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Low leaf N and P resorption contributes to nutrient limitation in two desert shrubs

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Abstract

Both water and nutrients are limiting in arid environments, and desert plants have adapted to these limitations through numerous developmental and physiological mechanisms. In the Mono Basin, California, USA, co-dominant *Sarcobatus vermiculatus* and *Chrysothamnus nauseosus* ssp. *consimilis* are differentially N and P limited. We hypothesized that low leaf N resorption contributes to N-limitation in *Sarcobatus* and that low leaf P resorption contributes to P-limitation in *Chrysothamnus*. As predicted, *Sarcobatus* resorbed proportionally 1.7-fold less N than *Chrysothamnus*, but reduced leaf P in senescent leaves to lower levels than *Chrysothamnus* (8.0 –10.8-fold lower based on leaf area or mass, respectively), consistent with N, but not P limitations in *Sarcobatus*. Again, as predicted, *Chrysothamnus* resorbed proportionally 2.0-fold less P than *Sarcobatus* yet reduced leaf N in senescent leaves to lower levels than *Sarcobatus* (1.8 –1.3-fold lower based on leaf area or mass, respectively), consistent with P, but not N limitations in *Chrysothamnus*. Leaf N and P pools were approximately 50% of aboveground pools in both species during the growing season, suggesting leaf resorption can contribute significantly to whole plant nutrient retention. This was consistent with changes in leaf N vs. P concentration as plants grew from seedlings to adults. Our results support the conclusion that N-limitation in *Sarcobatus* and P-limitation in *Chrysothamnus* are in part caused by physiological (or other) constraints that prevent more efficient resorption of N or P, respectively. For these species, differential nutrient resorption may be a key physiological component contributing to their coexistence in this saline, low resource habitat.

Introduction

Desert ecosystems are resource-poor environments. Not only does low and infrequent precipitation lead to low water availability, but it also decreases nutrient availability. Without sufficient leaching from precipitation, soil carbonates accumulate, increasing soil alkalinity and leading to low availability of P and other plant nutrients (Lajtha and Schlesinger 1988; Misra and Tyler 2000). In addition, low and pulsed precipitation limits biological N cycling, strongly limiting N availability (Noy-Meir 1973; Schimel and Parton 1986; Fisher et al. 1987).

Desert plants have adapted to these low nutrient conditions both developmentally and physiologically. Following precipitation-linked nutrient pulses, rapid root proliferation (Jordan and Nobel 1984; Jackson and Caldwell 1989) and changes in physiological uptake capacity (Jackson et al. 1990) may occur. In many desert perennials high nutrient use efficiency (Lajtha 1987), low growth rates, long green tissue life span (Aerts and Chapin 2000), and tight nutrient recycling (West 1991; Carrera et al. 2001) also contribute to nutrient conservation.

In the Great Basin Desert of western North America, two common shrubs, *Chrysothamnus-nauseosus* (Palla.) Britton ssp. *consimilis* (Greene) Hall and Clement (Asteraceae) and *Sarcobatus-vermiculatus* (Hook.) Torrey (Chenopodiaceae), often co-dominate saline, alkaline basin habitats, typified by our Mono Basin, California field site (West 1983; Fort and Richards 1998; Toft and Elliott-Fisk 2002). However, these phreatophytic shrubs differ greatly in water relations and nutrient physiology; *Sarcobatus* is a halophyte while *Chrysothamnus* is not (Donovan et al. 1996; Donovan and Richards 2000). Furthermore, despite similar rooting densities and significant root overlap in the upper 1 m of soil (Donovan et al. 1996, Donovan et al. 2003), previous research has documented N limitation in *Sarcobatus* and P and water co-limitation in *Chrysothamnus* (Drenovsky and Richards 2004). A factorial nutrient addition field experiment (N, P, N+P, control) showed that *Chrysothamnus*, although mycorrhizal, is water and P co-limited, with addition of these resources increasing stem growth by 70% relative to controls. In contrast, *Sarcobatus*, which is usually non-mycorrhizal, is strongly N-limited, with N additions increasing stem growth by as much as 170%. These contrasting nutrient limitations may be one additional component of physiological differences between these species that contributes to their coexistence.

Chrysothamnus and *Sarcobatus* have similar phenological characteristics. They initiate shoot growth in spring and grow most rapidly during May and June (Donovan et al. 1997; Drenovsky and Richards 2004). Similar growth patterns correspond with similar timing of N acquisition in spring (James and Richards 2005). Nighttime transpiration and hydraulic lift have been measured in both species (Donovan et al. 2001, 2003), which may contribute to nutrient acquisition in their low nutrient habitat. In addition, both species experience loss of nutrients due to leaf shedding in late summer and in autumn.

One important nutrient conservation strategy that has not been studied in these shrubs is nutrient recycling and storage. If *Chrysothamnus* and *Sarcobatus* differentially resorb N and P from senescing leaves, we would have evidence for a key physiological mechanism contributing to their contrasting nutrient limitations. Because more complete resorption may increase within-plant nutrient recycling and fitness-related traits (May and Killingbeck 1992; van Breemen 1995; Aerts 1996 and references cited therein; Eckstein et al. 1999; Aerts and Chapin 2000), we hypothesized that differential leaf nutrient resorption may contribute to these observed differences in nutrient limitation. Specifically, since *Chrysothamnus* is P-limited but not N-limited, we predicted that the lack of N-limitation in *Chrysothamnus* is associated with higher percent N resorption (greater N resorption efficiency) and lower N concentrations in senesced leaf tissue (higher N resorption proficiency, *sensu* Killingbeck 1996). In contrast, because *Sarcobatus* is N-limited, but not P-limited, we predicted that the lack of P-limitation in *Sarcobatus* is related to higher percent P resorption (greater P resorption efficiency) and lower P concentrations in senesced leaf tissue (higher P resorption proficiency). For both species, we hypothesized that low nutrient resorption efficiency and proficiency for their respective limiting nutrient (P in *Chrysothamnus* and N in *Sarcobatus*) contributes to the respective nutrient limitations in both shrubs.

The objectives of our experiment were (1) to determine whether *Chrysothamnus* and *Sarcobatus* differentially resorb N and P from leaves, consistent with our hypothesis that *Chrysothamnus* is more efficient and proficient at resorbing N and *Sarcobatus* is more efficient and proficient at resorbing P, (2) to determine the relative contribution leaf nutrient resorption makes to overall aboveground N and P pools in these shrubs to assess whether resorption is likely to affect plant nutrient status, and (3) to relate these physiological mechanisms to observed changes in leaf nutrient concentrations in different age classes of shrubs.

Methods

Our study site is part of the Mono Basin Ecosystem Research Site (MBERS) located in the Mono Basin, CA, USA, approximately 1.5 km north of the current lakeshore near two sites used previously (Sand Flat and Diverse Dunes, Donovan and Richards 2000). Although long-term climate change has caused the lake level to fluctuate, in 1941 inflow streams were diverted for agricultural and urban purposes causing the lake level to rapidly decline, exposing lakebed surfaces. Our site has been exposed for approximately 60 years (Toft and Elliott-Fisk 2002). Soil pH is approximately 9.6, and soil saturated paste electrical conductivity (EC_e) is 3.8 dS m^{-1} (Donovan and Richards 2000).

Previous data from this experiment demonstrated P and water co-limitation in *Chrysothamnus* and N-limitation in *Sarcobatus* (Drenovsky and Richards 2004). For the present study, control plants from the previous study were analyzed for resorption and storage patterns to test the hypothesis that low resorption contributes to the respective nutrient limitations of these two species. Eight blocks, across 0.5 km of the site, were selected in fall 1999 (Drenovsky and Richards 2004). The present study was initiated in spring 2001. Previous studies at this field site indicated mature leaf N and P concentrations are maximal in June (Donovan et al. 1997; R.E. Drenovsky, unpublished data). All mature leaves from 8 to 10 upper canopy stems were collected from shrubs of both species in all blocks in mid-June, and, similarly, senescent leaves were collected just prior to abscission in mid-October. Leaf samples were kept cold until leaf area could be determined from a subsample of 50–100 leaves from each plant (WinRhizo Pro, version 5.1A; Quebec, Canada). These leaves were oven-dried at 60 °C and weighed to determine leaf mass per area. Oven-dried leaves were ground and weighed for N and P analysis. Leaf N was measured on a CN analyzer (Carlo Erba; Milan, Italy). Samples for leaf P were dry-ashed and dissolved in 1 N HCl before ICP-AES analysis (Thermo-Jarrell Ash; Franklin, MA, USA).

Both resorption efficiency and resorption proficiency were measured in this study. Resorption efficiency was defined as in Lajtha and Klein (1988):

$$RE = \frac{\text{(June nutrient mass per unit leaf area -- October nutrient mass per unit leaf area)}}{\text{(June nutrient mass per unit leaf area)}}$$

Following the definition of Killingbeck (1996), resorption proficiency was the nutrient concentration in senesced leaves. In Killingbeck's (1996) comparison of 89 plant species, distinctions were made between relatively complete (i.e., lowest nutrient concentration at abscission), incomplete, and intermediate resorption. Complete and incomplete resorption are equivalent to high (< 50 µg cm^{-2} N or 3 µg cm^{-2} P) and low (> 75 µg cm^{-2} N or 8 µg cm^{-2} P) resorption proficiency, respectively. Intermediate resorption is the range between complete and incomplete resorption. Both resorption measures were calculated on an area basis (N or P concentration (g kg^{-1}) multiplied by leaf mass per area (kg m^{-2})). Determining nutrient resorption on an area basis, rather than a mass basis, removes the confounding effect of decreased leaf mass due to carbohydrate resorption in both species (Aerts 1996; van Heerwaarden et al. 2003) and salt accumulation in *Sarcobatus*, but not *Chrysothamnus*. Resorption proficiency, however, was also reported on a mass basis, to allow for comparison with other resorption proficiency values in the literature (see Killingbeck 1996).

As a relative measure, resorption efficiency provides a link between nutrient requirements (nutrient concentration in green, mature leaves) and nutrient withdrawal (nutrient concentration in senesced leaves). In contrast to resorption efficiency, resorption proficiency is an absolute measure of nutrient withdrawal. It has been suggested that resorption proficiency is more useful than resorption efficiency for assessing the evolution of resorption processes, since selection acts on traits (such as nutrient concentrations in senesced leaves) rather than proportions (such as the amount of nutrients in green vs. senesced leaves) (Killingbeck 1996). As such, resorption proficiency may provide insight into relationships between nutrient resorption, site fertility, and species traits.

To assess the relative contribution nutrient resorption makes to overall aboveground nutrient status, aboveground N and P pool sizes were estimated (where pool size equals biomass times nutrient mass concentration). The extensive root system overlap and morphological similarity of

Chrysothamnus and *Sarcobatus* fine roots pre-vented an assessment of root N and P pools. In June, samples containing old stems (> 1 year old) and young stems (current growing season) were collected from five of the experimental shrubs to determine N and P concentrations in stem mate-rial. These samples were separated into their component parts, dried at 60 °C, ground, and analyzed for N and P, using the analytical methods described above for leaf tissue. To obtain a June biomass estimate without destroying the experi-mental plants, relative biomass of old stems, young stems, and leaves were estimated in June by harvesting the aboveground biomass of five addi-tional shrubs per species similar in size and growing near the experimental shrubs. The N and P concentrations in leaves, young stems, and old stems from the experimental shrubs were averaged and then multiplied by the average biomass values from the reference shrubs to approximate nutrient pool sizes for the June sampling period. The same procedures were followed in October to determine nutrient pool sizes. In the community, *Chryso-thamnus* and *Sarcobatus* achieve the same sizes and root depth distribution (Donovan et al. 1996; Snyder et al. 2004). However, although the experimental plants were randomly selected within the same canopy volume classes, they did not ob-tain similar mass by the end of the growing season. To prevent the mass difference of the experimental plants from confounding our analysis of nutrient pools, we scaled each shrub to the same mass, maintaining the measured ratios of leaves, young stems, and old stems.

We also compared nutrient concentrations in leaves of seedling and adult *Chrysothamnus* and *Sarcobatus* to assess consistency with resorption differences (seedling data: L.A. Donovan and J.H. Richards unpublished data; *Chrysothamnus* adult data: Donovan et al. 1996; *Sarcobatus* adult data: Drenovsky and Richards 2005 and R.E. Drenovsky unpublished data). Due to variable precipitation between years, where available, data were averaged over below-average and average rainfall years. All leaf tissue was collected mid-growing season.

Differences between species resorption patterns were determined using analysis of variance (ANOVA), with species and block as the main effects. Assumption of normality was tested using the Shapiro–Wilks test, and weighted ANOVAs

were run when variance was unequal between species (Neter et al. 1996). Post-hoc Tukey's tests were used to determine differences between spe-cies means. *t*-tests were used to compare resorp-tion efficiency values in *Chrysothamnus* and *Sarcobatus* to average resorption efficiency values for shrubs and trees and to compare leaf N and P concentrations in different age classes of *Chrysothamnus* and *Sarcobatus*. All data were analyzed with SAS (SAS Institute 2001). Pool sizes were not statistically comparable, as average biomass values were multiplied by average nutrient concentrations.

Results

Nutrient resorption

Chrysothamnus and *Sarcobatus* differentially re-sorbed N and P whether calculated as resorption efficiency or as resorption proficiency on either a leaf area or a mass basis. Leaf N resorption effi-ciency was 1.7-fold greater in *Chrysothamnus* than in *Sarcobatus* (Figure 1a; Table 1). *Chrysothamnus* also was most proficient at resorbing N, with se-nesced leaf N concentrations 1.8 and 1.3-fold less based on leaf area or mass, respectively, than in *Sarcobatus* (Figure 1b and c; Table 1). Opposite to leaf N resorption, *Sarcobatus* was 2.0-fold more efficient at resorbing P than *Chrysothamnus* (Fig-ure 1d; Table 1). *Sarcobatus* also was extremely proficient at resorbing P, with senesced leaf P concentrations 8.0 and 10.8-fold less based on leaf area or mass, respectively, than in *Chrysothamnus* (Figure 1e and f; Table 1).

Nutrient pools

Aboveground N and P pools, based on biomass allocation and nutrient concentration patterns, were assessed to estimate the relative contribution leaf nutrient resorption could make to plant nutrient status (Figure 2a–j). In June, at the height of the growing season, leaf N and P pools ac-counted for 43–53% of aboveground N and P in both species. In June, *Chrysothamnus* N and P pools were greater in young stems (42% N pool, 37% P pool) than old stems (15% N pool, 13% P pool), whereas *Sarcobatus* N and P pools were
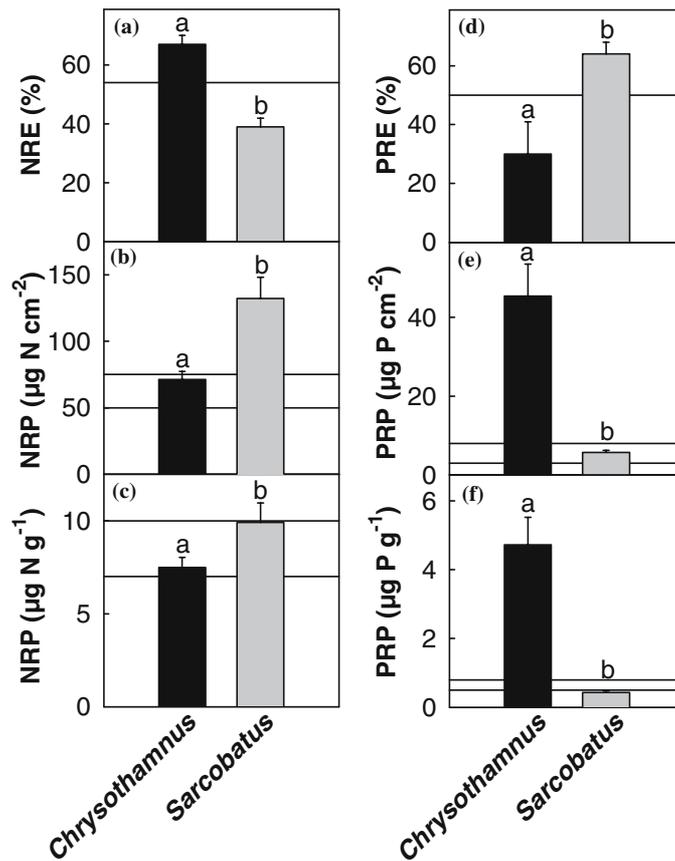
Figure 1. (a–f) N and P resorption efficiency (NRE and PRE, respectively) and N and P resorption proficiency (NRP and PRP, respectively) for *Chrysothamnus* and *Sarcobatus* (2001 growing season). Proficiency values are expressed both on an area basis (b, e) and mass basis (c, f). Data are means $\pm$ SE ($n = 8$). Letters indicate significant differences between species means following post-hoc Tukey's tests ($\alpha = 0.05$). In a and d, the reference line indicates the average resorption efficiency value for deciduous shrubs and trees (Aerts 1996). In b, c, e, and f, the area above the upper reference line is the incomplete resorption range, below the lower reference line is the complete resorption srange, and between the upper and lower reference lines is the intermediate resorption range (*sensu* Killingbeck 1996).

greater in old stems (36% N pool, 32% P pool) than young stems (11% N pool, 17% P pool) (Figure 2e, f, i and j). These differences in pool sizes between young stems and old stems were strongly influenced by biomass allocation between these components (Figure 2a and b).

Allocation of N and P shifted following leaf senescence in October. The percentage of the aboveground N pool lost to leaf litter was higher in *Sarcobatus* (37%) than in *Chrysothamnus* (19%), where the total October aboveground pool is the sum of young stem N, old stem N, and senesced leaf N (Figure 2e, f). In contrast, the opposite trends were observed for P pools, with larger P pools tied up in *Chrysothamnus* leaf litter than in

Sarcobatus leaf litter (53% vs. 33% of October aboveground P pools, respectively) (Figure 2i, j). Overall, aboveground N and P pools declined between June and October.

Ecological comparisons between age classes

Leaf nutrient concentrations in seedlings and adults were compared to determine whether differences in N and P resorption were consistent with patterns of nutrient concentration over a shrub's lifespan (Table 2). Consistent with expectations, leaf N was over 1.5-fold higher in *Chrysothamnus* adults than in seedlings, whereas there was no significant

Table 1. ANOVA of nutrient resorption efficiency (the proportion of nutrients withdrawn before leaf senescence) and nutrient resorption proficiency (the nutrient concentration in senesced leaf tissue). Degrees of freedom for numerator (dfn) and denominator (dfd) were (1,7) where species was the source and (7,7) where block was the source. *F* and *p* values are shown (significant values in bold).

Variable	Source	*F*	*p*
N resorption efficiency	Species	**46.41**	**0.0003**
	Block	0.86	0.58
N resorption proficiency (area basis)	Species	**12.43**	**0.01**
	Block	1.00	0.50
N resorption proficiency (mass basis)	Species	**8.37**	**0.02**
	Block	3.00	0.09
P resorption efficiency	Species	**13.97**	**0.007**
	Block	1.16	0.43
P resorption proficiency (area basis)	Species	**24.54**	**0.002**
	Block	1.06	0.47
P resorption proficiency (mass basis)	Species	**31.13**	**0.0008**
	Block	1.13	0.44

difference in leaf P between *Chrysothamnus* seedlings and adults (Tables 2 and 3). Although leaf N was significantly higher in *Sarcobatus* adults than in seedlings, there was only a 1.17-fold increase in leaf N concentration between the two age classes (Tables 2 and 3). Leaf P was significantly higher in *Sarcobatus* adults than in seedlings, translating into a 1.85-fold increase in leaf P between age classes (Tables 2 and 3).

Discussion

Most research suggests more efficient leaf nutrient resorption leads to increased nutrient use efficiency in deciduous plants from infertile environments (van Breemen 1995; Aerts 1996, 1997; Aerts and Chapin 2000). Consistent with our hypothesis that low resorption might contribute to nutrient limitation, both *Chrysothamnus* and *Sarcobatus* were less efficient and less proficient in resorbing the nutrient most limiting their growth than their non-limiting nutrient. Although *Chrysothamnus* is P-limited, it resorbed P poorly compared to *Sarcobatus* and other perennial species (i.e., it had incomplete P resorption proficiency vs. *Sarcobatus* having intermediate to complete P resorption proficiency, *sensu* Killingbeck 1996; Figure 1e and f). Although average P resorption efficiency in *Chrysothamnus* was lower than the average value
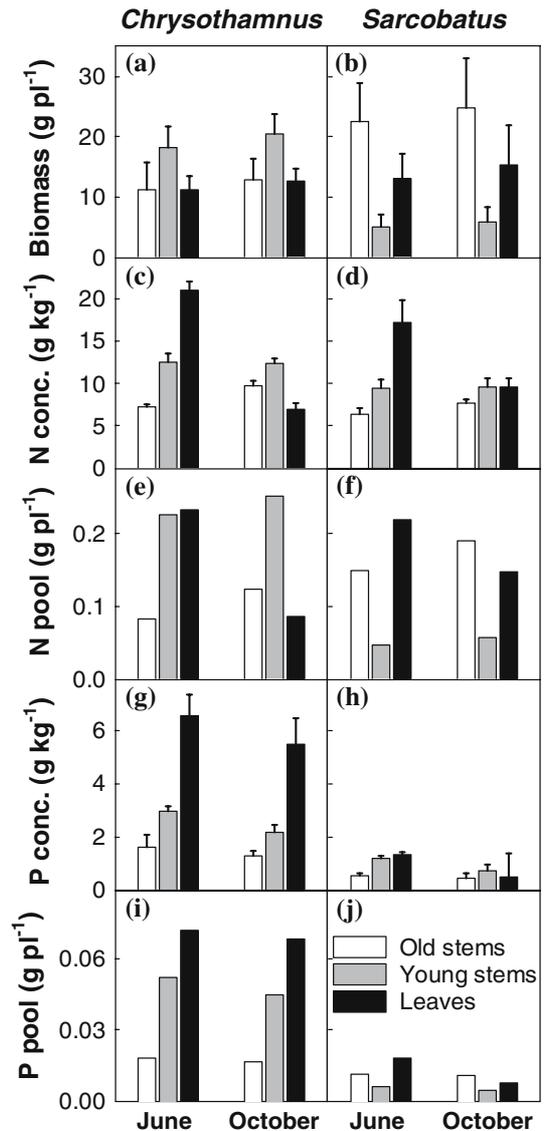

Figure 2. (a–j) Biomass, N and P concentrations, and N and P pool sizes of leaves, young stems (< 1 year old), and old stems (> 1 year old) of *Chrysothamnus* and *Sarcobatus* shrubs (June and October 2001). Leaf values in October are for senesced leaves. Data are means of five replicate shrubs. Total aboveground *Chrysothamnus* biomass was scaled to the same total aboveground biomass as *Sarcobatus* (see Methods for further text regarding estimation of shoot biomass and pool sizes). Data are means ± SE in Figure 2a–d, g and h ($n = 4$–5).

for deciduous shrubs and trees, this difference was not significant (Figure 1d, Table 3). In contrast, *Sarcobatus*, although N-limited, resorbed N poorly compared to *Chrysothamnus* and other perennial species (i.e., it had intermediate to

Table 2. *Chrysothamnus* and *Sarcobatus* leaf N and P concentrations from shrubs of different age classes growing in the Mono Basin, CA, USA. The sites included are non-saline to moderately saline, and the soil is very low in both total N and bicarbonate-extractable P (Donovan and Richards 2000; Drenovsky and Richards 2004).

Species	Age class	Leaf N (g kg^{-1})	Leaf P (g kg^{-1})
Chrysothamnus	Seedling ($n = 24$)	14.0 ± 0.05	4.1 ± 0.46
	Adult ($n = 6$)	21.2 ± 1.3	4.4 ± 0.6
Sarcobatus	Seedling ($n = 19$ for leaf N, $n = 11$ for leaf P)	11.8 ± 0.7	0.7 ± 0.1
	Adult ($n = 8$)	13.8 ± 0.3	1.4 ± 0.1

incomplete N resorption proficiency vs. *Chrysothamnus* having intermediate N resorption proficiency; Figure 1b and c). Additionally, compared to average N resorption efficiency for deciduous shrubs and trees, *Sarcobatus* resorbed significantly less N, while *Chrysothamnus* resorbed significantly more (Figure 1a, Table 3). In addition, June leaf N and P pools were approximately 50% of both species' aboveground nutrient pools, suggesting leaves can contribute significantly to N and P retention in these species. Together, these data support our hypothesis that *Chrysothamnus* and *Sarcobatus* differentially resorb N and P and that this low resorption is substantial enough to contribute to their respective nutrient limitations.

Low N resorption efficiency has been correlated with greater whole plant nutrient loss (Eckstein et al. 1999). Therefore, low leaf N resorption in *Sarcobatus* may contribute to its N-limitation at this site, due to cumulative N loss in litterfall and poor mineralization capacity in these dry soils.

Although high N litter increases site fertility in temperate ecosystems (van Breemen 1995; Aerts 1996, 1997), in deserts N mineralization is tightly linked to precipitation events, which are both infrequent and low (Noy-Meir 1973; Schimel and Parton 1986; Fisher et al. 1987). Therefore, the N in abscised leaves is lost to the slowly cycling organic matter pool and, as a result, only leads to higher microsite fertility after many decades or centuries (Schaber 1994).

Given these low N conditions, a strong selective pressure for more efficient and proficient N resorption in *Sarcobatus* should be expected. However, several physiological constraints may prevent more complete N resorption in *Sarcobatus* and thus contribute to its N limitation. First, during leaf senescence, N is required for enzymes and transporters necessary to metabolize leaf components and translocate them through the phloem. This sets a minimum pool of N that cannot be resorbed from leaves. In the desert shrub *Larrea tridentata*, resorption efficiency decreased concurrently with nutrient availability, suggesting the small pool of potentially remobilized nutrients impeded more efficient resorption (Lajtha 1987). Second, the halophytic and drought tolerant nature of *Sarcobatus* may prevent effective N retranslocation because of the need for N-containing compatible solutes. As soil water potential decreases through the season (Donovan et al. 1996), *Sarcobatus* accumulates Na in leaf cell vacuoles (Donovan et al. 1997), reducing plant water potential below soil water potential. To prevent osmotic imbalance, *Sarcobatus* concurrently accumulates the N-containing compound glycine-betaine in cytoplasm (T. W-M. Fan and J.H. Richards, unpublished data).

Table 3. Statistical comparisons of seedling and adult leaf nutrient concentrations in *Chrysothamnus* and *Sarcobatus* and N resorption efficiency (NRE) and P resorption efficiency (PRE) values with average values reported in the literature. Significant values, based on one-tailed *t*-tests, are in bold.

Null hypothesis	*Chrysothamnus*		*Sarcobatus*	
	t	*p*	*t*	*p*
Seedlings vs. adults				
No difference between seedling and adult leaf N concentrations	**−7.4**	**< 0.0001**	**−2.57**	**0.008**
No difference between seedling and adult leaf P concentrations	−0.59	0.28	**−5.43**	**< 0.0001**
Study species vs. average for deciduous species				
No difference between study species and average deciduous species leaf NRE	**4.89**	**0.0009**	**−5.10**	**0.0007**
No difference between study species and average deciduous species leaf PRE	−1.76	0.06	**3.60**	**0.004**

Without this cytoplasmically compatible solute accumulation, cellular and whole plant water relations would not be maintained, impeding metabolic activity necessary to sustain phloem export of catabolized substrates. In support, data from a separate experiment in a different year show that *Sarcobatus* leaf ash content was negatively correlated with N resorption efficiency and positively correlated with N resorption proficiency ($r^2 = 0.81$ and 0.67, respectively) (ash content reported in Donovan et al. 1997, resorption efficiency and proficiency calculated from seasonal data also included in that paper). As leaf ash content (including accumulated leaf Na) increased, *Sarcobatus* resorbed a smaller proportion of leaf N (lower resorption efficiency), and end-of-season leaf N concentrations were higher (poorer resorption proficiency). Further work investigating possible links between high leaf Na and low leaf N resorption in halophytic species is currently underway in our laboratory.

In contrast to *Sarcobatus*, *Chrysothamnus* is a drought stress avoider, functioning only at higher water potentials (Donovan et al. 1996) and abscising some leaves earlier in the season than *Sarcobatus* (R.E. Drenovsky, personal observation). *Chrysothamnus* also has greater selectivity against Na uptake and low leaf Na concentrations even under moderately saline conditions (< 1.8 g kg^{-1}; Donovan et al. 1996; R.E. Drenovsky, unpublished data). Therefore, by avoiding drought stress and minimizing Na accumulation, compatible solute accumulation likely is lower in *Chrysothamnus* than in *Sarcobatus*. As a result, *Chrysothamnus* may have less N invested in substrates that must remain in solution to maintain osmotic potential of leaf cytoplasm. This would allow greater N resorption, as we documented.

Contrary to N resorption, *Sarcobatus* was both highly efficient and proficient at resorbing P (Figure 1d–f). The low and ineffective mycorrhizal infection of *Sarcobatus*, compounded by the low soil P conditions at the site, create an expected selective pressure for low P concentrations in senesced leaf tissue (i.e., high P resorption proficiency). Therefore, it appears that internal P recycling may be critical to the success of *Sarcobatus*. Similarly, in the desert shrub *Larrea tridentata* it was hypothesized that tight internal recycling of leaf P may account for much of that shrub's P needs (Lajtha 1987).

Parallel to *Sarcobatus*, a selective pressure for more efficient and proficient P resorption in *Chrysothamnus* should be expected. However, we observed poor P resorption in *Chrysothamnus*, which we hypothesize contributes to its P limitation. There is not a clear mechanistic explanation for a physiological constraint preventing more complete P resorption in *Chrysothamnus*, nor is it clear why *Chrysothamnus* has such a high P requirement. In previous work at our site, mycorrhizal infection was extensive in juvenile *Chrysothamnus* shrubs (L.A. Donovan and J.H. Richards, unpublished data). However, even with high leaf P (> 5 g kg^{-1}), P and water co-limited *Chrysothamnus* shoot growth (Drenovsky and Richards 2004). Although not detected in their study, Chapin and Kedrowski (1983) suggested that differential nutrient resorption could lead to distinct nutrient requirements between species. As differential resource limitations may provide a mechanism for species coexistence (Tilman and Pacala 1993), it is possible that lower P resorption in *Chrysothamnus* than in *Sarcobatus* contributes to nutrient niche differentiation at our study site.

Nevertheless, both *Chrysothamnus* and *Sarcobatus* invest a significant proportion of their shoot N and P in leaves, suggesting incomplete N and/or P resorption may lead to significant nutrient losses through litterfall. Over the lifetime of these long-lived shrubs, P losses in *Chrysothamnus* and N losses in *Sarcobatus* may negatively affect their P and N status, respectively. Although a change in biomass allocation over time may contribute to these observed differences in leaf nutrient concentrations, allocation should affect N and P equally, whereas our data show that these nutrients are differentially affected over time. These observations are consistent with our resorption data suggesting that nutrient limitation is in part caused by the existence of physiological (or other) constraints that prevent more efficient and proficient resorption of nutrients. Together, it appears that low soil P availability and low P resorption may contribute to the P-limited status of *Chrysothamnus*. In contrast, low soil N availability and low leaf N resorption may contribute to the N-limited status of *Sarcobatus*. Further study of other species is needed to determine if this relationship is more widespread.

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