Nutrient reabsorption efficiency and the response to phosphorus fertilization in the desert shrub *Larrea tridentata* (DC.) Cov.

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Abstract. A field fertilization experiment demonstrated that growth of *Larrea tridentata* was not limited by phosphorus, even though soils contained high levels of pedogenic carbonates that can potentially fix high amounts of phosphorus. Nutrient reabsorption efficiencies in unfertilized shrubs ranged from 72–86% for P, making nutrient reabsorption a very effective nutrient conservation mechanism. Absolute amounts of N and P reabsorption increased with N and P concentrations in leaves, with reabsorption being greater during drought stress than during rapid leaf growth. However, only N reabsorption efficiency increased with increasing plant N status. A model was developed to explain patterns of nutrient reabsorption efficiencies over large gradients in nutrient availability.

Introduction

Ecologists have only recently begun to assess the importance of nutrients as controlling factors in the productivity of deserts (Crawford & Gosz 1982). To date, most studies of nutrient cycling in arid lands have focused on nitrogen. Fertilization experiments in various deserts of the southwestern US demonstrated that many plants respond to increased levels of nitrogen, showing greater production or higher tissue nutrient content (Wallace & Romney 1972; Ettershank et al. 1978; Williams & Bell 1981). Little is known about the effects of nutrient limitations on nutrient allocation within desert plants or on internal cycling and conservation of nutrients by plants. These physiological processes can affect nutrient cycling at the ecosystem level and indirectly affect carbon allocation and fixation.

Certain characteristic features of desert soils suggest that phosphorus might also be a limiting element to plant growth. Soils in the southwestern US, as well as many soils of arid regions worldwide, contain high levels of precipitated carbonates (Dregne 1976; Schlesinger 1982). Carbonates can

control phosphorus levels in the soil solution through ion pairing with calcium, physical sorption onto $CaCO_3$, and the precipitation of secondary calcium phosphate minerals (Cole & Olsen 1959; Marion & Babcock 1977; Avnimelech 1983). The fixation of phosphorus by pedogenic carbonates has been implicated in the lowered crop response to phosphorus fertilization in the Southwest (Chang 1953; McCaslin & Gledhill 1980). In greenhouse experiments, additions of $CaCO_3$ were shown to affect phosphorus uptake in *Larrea tridentata*, an evergreen shrub of southwestern deserts whose distribution is linked to soils with a calcic horizon at depth, but not significantly in *Parthenium incanum*, a shrub restricted to soils that are more strongly calcareous throughout the soil profile (Lajtha 1986). Although pedogenic $CaCO_3$ appears to effectively lower soil phosphorus availability, phosphorus may not limit productivity in sparsely vegetated desert communities given concurrent limitations by water and nitrogen.

The purpose of this study was threefold. Firstly, a fertilization experiment was conducted to determine if phosphorus is limiting to the primary production of a *Larrea tridentata*-dominated desert community that has been shown to respond both to water and to nitrogen amendments (Fisher et al. unpublished). Secondly, the effects of increased phosphorus availability on the internal cycling of phosphorus by *Larrea* were examined. Thirdly, the relationships between nutrient reabsorption, nutrient reabsorption efficiency, and plant nutrient status were examined in both natural and fertilized shrubs. Initial hypotheses were:

— Shrubs would respond to increases in P availability with increased growth and increased leaf longevity (cf. Miller et al 1976; but also see Shaver 1983).
— Nutrient reabsorption efficiency would decrease with increasing P availability (cf. Shaver & Melillo 1984).
— The relationship between reabsorption efficiency and plant nutrient status would be greatest during periods of rapid growth and least during periods of drought stress (cf. Hocking, 1982).

Methods

Study site

This study was conducted on the Jornada Experimental Ranch of New Mexico State University in the Jornada Del Muerto Basin, 40 km NNE of Las Cruces, New Mexico. The Jornada is located in the Mexican Highland section of the Basin and Range physiographic province, near the northern limits of the Chihuahuan Desert. The climate in the valley border area is

arid, with potential evaporation exceeding ten times the annual precipitation (Gile et al. 1981). Soils in the study area show 1–5% $CaCO_3$ throughout the profile, with an indurated caliche layer at 37 cm depth.

During the summer of 1983, a 20 m × 10 m plot was established on a bajada slope of Mt. Summerford in a community dominated by *Larrea tridentata*, an evergreen xerophytic shrub that is one of the most widespread shrubs of the warm deserts of North America (Shreve 1942). Growth in *Larrea* occurs both in spring in response to warming and soil moisture that has accumulated during the winter, and in late summer in response to significant rainstorms. Pairs of bifoliate leaves are produced on nodes that remain visible even after leaf abscission, making *Larrea* an ideal shrub for phenological studies. The plot was fenced to protect shrubs from grazing, and was subdivided into a central experimental fertilization plot (10 m × 10 m) with two control plots (10 m × 5 m) on each side. Trenches were dug between these subplots to a depth several cm below the top of the indurated carbonate layer, then lined with plastic and backfilled. The experimental plot was fertilized with triple superphosphate (0-46-0) at the rate of 25 g m^{-2} P. The fertilizer was applied in late July, just prior to the expected summer rainy season.

Phenology

Within these plots, 15 control (7 in one subplot, 8 in the other) and 15 fertilized *Larrea* shrubs were randomly selected from the 26 (control) and 25 (fertilized) shrubs present in the plots. On each shrub 10 stems were tagged and the year's earliest internode (identified by the pale color of stipules) was marked for growth analyses, following the methods of Burk & Dick-Peddie (1973). Phenological parameters were monitored monthly from May–September during the following two years, which included spring growing seasons and late-summer rainy seasons:
— shoot elongation
— total # nodes/branch
— total # live leaves/branch
— # empty nodes/branch

Nutrient analyses

At each sampling date, both fully expanded live leaves and attached, dead leaves whose abscission layer was formed were collected for nutrient analyses. Leaf area was determined on a LICOR 3100 area meter. Because *Larrea* leaves generally curl when dried upon storage after collection, leaves were autoclaved briefly, pressed between glass plates, and air-dried prior to leaf

area determinations. Leaves were then dried at 70 °C for 48 h prior to weighing. Tissues were digested in a Technicon block digestor using a sulfuric acid-hydrogen peroxide flux (Lowther 1980), and analyzed for total N and P on a Technicon AutoAnalyzer using standard methods (Technicon 1977).

Tissue nutrient contents were measured both on a leaf weight and a leaf area basis to take into account changes in specific weight that might occur over the growing season. Reabsorption efficiency was expressed as a percentage of the nutrient content of live leaves:

$$\% \text{ reabsorption} = \frac{\text{LL--DL}}{\text{LL}} \times 100$$

where: LL = maximum nutrient concentration of live leaves during the growing season
DL = nutrient content of dead leaves collected each month
The absolute amount of nutrient withdrawal was defined as LL–DL, measured on a leaf area basis. Leaching losses of N and P were assumed to be negligible, as has been found in other studies (Ryan & Bormann 1982; Lennon et al. 1985).

Statistical analyses

The GLM procedure of SAS (SAS Institute Inc. 1982) was used to perform linear regressions between variables and for between plot comparisons within individual sampling dates. In order to avoid problems of temporal pseudoreplication through the repeated measurement of the same individuals over time (Hurlbert 1984), the GLM procedure was modified to perform a profile analysis of variance (Simms & Burdick, in press) for comparing nutrient concentrations and nutrient reabsorption over time.

It must be noted that as only one fertilized plot was established due to the difficulty and expense of fencing and trenching large areas of sparsely vegetated desert land, the 15 shrubs within the experimental plot are sub-samples of a single plot and are not technically independent replicates. Statistical differences between plots, then, cannot be definitively attributed to differences in experimental fertilization. The establishment of the 2 interspersed control plots was done in part to compensate for this. This nonreplication of experimental treatment does not, however, affect regression analyses that were plot-independent.
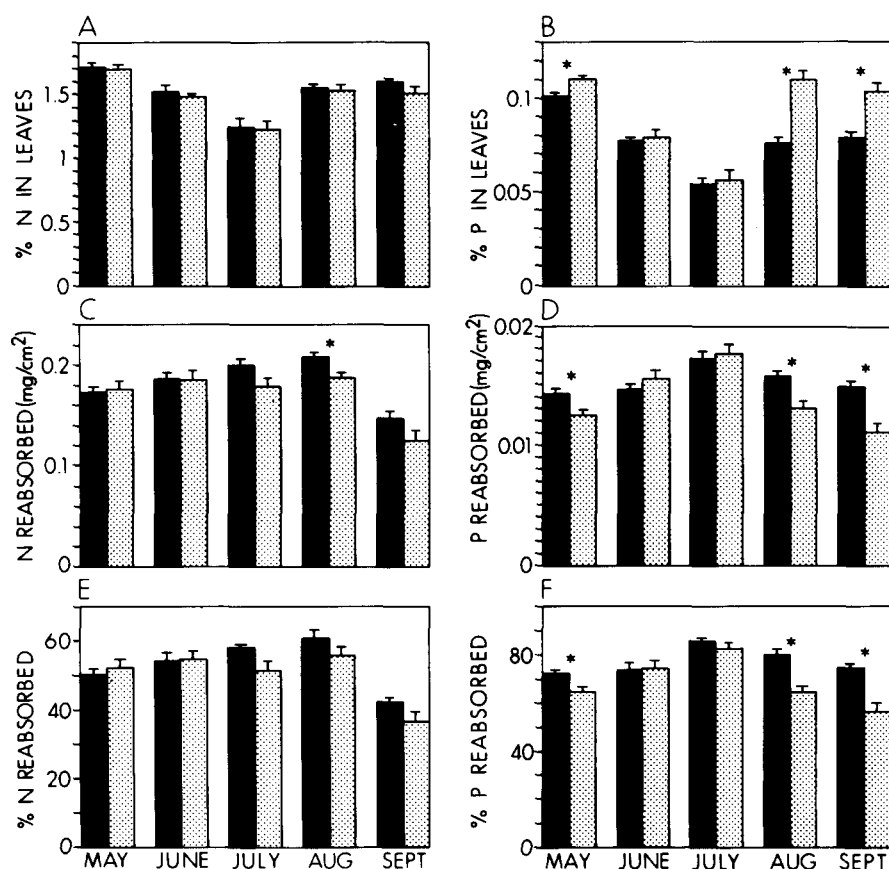
Fig. 1. Nutrient content, nutrient reabsorption, and % nutrient reabsorption ($\pm$ SE) in control (solid bars) and fertilized (stippled bars) *Larrea tridentata* shrubs during the summer of 1985. Each bar represents the mean of 15 shrubs. * indicates months in which treatment means are significantly different ($p < 0.05$).

Results

The experimental plot was fertilized in the late summer of 1983, but very little rain fell during the autumn rain season. Elevated levels of soil P in the B horizon and increased tissue P concentrations in shrubs in the fertilized plot were not detected until late summer 1984. Thus, comparisons of growth and nutrient cycling between plots were analyzed only for the 1985 growing season.

No differences between fertilized and control treatments were detected in shoot elongation, leaf production, or leaf longevity (Table 1). In all plots, the lifespan of a leaf averaged about 11 months.

Table 1. Shoot elongation, leaf node production, and leaf lifespan ($\pm$ SE) for control and fertilized *Larrea tridentata* shrubs after 3 years. Each value is the mean of 15 shrubs.

	control shrubs	fertilized shrubs
mean elongation/shoot	10.6 (± 2.1) cm	10.1 (± 3.0) cm
mean # leaf nodes produced/shoot	42 (± 8)	46 (± 8)
mean leaf lifespan	11.1 (± 2.0) months	10.6 (± 1.7) months

During the 1985 growing season, foliar concentrations of both N and P were highest at the start of the growing season and lowest in July during the mid-summer dry period (Fig. 1a,b). Concentrations then increased in August and September, although this increase was significant only for N. Tissue N concentrations did not vary significantly between treatments during any month. However, P concentrations were significantly higher in
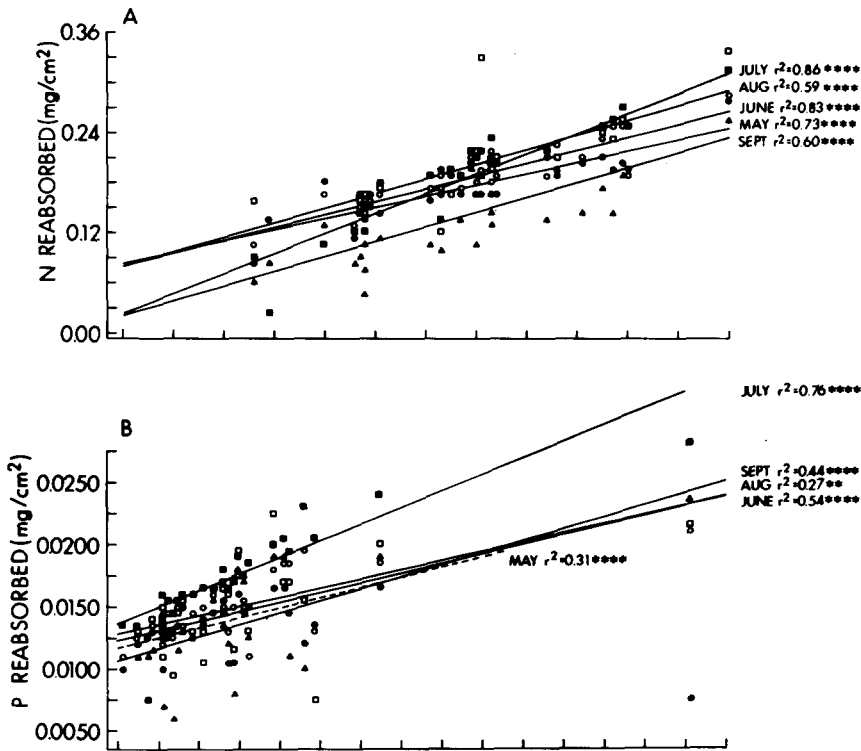

Fig. 2a,b.

the fertilized plot during all months except June and July, when tissue P concentrations in all leaves were very low.

Reabsorption efficiencies were very similar on a leaf area or leaf weight basis for both elements, with efficiencies calculated on a leaf area basis about 3–5% higher than efficiencies calculated on a leaf weight basis. Only efficiencies based on leaf area are discussed here, as these values are more sensitive to seasonal changes in specific leaf weight.

Neither the absolute amount (mg/cm^2) nor the %N reabsorbed varied significantly between treatments (Fig. 1c,e), although both the absolute amounts and the percentages of P reabsorbed were greater in unfertilized plants during all months except June and July, when P reabsorption was very high for all shrubs (Fig. 1d,f). There were no statistically significant differences among months for either the absolute amount or the percent reabsorption for either N or P.
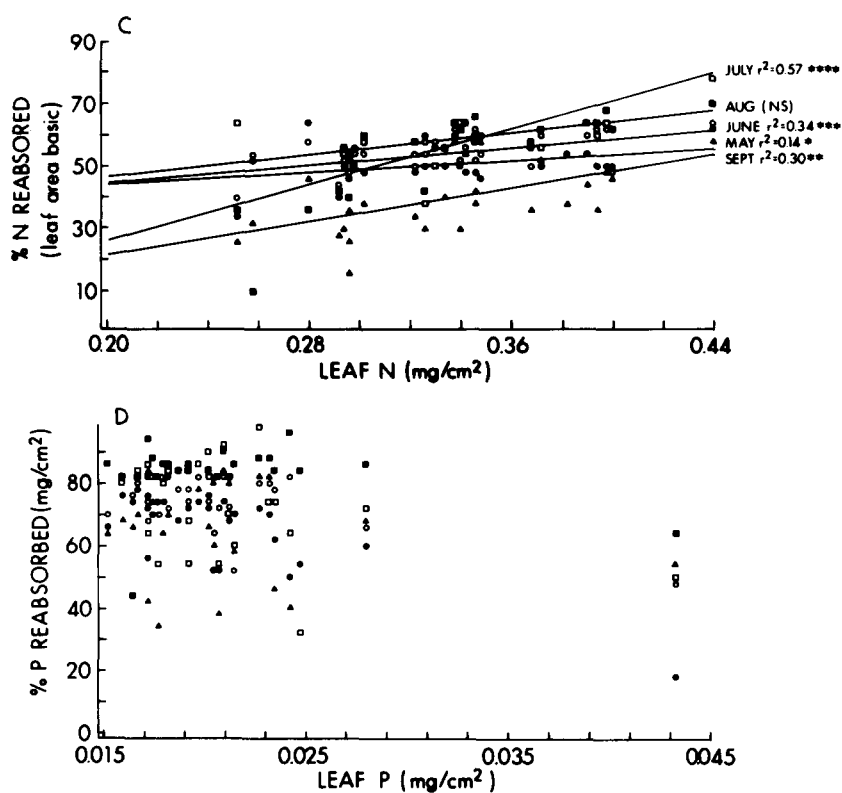

Fig. 2c,d.

Fig. 2. Correlations of absolute amounts of nutrient reabsorption and nutrient reabsorption efficiency with nutrient status of both control and fertilized *Larrea* shrubs during each month of the 1985 growing season. Broken regression line indicates regression performed after eliminating outliers. ● = May, ○ = June, ■ = July, ◻ = August, ▲ = September
*p < 0.05,**p < 0.01, ***p < 0.001, ****p < 0.0001

The absolute amounts of both N and P reabsorbed were highly correlated to shrub nutrient status at each sampling date, with correlations being slightly stronger for N (Fig. 2a,b). Slopes of the regressions as well as r^2 values were highest for both N and P during July. The %N reabsorbed, or N reabsorption efficiency, increased with increasing plant N status (Fig. 2c). Regression slopes again were greatest during July. The reabsorption efficiency of P did not vary significantly with plant P status either in control shrubs or in all shrubs considered together, although all regression slopes were negative (Fig. 2d).

Discussion

In a greenhouse study, the presence of $CaCO_3$ in the soil significantly inhibited the availability of P to *Larrea tridentata* seedlings (Lajtha 1986). In this field fertilization experiment, however, P did not appear to be a limiting element for growth in mature *Larrea* shrubs. It is possible that potential limitations of P in the field are overshadowed by the more severe limitations of both water and N. Alternatively, despite fixation of P by pedogenic carbonates, levels of total P in the soil may be high enough that relatively high levels of available P are maintained.

Reabsorption of nutrients by *Larrea* is an effective nutrient conservation mechanism, so that nutrient limitations may be avoided even under conditions of low nutrient availability. Leaf initiation and senescence occur year-round in this species, with no distinct season of leaf fall. Jonasson & Chapin (1985) stressed the significance of sequential leaf production for
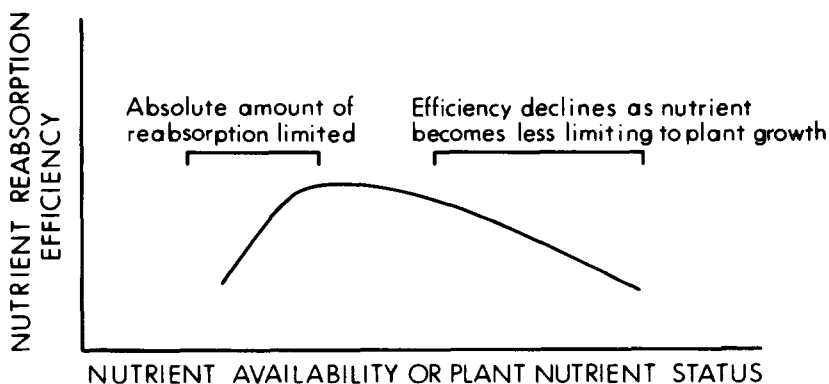

Fig. 3. A model of the relationship between nutrient availability and nutrient reabsorption efficiency. When tissue nutrient concentrations are very low, the pool of potentially re-mobilized nutrients limits the absolute amount of reabsorption. As tissue nutrient concentrations increase, the absolute amount of nutrient reabsorption increases at first but then levels of as nutrients become less limiting to growth.

nutrient conservation, and demonstrated that nutrients reabsorbed from senescing leaves could account for over 85% of the nutrients required for the production of concurrently growing leaves in *Eriophorum vaginatum* in a wet tundra ecosystem.

Nutrient reabsorption efficiency in unfertilized shrubs, measured on a leaf area basis, ranged from a monthly average of 72–86% for P and 42–61% for N. This efficiency for P is extremely high and is comparable to efficiencies in P-limited ecosystems such as Australian *Eucalyptus* forests (mean of 73%, Attiwill et al. 1978), Alaskan black spruce understory (72%; Chapin 1983), Alaskan taiga (44–81%; Chapin & Kedrowski 1983), and southeastern coastal plain pocosins (53–87%; Walbridge 1986). In a survey of a wide variety of plant communities, Chapin & Kedrowski (1983) calculated a mean P reabsorption efficiency of 43%. Thus even under relatively low P availability, *Larrea* could meet much of its nutrient requirement through internal nutrient recycling.

Many studies have attempted to correlate nutrient reabsorption efficiency with plant nutrient status and soil nutrient availability. While some authors, working with fertilized plots, natural fertility gradients, or greenhouse experiments have found that nutrient reabsorption efficiency decreases with' increasing nutrient availability or plant nutrient status (Stachurski & Zimka 1975; Miller et al. 1976; Turner 1977; Shaver & Melillo 1984, Lennon et al. 1985), others have found no such relationship or the reverse (Staaf 1982; Ostman & Weaver 1982; Chapin & Kedrowski 1983; Birk & Vitousek 1986). In the present study, absolute amounts of N and P reabsorbed consistently increased with increasing plant nutrient status. N reabsorption efficiency increased significantly with increasing plant N status, in contrast with most of the above cited studies. However, P reabsorption efficiency did not show a statistically significant pattern with plant P status, although there was a slight trend for decreasing efficiencies with increasing P status.

There are several potential explanations for these apparently anomalous patterns. Nitrogen concentrations measured in these shrubs were extremely low compared to mean values for desert shrubs in general (El-Ghonemy et al. 1978), and N fertilization of *Larrea* in adjacent plots increased biomass production by over 100% (Fisher et al. unpublished). Leaves with more favorable N status undoubtedly contain a higher proportion of proteins, particularly C-fixing enzymes. Protein that was hydrolyzed and subsequently reabsorbed accounted for the vast majority (82–91%) of the total N removed from senescing leaves in 4 taiga tree species studied by Chapin & Kedrowski (1983). As nutrient status increases in nutrient stressed plants, the pool of potentially remobilized nutrients increases, and thus calculated efficiencies increase. However, in more fertile sites, the cost of reabsorbing a nutrient may exceed the cost of nutrient uptake from the soil, and nutrient reabsorption efficiency may decrease (Fig. 3). Previous workers may have

reached contradictory interpretations regarding the response of plants to nutrient stress because the status of experimental sites along the full gradient of nutrient availability (Fig. 3) was unknown. Desert ecosystems may represent an extreme in nitrogen limitation, at which the quantity of non-structural leaf N that can be reabsorbed is minimal and increases with increasing availability. Phosphorus, however, was found not to be a limiting element in this system, and thus the observed patterns of decreasing reabsorption efficiency with increasing P status and in P-fertilized shrubs are consistent with this model.

Various authors have postulated a positive feedback towards the maintenance of nutrient stress in nutrient-poor ecosystems (Vitousek 1982; Shaver & Melillo 1984). Litterfall with a high C:N ratio is relatively resistant to decomposition in the soil, potentially reducing soil nutrient availability. Plants might then respond to the lowered nutrient availability by increasing reabsorption efficiency, thus further increasing resistance of litter to decomposition. Two lines of evidence suggest that this pattern might not occur in desert ecosystems. Firstly, there is relatively little build-up of organic matter in desert soils, such that organic matter is not a significant pool of soil nutrients (Lajtha 1986). Secondly, this study, in contrast to studies in many other ecosystems, has demonstrated that nutrient withdrawal and nutrient withdrawal efficiency decrease, rather than increase, under increasing nutrient stress.

An initial hypothesis of this experiment was that the relationship between resorption and plant nutrient status would be greatest during seasons of rapid growth and least during mid-summer drought. This hypothesis was based on the observation that leaves of this species turn over most rapidly during periods of new growth (Burk & Dick-Peddie 1973; Bamberg et al. 1976), presumably because N and P stored in old leaves are mobilized for the nutrient requirements of young leaves. This phenomenon has been observed in other species as well (Fife & Nambiar 1984; Comstock & Ehleringer 1986). Leaves are also shed in response to periods of severe drought (Chew & Chew 1965; Ludwig & Whitford 1981) and these leaves may not have sufficient time for the complete reabsorption of nutrients (Hocking 1982). However, mean reabsorption efficiencies were highest (although this is not statistically significant by profile ANOVA) and the relationship of nutrient reabsorption versus plant nutrient content was greatest during the mid-summer drought of July. Regression slopes and r^2 values were lower in September and May, seasons of growth from autumn rains and winter soil moisture accumulation, respectively. Thus leaves that abscise during periods of drought are able to remobilize greater amounts of nutrients than leaves that abscise during periods of greater water availability and new leaf growth.

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