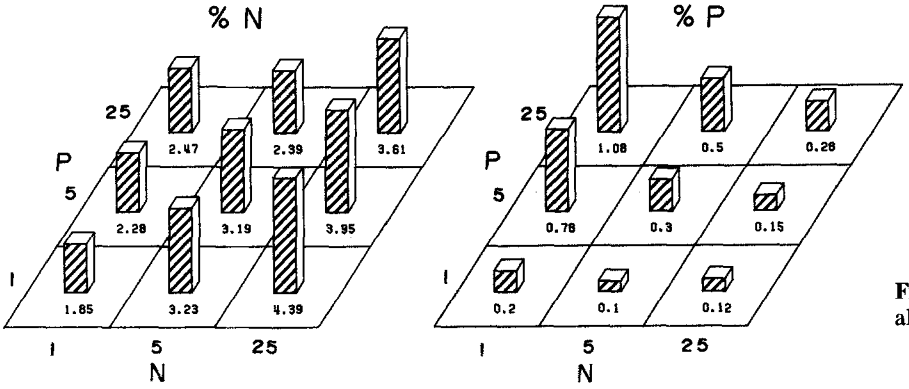

Fig. 2. % N and % P in *Larrea* seedlings along the N and P supply gradients

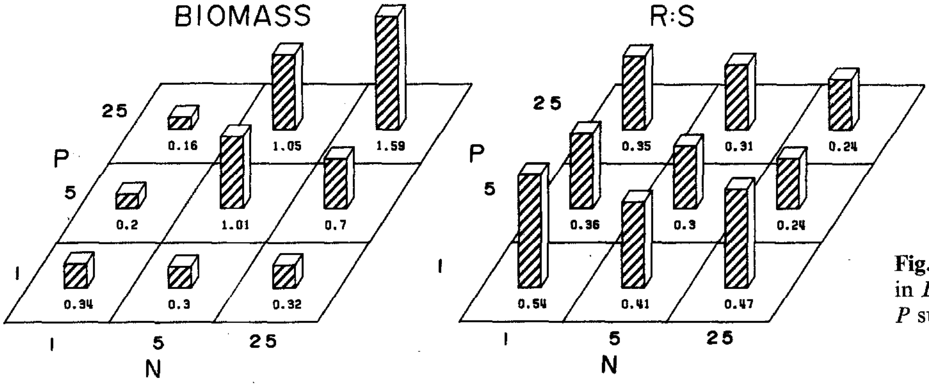

Fig. 3. Biomass and root:shoot ratios in *Larrea* seedlings along the N and P supply gradients

Biomass

Root, shoot, and total plant biomass were significantly positively correlated to both N and P supply ($P < 0.0001$). There was a 2.5-fold increase in biomass with increasing levels of P, and an even greater increase for N (Fig. 3). Neither nutrient alone controlled growth; low levels of either N or P resulted in low biomass. Within the bounds of a given N:P supply ratio, increased total nutrient concentration resulted in increased biomass. In the low N treatments, plants seemed to exhibit a "ratio toxicity" effect; as the level of P increased, biomass decreased, which most likely caused the significant $N*P$ interaction.

The total leaf area and leaf weight per leaf were significantly greater ($P < 0.004$ and $P < 0.0009$, respectively; Table 2) at intermediate and high levels of N. Phosphorus alone had no significant effect although there was a significant $N*P$ interaction for both leaf area and weight ($P <$ 0.003 and $P < 0.04$). Within any given nutrient supply ratio, increased total nutrient level resulted in a slight, although not statistically significant increase in leaf area and leaf weight.

Root: shoot ratio

Root:shoot ratios tended to decrease with increasing availability of either nutrient, although this effect was significant only for P ($P < 0.0005$, Fig. 3). This decrease was not due to an absolute decrease in root mass at higher nutrient treatments, but rather to a relatively larger increase in allocation to aboveground biomass. Root:shoot ratios did not vary predictably with N:P supply ratios.

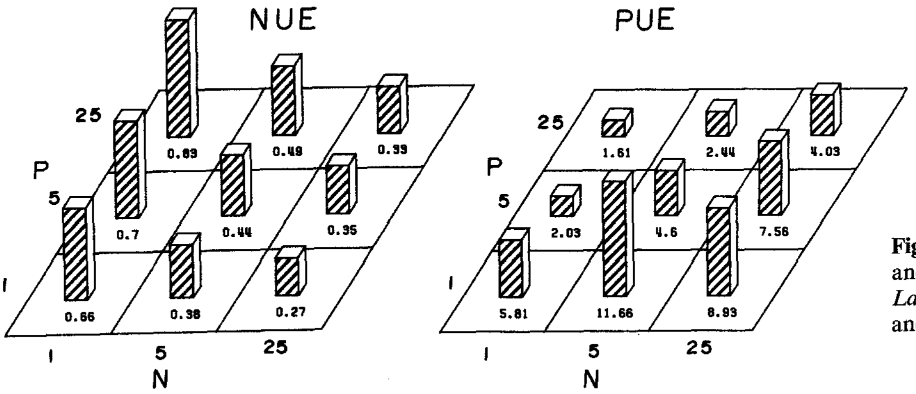

Fig. 4. Nitrogen use efficiency (NUE) and phosphorus use efficiency (PUE) in *Larrea* seedlings along the *N* and *P* supply gradients

Table 3. Efficiency of nutrient resorption and absolute amount of nutrient resorption at each nutrient supply treatment

Treatment	*N* resorption efficiency (%)	*P* resorption efficiency (%)	Amount of *N* resorption (g/cm^2)	Amount of *P* resorption (g/cm^2)
1N1P	54.2	65.1	0.099	0.013
5N1P	40.8	33.3	0.174	0.004
25N1P	51.0	41.0	0.272	0.006
1N5P	22.8	36.6	0.054	0.030
5N5P	66.5	37.0	0.235	0.013
25N5P	25.7	36.0	0.125	0.007
1N25P	22.3	39.4	0.064	0.050
5N25P	41.9	−33.0	0.108	−0.018
25N25P	34.2	−10.5	0.122	−0.003

Nutrient use efficiency

Nitrogen use efficiency (NUE; g biomass/g *N*) increased significantly ($P < 0.0001$) with decreasing levels of *N* supply (Fig. 4). NUE showed no significant correlation with *N:P* ratio in the supply solutions. Within a given *N:P* ratio, however, decreased *N* concentration resulted in an increase in NUE ($P < 0.05$). Although NUE was not significantly correlated with *P* supply rate, within any given *N* supply rate, NUE at intermediate and high levels of *P* supply were significantly higher than at low *P* supply rate ($P < 0.05$). Phosphorus use efficiency (PUE) similarly decreased with increasing levels of *P* and increased with increasing *N* supply, with a significant $N*P$ interaction ($P < 0.0001$ for all; Fig. 4).

Both NUE and PUE were significantly correlated to the concentrations of nutrients in plant tissues. NUE was negatively correlated to %*N* in leaves and positively correlated to %*P* ($P < 0.0001$ for both), with no significant N*P interaction. PUE was negatively correlated to %*P* and positively correlated to %*N* in leaves ($P < 0.0001$ and $P < 0.0008$, respectively), again without an $N*P$ interaction.

Nutrient resorption

Data could not be analyzed statistically, as individual samples were pooled within each nutrient treatment due to low abscised leaf weights for individual plants. In general, however, the greatest absolute amounts of *N* resorption were at the high *N* supply rate, and the smallest absolute amounts were at the low *N* supply rate (Table 3). However, the efficiency of *N* resorption did not demonstrate a trend with increasing *N* supply. Similarly, there did not appear to be a trend in absolute amounts of *P* resorption with either *N* or *P* supply. Although the efficiency of *P* resorption generally decreased with increasing *P* supply rate (with mean efficiencies of 46.5, 36.5, and −1.5% for high, intermediate, and low *P* supply rates, respectively), individual values were quite scattered, and thus the trend in mean efficiencies was not considered to be significant. In two of the high-*P* treatments *P* resorption had a negative value, indicating that *P* was translocated *to* the leaves prior to abscission.

Discussion

N:P ratios in photosynthetic tissue are typically measured in the range of 10–14 for optimal productivity (Rundel 1982; Ingestad 1979; van den Driessche 1974). In this study, the *N:P* ratio of both whole plants and leaves closely followed the *N:P* ratio of the nutrient supply solution, with the *N:P* ratio in the highest nutrient supply treatment averaging 13.2 for leaves and 12.1 for whole plants. Within each nutrient supply ratio, increasing absolute concentrations of nutrients tended to cause the plants to accumulate *N* and *P* such that internal *N:P* concentrations approached this value. This pattern of an "optimal" *N:P* ratio within plant tissues suggests that the uptake of *N* and *P* are not completely independent of each other, a conclusion reached by Shaver and Melillo (1984) in a similar experiment.

Nitrogen and phosphorus use efficiencies (g biomass/g nutrient) decreased with increasing supply of the individual nutrient, as has been found both in the field and in experimental greenhouse studies (Pastor et al. 1984; Shaver and Melillo 1984; Gray and Schlesinger 1983; Vitousek 1982; Ingestad 1979). In addition, NUE significantly increased with increasing *P* availability, just as PUE increased with increasing *N* availability. In effect, then, it appears that increased availability of *N* or *P* had the same effect on PUE or NUE, respectively, as did decreased *P* or *N* availability. There are two possible causes of these nutrient interaction effects:

1) Increased availability of one nutrient stimulates photosynthesis such that the concentration of other nutrients in foliage are diluted by growth and the accumulation of carbohydrates.

2) Plants respond directly to nutrient ratios, and thus an increase in the availability of one nutrient decreases the *relative* availability of other nutrients.

The first hypothesis was partially tested by regressing NUE and PUE against the concentration of *N* and *P* in photosynthetic tissues, thus removing the effect of dilution by growth. In both cases, nutrient use efficiency significantly increased with increasing concentrations of the other nutrient in leaves, suggesting that dilution alone did not account for these patterns. Parallel support for the second hypothesis was given by Davidson (1969), who found that for plants limited by a specific nutrient, increases in the availability of another nutrient caused a further decrease in the relative availability of the limiting nutrient, which led to an increase in root:shoot ratio. However, no similar pattern in root:shoot ratio was observed in this study.

Patterns of nutrient resorption were not as clear-cut. Although *N* resorption was greatest in the high *N* supply treatments, *P* resorption did not demonstrate a trend with *P* availability. There was no firm trend in either *N* or *P* resorption efficiency with either *N* or *P* availability.

Results from the literature on nutrient resorption efficiency are similarly inconclusive. Some studies have reported decreased resorption efficiency with increased nutrient availability (Turner 1977; Miller et al. 1976; Stachurski and Zimka 1975). Others have found either the reverse or else no clear pattern (Birk and Vitousek 1986; Chapin and Kedrowski 1983; Ostman and Weaver 1982; Staaf 1982). Patterns seen in this greenhouse experiment with seedlings do not match those observed in the field by Lajtha (1987), who found that *N* resorption efficiency increased significantly with increased *N* status although *P* resorption efficiency did not show a consistent pattern with plant *P* status. In that study, however, *N* availability was consistently relatively low compared to *P* availability, which was never limiting to plant growth.

These results may have important ecosystem-level implications. Several authors have postulated a positive feedback towards the maintenance of nutrient stress in nutrient-poor ecosystems (Shaver and Melillo 1984; Vitousek 1982). Critical to these arguments is the assumption that with decreased nutrient availability, increased nutrient use and nutrient resorption efficiencies lead to litterfall with a high *C:N* ratio that is relatively resistant to decomposition, further reducing soil nutrient availability. Evidence suggests that this pattern might not occur in *Larrea*-dominated ecosystems. First, there is relatively little buildup of organic matter in desert soils, such that organic matter is not a significant pool of soil nutrients (Lajtha and Schlesinger 1988). Second, although nutrient use efficiency increases with decreasing nutrient availability in *Larrea,* both this study and that of Lajtha (1987) have shown that this does not always result in increased resorption and thus the production of nutrient-poor litter.

Few authors have examined the role of nutrient interactions and nutrient availability ratios on the cycling and use of nutrients by plants. In this study, nitrogen use efficiency in *Larrea tridentata* was significantly affected by the availability of phosphorus and vice versa. In contrast, Shaver and Melillo (1984) found that nutrient availability ratios did not affect nutrient use efficiency in four species of marsh graminoids, although nutrient interactions significantly affected nutrient uptake efficiency. Clearly, more studies of nutrient ratio effects on nutrient cycling parameters of different plant species are needed before clear generalizations can be made.

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