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Short Communication

Variation in nutrient resorption by desert shrubs

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A B S T R A C T

Plant nutrient resorption prior to leaf senescence is an important nutrient conservation mechanism for aridland plant species. However, little is known regarding the phylogenetic and environmental factors influencing this trait. Our objective was to compare nitrogen (N) and phosphorous (P) resorption in a suite of species in the Asteraceae and Chenopodiaceae and assess the impact of soil salinity on nitrogen resorption. Although asters and chenopods did not differ in N resorption proficiency, chenopods were more proficient than asters at resorbing P. Plant responses to salinity gradients were species-specific and likely related to different salt-tolerances of the species. During the three year study, precipitation varied 6.4- and 9.9-fold from the long term averages at our two desert sites; despite these differences, annual variation in nutrient resorption was not linked to annual precipitation. More detailed studies are required to understand the influence of salinity and precipitation on resorption. Understanding controls on this trait may give insight into how species will respond to anthropogenic soil salinization and desertification.

Keywords:

Drought
Phylogenetic comparison
Resorption proficiency
Senesced leaf nitrogen
Senesced leaf phosphorus
Salinity

In arid, nitrogen and phosphorus-limited systems, plant performance depends on nutrient conservation. During leaf senescence, plants break down biomolecules and translocate nutrients to storage tissues. This process (resorption) is considered one of the most important plant nutrient conservation mechanisms (Eckstein et al., 1998; Killingbeck, 1996; van Heerwaarden et al., 2003). In aridlands, resorption may be particularly important to whole-plant nutrient budgets due to slow decomposition rates and variable soil nutrient supply (Noy-Meir, 1973). Comparing data from seven desert shrubs to average values for non-desert shrubs, resorption was higher in desert species, suggesting tight internal nutrient recycling is key in arid habitats (Killingbeck, 1993). Despite its significance, there is little information examining phylogenetic and environmental controls influencing resorption in aridland species. Such understanding is fundamental for predicting plant community responses to anthropogenic disturbance as well as understanding selection pressures leading to variation in this trait.

Resorption potential is not a simple function of habitat nutrient availability. Instead, resorption may be influenced by phylogeny and/or environmental factors, including both drought and salinity stress (Killingbeck, 1996). Some research suggests resorption may be more similar among closely related than distantly related

species (Killingbeck, 1996; Wright and Westoby, 2003); however, resorption varied greatly in some congeners, suggesting evolutionary history is not the only factor driving resorption (Killingbeck, 1996). Despite the predicted importance of resorption in arid systems, little research has focused on this trait in arid environments. Both drought (Bertiller et al., 2005; Wright and Westoby, 2003) and soil salinity (Drenovsky and Richards, 2006) may decrease resorption, due to rapid leaf senescence and the need for N-rich compatible solute accumulation in leaves (e.g., glycinebetaine). Desert systems thus provide a unique test of environmental constraints on resorption, as they are water-limited and often saline.

Our objective was to compare nitrogen (N) and phosphorus (P) resorption in widely distributed desert shrubs from two families (Asteraceae and Chenopodiaceae) and to determine the effects of soil salinity on resorption. Previous data suggested that the aster, *Chrysothamnus nauseosus* ssp. *consimilis*, was more proficient at N, but not P, resorption, compared to the chenopod, *Sarcobatus vermiculatus* (Drenovsky and Richards, 2006). These differences were attributed to their relative requirement for N-containing compatible solutes for drought and salinity tolerance (*C. nauseosus* ssp. *consimilis* is less drought and salinity tolerant than *S. vermiculatus*) and their mycorrhizal status (*C. nauseosus* ssp. *consimilis* is mycorrhizal, *S. vermiculatus* is not) (Drenovsky and Richards, 2004). Based on these two model species, we hypothesized that asters would resorb more N but less P than chenopods. To examine the influence

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of soil salinity on resorption, we sampled a subset of species growing along natural salinity gradients. We hypothesized that N concentration in senesced leaf tissue would increase as soil salinity increased due to compatible solute accumulation but that these responses would depend, in part, on the salt tolerance of the species.

Our study was conducted at the Mono Basin Ecosystem Research Site (MBERS), near Mono Lake, and around the Owens Lake playa, California, USA during Fall 2005, 2006, and 2007. MBERS is located on the western edge of the Great Basin Desert, USA, and the Owens playa is on the northern edge of the Mojave Desert, USA. Vegetation at both sites is dominated by shrubs in the Asteraceae and Chenopodiaceae. Annual precipitation at MBERS averages 160 mm (Snyder et al., 2004). During our study, precipitation varied 6.4-fold (2005: 289 mm; 2006: 416 mm; 2007: 65 mm); precipitation was determined from records at Cain Ranch (24 km from the study area). Average annual rainfall around the Owens playa is 149 mm (Snyder et al., 2004); during our study, precipitation varied 9.9-fold (2005: 200.0 mm; 2006: 75.6 mm; 2007: 20.3 mm). Precipitation was determined from the average of two Owens Lake CIMIS weather stations (<http://www.cimis.water.ca.gov/cimis/welcome.jsp>).

Both systems are closed hydrologic basins that have experienced natural and anthropogenic lake level change. MBERS is composed of a series of dunes representing previous shorelines. Old Growth Dunes and Diverse Dunes represent shorelines exposed due to natural climatic changes. These sites have lower soil pH, lower soil salinity, and higher plant diversity than Sand Shadow Dunes, which are closer to Mono Lake and represent a shoreline exposed due to water diversion for urban use (Aanderud et al., 2008; Donovan et al., 1997; Toft and Elliott-Fisk, 2002). The Owens playa also represents both ancient and recent shorelines, as well as exposed lakebed; Owens Lake has been dried completely since 1926 due to re-routing of tributary waters to urban areas (Saint-Amand et al., 1986). Similar to MBERS, upland sites are lower in soil pH and salinity and higher in plant diversity than playa sites (Dahlgren et al., 1997). Both sites are periodically grazed by cattle, and most asters are grazed by herbivorous mammals, predominantly jackrabbits. At MBERS and the Owens playa, we sampled a total of seven aster species (MBERS: *Artemisia tridentata*, *Chrysothamnus nauseosus* ssp. *albicaulis*, *C. nauseosus* ssp. *consimilis*, *Chrysothamnus viscidiflorus*, *Tetradymia glabrata*, *Tetradymia tetrameres*; Owens playa: *Artemisia spinescens*, *A. tridentata*) and six chenopods (MBERS: *Atriplex canescens*, *Atriplex confertifolia*, *S. vermiculatus*; Owens playa: *A. canescens*, *A. confertifolia*, *Atriplex hymenelytra*, *Atriplex parryi*, *Sarcobatus baileyi*, *S. vermiculatus*) in low salinity, high diversity areas and select asters and chenopods that could be found at multiple locations along salinity gradients (*C. nauseosus* ssp. *consimilis*, *C. viscidiflorus*, *A. parryi*, and *S. vermiculatus*). Nomenclature follows that of the Jepson Manual (Hickman, 1993). Adult shrubs of similar size were randomly selected. Due to strong winds, no senesced leaves were available from *A. parryi* during 2007 at the high salinity site. All sampled genera include species varying in salinity tolerance based upon their relative dominance along salinity gradients and previous experimental work (Donovan and Richards, 2000; Richards, 1994).

Senescent leaves were collected by gently shaking branches. Each year, 3–7 shrubs per species were sampled. Different shrubs were sampled each year. Prior to analysis, leaves were dried at 60 °C, triple-rinsed in deionized water to remove surface salts and dust, dried again at 60 °C, and finely ground. Leaf N was analyzed on a CN analyzer. Leaf P was measured by ICP-AES on dry-ashed samples suspended in 1 N HCl. We used N and P resorption proficiency, the N or P concentration in senesced leaf tissue, as our measure of resorption (N_{PROF} and P_{PROF} , respectively; Drenovsky and

Richards, 2006; Killingbeck, 1996). Lower values represent less nutrient loss from the plant and thus, high proficiency.

During November 2007, three soil subsamples (0–30 cm depth to represent the main rooting zone) were collected below the canopy dripline of each shrub ($n = 3\text{--}4$ shrubs per species per sampling site). Subsamples were composited, air-dried, and sieved (2 mm). Total N was measured on a CN analyzer, and Olsen's extractable P was measured by flow injection analysis. Soil pH and electrical conductivity (E.C.) was measured on 1:5 soil-water extracts.

To address hypothesis one, we compiled data from seven asters and six chenopods from high diversity, low salinity sites. We used a randomized block design in which we pooled annual data from individual shrubs of each species. Sampling year was the block factor, and the main effect was family (Asteraceae or Chenopodiaceae). To address hypothesis two, we analyzed N_{PROF} data from two asters (*C. nauseosus* ssp. *consimilis* and *C. viscidiflorus*) and two chenopods (*A. parryi* and *S. vermiculatus*) that grow along salinity gradients. In this analysis, the main effects were site and block; sampling year was the block factor. Data were analyzed with SAS (SAS, 2002).

Total soil N did not differ between aster and chenopod soil microsites ($P = 0.44$; Table 1), but extractable soil P was higher in aster compared to chenopod soil microsites ($P = 0.04$; Table 1). Soil pH and E.C. were lower in aster compared to chenopod microsites ($P = 0.0003$ and $P = 0.0015$, respectively; Table 1). At MBERS, total soil N increased over 3.3-fold with substrate age ($P = 0.0015$; Table 1). Around the Owens playa, soil N was 5.2-fold higher at the Upland site compared to the Playa site ($P = 0.005$; Table 1). Extractable soil P increased 3.4-fold with substrate age at MBERS ($P = 0.03$; Table 1), but it did not differ among soils from around the Owens playa ($P = 0.39$; Table 1). Soil pH and E.C. decreased with substrate age at both MBERS ($P = 0.0002$ and $P < 0.0001$, respectively; Table 1) and around the Owens playa ($P = 0.01$ and $P = 0.03$, respectively; Table 1).

N_{PROF} did not differ between asters and chenopods ($P = 0.27$; Fig. 1A). In contrast, P_{PROF} was 4.3-fold higher in asters than chenopods ($P = 0.015$; Fig. 1B). N_{PROF} varied 1.5-fold among sampling years ($P = 0.0012$; Fig. 1A) but was similar among years for P_{PROF} ($P > 0.05$).

N_{PROF} did not differ between sites varying in salinity for either *C. viscidiflorus* ($P = 0.79$; Fig. 2A) or *C. nauseosus* ssp. *consimilis* ($P = 0.53$; Fig. 2B). Year was not a significant factor for *C. viscidiflorus* ($P = 0.26$; Fig. 2A) but was for *C. nauseosus* ssp. *consimilis* ($P = 0.0007$; Fig. 2B). N_{PROF} significantly differed between sites for both chenopods, but species responses were in opposite directions. Across all years, N_{PROF} was 1.4-fold higher for *S. vermiculatus* at Sand Shadow Dunes (higher salinity site) than at Old Growth Dunes (lower salinity site) ($P = 0.0017$; Fig. 2C). For *A. parryi*, N_{PROF} was 1.9-

Table 1

Soil chemistry (0–30 cm) associated with different shrub microsites (aster and chenopod microsites, as well as different sampling locations along the salinity gradient at MBERS and around the Owens playa). Data are means \pm SE ($n = 6\text{--}7$ for family microsites; $n = 3\text{--}15$ for MBERS and Owens Valley microsites).

Shrub microsite	N (g kg ⁻¹)	P (mg kg ⁻¹)	pH	E.C. (dS m ⁻¹)
Family				
Asteraceae	0.49 \pm 0.09	25.4 \pm 7.5	8.4 \pm 0.3	0.23 \pm 0.06
Chenopodiaceae	0.39 \pm 0.07	6.5 \pm 1.8	9.9 \pm 0.1	0.59 \pm 0.06
MBERS				
Old Growth Dunes	0.67 \pm 0.07	33.2 \pm 5.8	8.5 \pm 0.2	0.44 \pm 0.10
Diverse Dunes	0.40 \pm 0.03	17.2 \pm 3.2	9.4 \pm 0.1	0.43 \pm 0.08
Sand Shadow Dunes	0.20 \pm 0.0	9.6 \pm 2.0	10.4 \pm 0.1	4.72 \pm 1.49
Owens Valley				
Upland	0.52 \pm 0.08	4.9 \pm 2.7	9.8 \pm 0.1	0.63 \pm 0.04
Playa	0.1 \pm 0.0	7.9 \pm 1.7	10.0 \pm 0.0	2.18 \pm 0.99

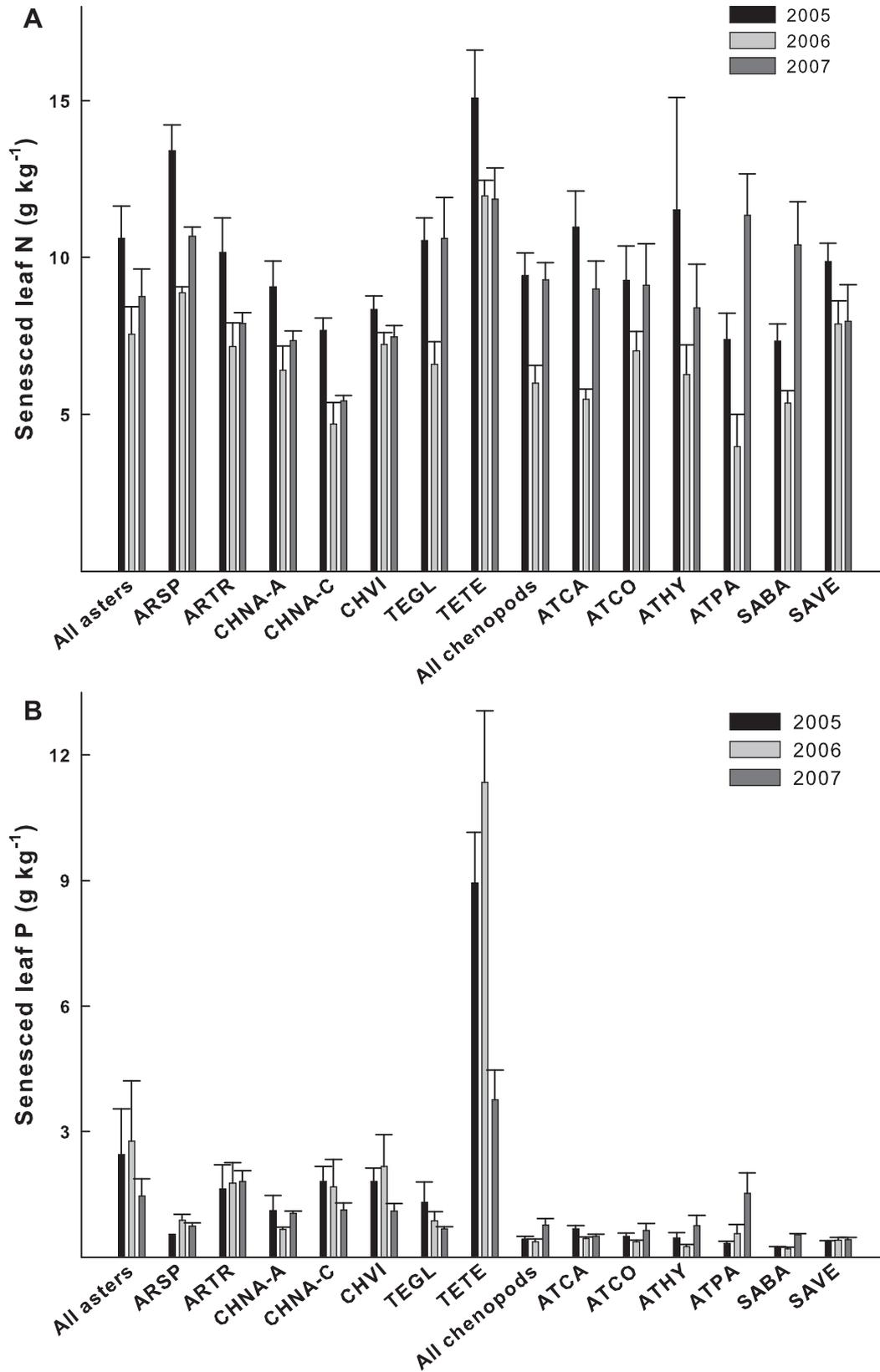


Fig. 1. Senesced leaf N (N_{PROF}) (A) and senesced leaf P (P_{PROF}) (B) of asters and chenopods from the 2005, 2006, and 2007 growing seasons. Data are means + SE ($n = 6-7$ for composited family data as described in methods; $n = 1-13$ for species data, leaf tissue for the 2005 *A. spinescens* leaf P data was composited from multiple shrubs limiting the replication to one for that sampling year). Abbreviations are as follows: ARSP, *Artemisia spinescens*; ARTR, *A. tridentata*; CHNA-A, *Chrysothamnus nauseosus* ssp. *albicaulis*; CHNA-C, *C. nauseosus* ssp. *consimilis*; CHVI, *C. viscidiflorus*; TEGL, *Tetradymia glabrata*; TETE, *T. tetrameris*; ATCA, *Atriplex canescens*; ATCO, *A. confertifolia*; ATHY, *A. hymenelytra*; ATPA, *A. parryi*; SABA, *Sarcobatus baileyi*; SAVE, *S. vermiculatus*).

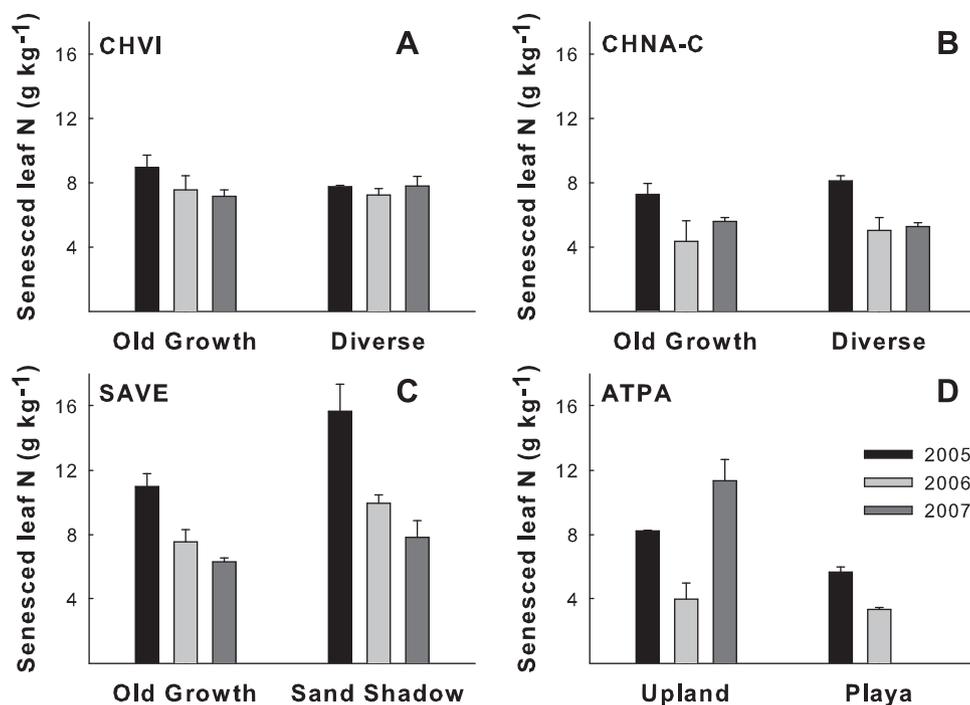


Fig. 2. Senesced leaf N (N_{PROF}) of *Chrysothamnus nauseosus* ssp. *consimilis* (CHNA-C, A), *C. viscidiflorus* (CHVI, B), *Sarcobatus vermiculatus* (SAVE, C), and *Atriplex parryi* (ATPA, D) growing along natural salinity gradients. Data are means \pm SE ($n = 3-6$). In all panels, data from the lower salinity site are presented to the left. *C. nauseosus* ssp. *consimilis* and *C. viscidiflorus* were sampled at Old Growth Dunes (lower salinity site) and Diverse Dunes (higher salinity site), *S. vermiculatus* was sampled at Old Growth Dunes (lower salinity site) and Sand Shadow Dunes (higher salinity site), and *A. parryi* was sampled at Upland (lower salinity) and Playa (higher salinity) locations. No data were available for *A. parryi* at the high salinity site in 2007.

fold higher at the Upland site (lower salinity site) than at the Playa site (higher salinity site) ($P = 0.0002$; Fig. 2D). Year was significant for *S. vermiculatus* ($P < 0.0001$; Fig. 2C) and *A. parryi* ($P = 0.0002$; Fig. 2D).

In support of our first hypothesis, P_{PROF} varied significantly between asters and chenopods. These results extend previous observations of *C. nauseosus* ssp. *consimilis* and *S. vermiculatus*, in which the aster was less proficient at resorbing P than the chenopod. Unlike asters, chenopods either do not form functional mycorrhizal relationships or are only weakly mycorrhizal (Allen and Allen, 1990). Combined with very low soil P at these sites, there is a strong selection pressure for highly proficient P resorption in chenopods. Comparing chenopod P_{PROF} from this study to published literature results, in 2005 and 2006, the chenopods completely resorbed P (*sensu* Killingbeck, 1996), and in 2007, P_{PROF} was just above the complete resorption range. Although P_{PROF} was highly variable among asters, it was well above the incomplete range ($>0.8 \text{ g kg}^{-1}$; *sensu* Killingbeck, 1996) in all years sampled. In Andean-Patagonian trees there was a correlation between mycorrhizal colonization (and thus adequate P supply) and poor P_{PROF} (Diehl et al., 2008). In contrast to their work, despite its mycorrhizal status, at least one of the asters included in this study is co-limited by P and water (Drenovsky and Richards, 2004). Given the importance of resorption in nutrient conservation, our data suggest other factors may limit P resorption in these desert asters. *Artemisia*, *Chrysothamnus*, and *Tetradymia* species produce a variety of secondary compounds, including terpenes (Hegazy et al., 2007; Jennings et al., 1974; Kelsey et al., 1982; Personius et al., 1987), the intermediates of which require phosphate (Croteau et al., 2000). It is possible that these compounds preclude more proficient P resorption.

In contrast with P_{PROF} , N_{PROF} did not vary between families. Previous research comparing resorption in *C. nauseosus* ssp. *consimilis* and *S. vermiculatus* indicated the aster, *C. nauseosus* ssp.

consimilis, was more proficient at resorbing N than the salt-accumulating chenopod, *S. vermiculatus* (Drenovsky and Richards, 2006). As salts accumulate in leaf vacuoles, compatible solutes are synthesized in the cytoplasm, in part, to maintain cellular water relations (Bartels and Sunkar, 2005). Since functional cells are necessary for nutrient export, we hypothesized that the salt-tolerant chenopods, due to compatible solute accumulation, would have a smaller potential pool of resorbable N than the relatively more salt sensitive asters. However, even within the chenopods, there is a range of salt tolerance (Reimann and Breckle, 1993). These differences may influence the size of the compatible solute pool and thus the amount of potentially resorbable N, masking any trend between N_{PROF} and salt tolerance.

N_{PROF} responses of *A. parryi* and *S. vermiculatus* along salinity gradients were in opposite directions. *A. parryi* had lower, and *S. vermiculatus* had higher, senesced leaf N at their respective high salinity sites. As a C_4 species, *A. parryi* has lower N requirements than *S. vermiculatus*, a C_3 species; thus, green leaf N concentrations, and subsequently senescent leaf N concentrations should be lower in *A. parryi* (Lambers et al., 2008). Additionally, *A. parryi* grows on extremely N poor soils at the high salinity site; previously measured green leaf concentrations were similar to the senescent leaf concentrations observed in this study (James et al., 2005). Therefore, there may be little non-structural N that can be resorbed in this species at this site. In contrast, high leaf N has been measured in *Sarcobatus* at more saline sites (Drenovsky and Richards, 2005), providing a larger pool of potentially resorbable N.

N_{PROF} was similar at the lower and higher salinity sites for both asters (*C. nauseosus* ssp. *consimilis* and *C. viscidiflorus*). Although *C. nauseosus* ssp. *consimilis* is moderately salt-tolerant, neither species likely accumulated sufficient leaf salt to necessitate extensive compatible solute accumulation. Additionally, the difference in salinity between sites may have been insufficient to observe any

significant effect on resorption. Little difference in soil E.C. was observed in this study between Diverse and Old Growth Dunes, although differences between these sites have been detected in previous work (Aanderud et al., 2008). More detailed studies under controlled conditions are necessary to parse out effects of salinity, salt tolerance, and resorption.

Although our study was not designed to address the effect of water availability on resorption, it encompassed both above and below average rainfall years. Despite this variation, we did not observe any correlation between precipitation and resorption. Some researchers have noted poorer resorption at drier sites or under water-stressed conditions (Bertiller et al., 2005; Wright and Westoby, 2003), while other authors have observed no relationship (Diehl et al., 2008) or a negative relationship (Lajtha, 1987) between these variables. These discrepancies may be related to differences in soil texture, which influence infiltration rates and water holding capacity. Additionally, if plants can root to groundwater, resorption processes may continue unaffected, even while surface soils dry. More detailed studies are necessary to understand relationships between soil water availability, plant morphology, and resorption processes.

Our research suggests both phylogeny and salinity influence nutrient resorption in aridland asters and chenopods. These data suggest it may be difficult to predict, at the family-level, species responses to environmental perturbations and stressors. However, some inferences may be made based on specific physiological traits (e.g., level of salinity tolerance). Additionally, low-nutrient adapted species may be limited by the amount of non-structural N that can be recycled. Future work should focus on the role of nutrient resorption in whole-plant nutrient budgets, as well as controlled greenhouse studies, in which soil nutrients are not limiting but soil salinity or moisture varies. Understanding links between plant nutrient budgets, soil salinity, drought, and resorption may help us better predict species responses to anthropogenic soil salinization and desertification.

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