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Potential and realized nutrient resorption in serpentine and non-serpentine chaparral shrubs and trees

Rebecca E. Drenovsky · Catherine E. Koehler ·
Kathryn Skelly · James H. Richards

Abstract Low-nutrient adapted species have numerous mechanisms that aid in nutrient conservation. Hypothetically, species adapted to nutrient-poor soils should have tighter internal nutrient recycling, as evidenced by greater resorption. However, literature results are mixed. We suggest methodological factors may limit our understanding of this process. We hypothesized that plants adapted to serpentine soils would be more proficient in resorbing N and P than plants adapted to non-serpentine soils, although there would be differences among functional groups within each soil type. For six growing seasons, we sampled senescent leaf tissue from the dominant and co-dominant shrubs and trees found in serpentine and non-serpentine chaparral communities in the California Coast Range. Our study also explicitly included congener pairs found on both soil types. Most species were highly N proficient, but species adapted to serpentine soils were more P proficient.

Surprisingly, two of the three potential N-fixing species were also highly N proficient. Evergreen *Quercus* congeners were more N proficient than their deciduous congener pairs, although there was no difference in P resorption proficiency. Overall, large inter-annual variation was observed among most species sampled, but at least in some years, maximum potential resorption likely was reached. However, climate (temperature and precipitation) was not strongly correlated with either N or P resorption proficiency. Our data suggest that controlling for phylogeny can aid in interpretation of resorption patterns. More importantly, our study clearly shows that resorption patterns can only be discerned through long-term datasets, of which few exist in the literature.

Keywords Resorption proficiency · Senesced leaf nitrogen · Senesced leaf phosphorus · Phylogenetic comparison · Plasticity

Introduction

Low soil nutrient availability, particularly N and P, limits plant growth and reproduction worldwide (Lambers et al. 2008). However, low-nutrient adapted plant species (LNAPs) express a suite of traits that promote their continued success on impoverished soils, including slow growth rates, extensive root allocation, and efficient nutrient conservation (Aerts and Chapin 2000). Multiple leaf-level traits are thought to promote nutrient conservation, including long leaf lifetimes, long nutrient residence times, large nutrient storage pools, and tight internal nutrient recycling (i.e., leaf nutrient resorption during leaf senescence). By internally recycling nutrients, plants can “uncouple” themselves from inter-annual variability in soil nutrient supply and circumvent delays in nutrient

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availability related to decomposition and mineralization of litter. However, despite the inherent logic and appeal of the importance of leaf nutrient resorption for LNAPs, there are mixed results for this hypothesis, with research suggesting increased, decreased, or unaffected resorption with decreasing nutrient availability (Aerts 1996; Aerts and Chapin 2000).

Why has it been so difficult to document trends between soil and/or plant nutrient status and resorption? In part, it may be the metric used to describe resorption patterns. In his classic review on resorption, Aerts (1996) observed no discernible pattern in resorption efficiency (the proportion of nutrients resorbed prior to leaf senescence) between plants found on nutrient-rich and nutrient-poor soils. However, interpreting efficiency data can be problematic, particularly when probing evolutionary questions, as resorption efficiency is a proportion based on two measured values: green and senesced leaf nutrient concentrations (Aerts 1996). Since selection acts upon traits, not proportions, resorption proficiency (the nutrient concentration in senesced leaf tissues) may be a better metric for testing hypotheses regarding the evolutionary significance of resorption (Killingbeck 1996; Eckstein et al. 1999). In multiple studies, resorption proficiency has been more sensitive to short-term and long-term changes in nutrient availability than resorption efficiency (Feller et al. 2002; van Heerwaarden et al. 2003; Rejmánková 2005). Second, the conclusion that resorption is not influenced by soil nutrient availability often has been based on results from short-term fertilization experiments (Aerts 1996; Aerts and Chapin 2000), which do not adequately represent long-term selective forces of low or high nutrient availability on plants, especially in long-lived species. Instead, short-term experiments may highlight lack of plasticity in slow-growing LNAPs rather than reflecting a true effect on resorption processes. Studies focusing on species responses to long-term differences in nutrient availability along successional or latitudinal gradients suggest more proficient resorption in low-nutrient systems (e.g., Oleksyn et al. 2003; Wright and Westoby 2003; Rejmánková 2005; Denton et al. 2007; Norris and Reich 2009). Third, the effect of phylogeny often is not considered, potentially masking the adaptive significance of the trait. Typically, studies focus more on functional traits such as leaf habit (e.g., Grelet et al. 2001; Diehl et al. 2003) or functional groups (e.g., Carrera et al. 2003; Bertiller et al. 2005; Ratnam et al. 2008) than on potential phylogenetic effects. Those studies including phylogenetic effects often have been at broad taxonomic scales (i.e., angiosperms vs. gymnosperms; Yuan and Chen 2009) or were not concurrently addressing potential effects of both site fertility and phylogeny (Killingbeck 1996).

Overall, a number of patterns have emerged from resorption proficiency data. These observations point to

necessary methodological improvements to resorption studies, as well as the potential influence of long-term nutrient availability on this process. First, large year-to-year variability in resorption is observed within species and sites (Nordell and Karlsson 1995; Killingbeck 1996; Drenovsky et al. 2010), indicating a difference between potential resorption (the amount of physiologically resorbable nutrients) and realized resorption (the amount of nutrients resorbed in any given year) (Killingbeck 2004). This emphasizes the need for multiple years of data to recognize resorption patterns. Second, phylogeny does exert some influence over resorption proficiency, with more closely related taxa having more similar resorption patterns than more distantly related taxa (e.g., comparison of eight angiosperm or gymnosperm genera; Killingbeck 1996; and comparison of angiosperms and gymnosperms; Yuan and Chen 2009). Potential phylogenetic effects stress the importance of incorporating phylogeny into the design and analysis of resorption experiments. Without recognizing evolutionary history, it is not possible to determine the adaptive significance of this trait (Ackerly et al. 2000). Lastly, specific functional groups may differ in their N and/or P resorption proficiency, with important consequences for ecosystem nutrient recycling, as nutrient-rich litter generally decomposes more rapidly than nutrient-poor litter (Aerts 1996, 1997). Typically, evergreen species are more proficient at resorbing P than deciduous species (Killingbeck 1996; Yuan and Chen 2009). However, the results are mixed for N resorption. Some datasets indicate greater N proficiency in evergreen compared to deciduous species (Yuan and Chen 2009), whereas other datasets indicate no significant difference among these groups (Killingbeck 1996). Also, multiple studies have detected poorer N resorption proficiency (i.e., higher senesced leaf N concentration) in N-fixing plants than in plants unable to fix N (Killingbeck 1996; Yuan et al. 2005; Stewart et al. 2008), likely because N-fixers have little need for tight internal N recycling. Together, these differences among functional groups suggest plant and/or soil nutrient status exerts some control over proficiency, given the preponderance of evergreen species on nutrient-poor soils and the high leaf N concentrations of N-fixing species.

Given these observed trends between environmental and phylogenetic factors and resorption, we wanted to test how species growing in climatically similar, but edaphically dissimilar, sites differ in their N and P resorption patterns. For six growing seasons, we documented N and P resorption proficiency in long-lived, woody species growing on and off serpentine soils in the California Coast Range. To assess community-wide patterns in resorption proficiency, we assessed N and P resorption proficiency in 19 dominant and co-dominant woody species in these communities. Through this exercise, we documented intra- and inter-

species differences in resorption and compared them to published literature values (sensu Killingbeck 1996) to assess whether or not complete resorption had occurred. We then focused on four congener pairs of evergreen shrubs growing on and off serpentine soils to explicitly test for relative effects of phylogeny and environment on nutrient resorption. Within this focal group, we also assessed relationships between green leaf nutrient status and resorption, during the final year of the study. We compared resorption responses within a species, *Heteromeles arbutifolia*, which grows both on and off serpentine soils. Although such a study cannot test potential phenotypic plasticity, it can indicate the ecological breadth within a species. We then compared resorption responses among deciduous and evergreen congeners found off serpentine soils to explicitly test the relative influence of phylogeny and leaf habit. Lastly, we correlated climate (i.e., temperature and precipitation) to resorption proficiency in our congeners. Overall, we hypothesized species and plants found on serpentine soils would be more N and P proficient than their non-serpentine counterparts, resulting in more nutrient-poor litter. Additionally, we hypothesized that evergreen species would be more N and P proficient than deciduous species. Lastly, we hypothesized that precipitation and temperature would be correlated with both N and P resorption proficiency and thus influence realized resorption.

Materials and methods

Study site

The University of California's Donald and Sylvia McLaughlin Natural Reserve is located in Yolo, Lake, and Napa Counties, California, USA. The climate is Mediterranean, with warm, dry summers and cool, wet winters. Mean annual precipitation is 620 mm. The reserve is composed of a mosaic of serpentine and non-serpentine soils, which differ dramatically in their physical and chemical properties (Safford and Harrison 2004). Serpentine soils are derived from ultramafic parent material, and as such have a low Ca:Mg ratio and may contain toxic concentrations of heavy metals such as chromium and nickel. They also are low in N and P, and are frequently shallow, very stony, and heavy in clay content. In contrast, the non-serpentine soils at McLaughlin are derived from marine sedimentary parent material associated with the Great Valley Sequence. These loamy to clay-loamy soils are typically, but not always, higher in N and P, are enriched in Ca relative to Mg, and lack the presence of heavy metals. They are also generally deeper, less stony, and lower in clay. While both soil types are dominated by

low-nutrient-adapted woody species, species composition and plant communities vary in response to these stark edaphic differences. Most plants found on non-serpentine soils cannot be found on serpentine soils (although there are exceptions, such as *Heteromeles arbutifolia* and *Umbellularia californica*), while plants on serpentine tend to primarily associate with serpentine soils. However, congeners can be found off and on serpentine soils (e.g., *Arctostaphylos manzanita*–*A. viscida*, *Ceanothus cuneatus*–*C. jepsonii*, *Quercus berberidifolia*–*Q. durata*, and *Rhamnus californica*–*R. tomentella*; non-serpentine species in each pair listed first), allowing for comparisons of species responses to soil type between related species. In this paper, nomenclature follows Hickman (1993).

Sampling design

Beginning in late autumn 2003 and continuing for 6 years, we sampled senescent leaf tissue from a suite of species found on and off serpentine soils. We focused our collections on the aforementioned four congener pairs, as well as other community dominants and sub-dominants found on each soil type (non-serpentine soils: *Aesculus californica*, *Cercocarpus betuloides*, *H. arbutifolia*, *Q. chrysolepis*, *Q. douglasii*, *Q. kelloggii*, *Q. lobata*, *Q. wislizenii*, *U. californica*; serpentine soils: *Garrya congdonii*, *H. arbutifolia*, *R. crocea*). Three of these species are actinorhizal, and thus are potential N-fixers: *Cercocarpus betuloides*, *Ceanothus cuneatus*, and *Ceanothus jepsonii*. Over the 6 years of sampling, we noted species-specific differences in leaf shedding, with most evergreen and some deciduous species shedding leaves predominantly in the summer (late June/early July) and some evergreen and most deciduous species shedding leaves in late autumn (late November/early December). In some years, some evergreen species shed so few leaves that samples were not collected for that species (e.g., 2004: *Ceanothus jepsonii* and *G. congdonii*). For other species, populations were not located until later in the study (e.g., the *Rhamnus* species). In most cases, three to four individuals of each species were sampled each year.

Senescent leaves were collected by gently shaking branches over a drop cloth. Following collection, leaves were sorted to remove fruits, seeds, twigs, and any non-senescent leaves (i.e., green leaves) that may have been brushed off the branches accidentally. To maximize the number of individuals included in the study, different shrubs were sampled between years. In the final year of the study (2008), green sun-exposed leaves were collected from all congener shrubs, allowing us to relate resorption proficiency (the concentration of nutrients in senesced leaf tissue) to resorption efficiency (the proportion of nutrients resorbed from leaf tissue) and green leaf N:P. Air-dried leaves were oven dried at 60 °C for consistent sample

treatment prior to triple-rinsing in deionized water to remove surface residues (rinsing time <10–15 s). Leaves were dried again at 60 °C and finely ground with a ball mill. Total N was determined by micro Dumas combustion on a CN analyzer (ECS 4010, Costech Analytical). For P analysis, samples were ashed, dissolved in 1.0 N HCl, diluted, and analyzed by ICP-AES (Plasma 400; Perkin Elmer).

Soils under the congener pair species were collected in July 2007. Under each shrub at three to four locations, soil from the surface 10 cm was collected and composited in the field. The soils were air dry when collected; thus, they were stored under ambient conditions in the laboratory. Soils were sieved (2 mm), and samples for total C and N and Olsen's P were ground with a ball mill prior to analysis. Soil pH and electrical conductivity (EC) were measured on 1:5 soil:water extracts. Total N was measured by micro Dumas combustion on the CN analyzer, and Olsen's extractable P was measured by flow injection analysis.

Climate variables

Seasonal and annual temperature and precipitation data were obtained from the Morgan Valley Weather Station, maintained by the Western Weather Group (<http://www.westernwx.com/Lakeco/historicalLakeCo.html>). This weather station is on the reserve property, near the field station. Mean quarterly and annual temperature, as well as quarterly and annual precipitation, were obtained from this site.

Statistical analyses

Soil data were compared using ANOVA, with soil type and genus as main effects. To assess community-wide trends, data for individual species found on and off serpentine soils were averaged across years; standard errors, coefficients of variation, and minimum and maximum values were also determined. To assess whether N and P resorption differed among congeners found on and off serpentine soils, a mixed-model ANOVA including the following factors was used: congener pair (to account for phylogenetic effects; Harvey and Pagel 1991; fixed effect), soil type (serpentine or non-serpentine; fixed effect), year (2003–2008; random effect), and the interaction of congener pair and soil type. To assess relationships between resorption proficiency and resorption efficiency, linear regression analyses were run on the mean values for the eight focal congener species. To compare resorption responses in *H. arbutifolia* found on serpentine and non-serpentine soils, we included the following factors in our mixed model: soil type (non-serpentine and serpentine; fixed effect) and year (2004–2008; no *H. arbutifolia* individuals were sampled on serpentine

soils in 2003; random effect). For comparison of deciduous and evergreen *Quercus* species, we included leaf habit (deciduous or evergreen; fixed effect) and year (2004–2005 to ensure all species were sampled in all years included in the analysis; random effect) in the mixed model. Bivariate correlations between climate variables (i.e., temperature and precipitation) and N and P resorption were conducted. Both seasonal (i.e., quarterly) and annual measurements were correlated with N and P resorption in the four congener pairs. Given the large number of correlations (20 in total), a Bonferroni correction was used to assess significance of the Pearson product moment correlations. Normality was tested using the Shapiro–Wilks test, and equal variance, with Levene's test. All ANOVA, correlation, and linear regression models were analyzed with SAS (SAS Institute 2002). Non-linear regression analyses were analyzed with Sigma Plot (Systat Software 2010).

Results

Soil nutrients

Soil pH was slightly lower on non-serpentine compared to serpentine soils ($P = 0.002$), and it was lower under the *Arctostaphylos* and *Quercus* species compared to the *Ceanothus* and *Rhamnus* species ($P < 0.0001$) (Table 1). Overall, there was a significant genus \times soil type interaction, with soil pH tending to be higher within a genus on serpentine soils ($P = 0.04$). Soil EC was slightly lower on non-serpentine compared to serpentine soils ($P = 0.04$). There were no differences among genera ($P > 0.05$), nor was there a significant genus \times soil type interaction. Total soil C was lower on non-serpentine than serpentine soils ($P = 0.008$). Total soil C was also higher under the *Arctostaphylos* and *Rhamnus* species and lower under the *Ceanothus* and *Quercus* species ($P = 0.02$). There was no significant genus \times soil type interaction for total soil C ($P > 0.05$). Total soil N was significantly lower on non-serpentine compared to serpentine soils ($P = 0.001$), and it was higher under *Arctostaphylos* and *Rhamnus* species and lower under *Ceanothus* and *Quercus* species ($P = 0.01$). However, the strength of these trends depended on soil type. For example, total soil N under *Rhamnus* species was over twofold higher on serpentine compared to non-serpentine soils. Soil C:N was lower on non-serpentine than serpentine soils ($P < 0.0001$) and was higher under *Arctostaphylos* species compared to *Ceanothus*, *Quercus*, and *Rhamnus* species ($P = 0.01$) (Table 1). There was no significant genus \times soil type interaction for soil C:N ($P > 0.05$). Lastly, extractable soil P was ≈ 1.9 -fold higher on non-serpentine compared to serpentine soils ($P = 0.0002$). Extractable soil P tended to be higher under

Table 1 Summary of chemical properties of soils sampled under shrubs found on non-serpentine and serpentine soils

	pH	EC (dS m ⁻¹)	C (g kg ⁻¹)	N (g kg ⁻¹)	C:N	P (mg kg ⁻¹)
Non-serpentine soils	6.9 ± 0.1	0.09 ± 0.01	22.7 ± 2.9	1.6 ± 0.2	14.0 ± 0.6	15.6 ± 1.9
<i>A. manzanita</i>	6.5 ± 0.10	0.09 ± 0.01	37.2 ± 2.3	2.3 ± 0.2	16.4 ± 0.4	21.8 ± 1.8
<i>C. cuneatus</i>	7.0 ± 0.07	0.10 ± 0.02	14.7 ± 4.6	1.3 ± 0.3	11.0 ± 1.3	12.6 ± 1.6
<i>Q. berberidifolia</i>	6.8 ± 0.06	0.07 ± 0.01	16.9 ± 1.8	1.2 ± 0.1	14.8 ± 0.7	9.3 ± 1.2
<i>R. californica</i>	7.2 ± 0.11	0.09 ± 0.02	22.0 ± 5.8	1.5 ± 0.3	13.8 ± 0.8	18.6 ± 6.0
Serpentine soils	7.0 ± 0.0	0.10 ± 0.01	34.3 ± 3.9	1.9 ± 0.2	17.2 ± 0.5	8.2 ± 0.9
<i>A. viscida</i>	6.9 ± 0.09	0.10 ± 0.01	37.0 ± 7.9	1.9 ± 0.2	18.5 ± 1.3	10.5 ± 1.5
<i>C. jepsonii</i>	7.2 ± 0.03	0.11 ± 0.01	21.2 ± 4.0	1.2 ± 0.2	16.8 ± 0.8	4.6 ± 1.3
<i>Q. durata</i>	7.0 ± 0.05	0.08 ± 0.01	33.4 ± 3.8	2.0 ± 0.2	16.6 ± 0.4	7.1 ± 0.8
<i>R. tomentella</i>	7.2 ± 0.10	0.13 ± 0.01	55.0 ± 16.0	3.2 ± 0.8	16.7 ± 0.6	12.4 ± 3.5

Data are mean ± SE ($n = 4-8$ for shrub means and $n = 16-28$ for soil type means)

Arctostaphylos and *Rhamnus* species and lower under *Ceanothus* and *Quercus* species ($P = 0.0004$). However, extractable soil P responses depended on both the genus under which the soil was sampled, as well as the soil type. For example, extractable soil P was lowest under *Quercus berberidifolia* in non-serpentine soils, but it was lowest under *Ceanothus jepsonii* in serpentine soils.

Community responses

Mean nitrogen resorption proficiency (N_{prof}) varied 3.9-fold among all species sampled (Table 2), with minimum values of 1.7 g kg⁻¹ observed in two *Arctostaphylos* individuals (one of each species) and a maximum value of 28.2 g kg⁻¹ observed in one *G. congdonii* individual. Mean N_{prof} was in the complete resorption range (<7 g kg⁻¹; sensu Killingbeck 1996) for 6 of the 12 non-serpentine species observed and for all 7 of the serpentine species observed. Two of three species able to form symbiotic relationships with *Frankia* symbionts (*Ceanothus cuneatus* and *Ceanothus jepsonii*) had mean N_{prof} values near or below the complete resorption range; in contrast, mean N_{prof} was above the incomplete resorption range (>10 g kg⁻¹; sensu Killingbeck 1996) in *Cercocarpus betuloides*. Mean phosphorus resorption proficiency (P_{prof}) varied 9.5-fold among all species sampled (Table 2), with a minimum value of 0.1 g kg⁻¹ observed in one *Ceanothus jepsonii* individual and a maximum value of 4.3 g kg⁻¹ observed in one *Q. kelloggii* individual. Mean P_{prof} was in the complete resorption range (<0.4 and <0.5 g kg⁻¹ for evergreen and deciduous species, respectively; sensu Killingbeck 1996) for none of the non-serpentine species measured and for 4 of the 7 serpentine species observed. In fact, all non-serpentine species were near or well above the incomplete resorption range (>0.5 and >0.8 g kg⁻¹ evergreen and deciduous species, respectively; sensu Killingbeck 1996). Overall, large variation in N_{prof} and P_{prof} was observed among replicates within species, with N_{prof}

varying as much as 9.1-fold within species and P_{prof} varying as much as 16.4-fold within species. This variation is evident by the large CVs and plasticities observed for most species for both N_{prof} and P_{prof} (Table 2).

Congener comparisons

N_{prof} did not differ between soil types ($P > 0.05$) but varied 2.4-fold among congener groups ($P < 0.0001$; Fig. 1a), with N_{prof} below the complete resorption range in both serpentine and non-serpentine species. There was no significant interaction between soil type and congener group for N_{prof} . In contrast, non-serpentine species were less P_{prof} than serpentine species ($P < 0.0001$), and only serpentine species were able to meet complete P_{prof} in at least some years (Fig. 1b). P_{prof} varied 9.5-fold among the congener groups ($P < 0.0001$), although there was not a significant interaction between soil type and congener group ($P > 0.05$). In the final year of the study, there was an inverse relationship between nitrogen resorption efficiency (N_{eff}) and N_{prof} ($R^2 = 0.63$, $P = 0.018$, $df = 1,6$; Supplementary Fig. 1A) and between phosphorus resorption proficiency (P_{eff}) and P_{prof} ($R^2 = 0.81$, $P = 0.002$, $df = 1,6$; Supplementary Fig. 1B). As such, plants that resorbed proportionally more N and P also had lower N and P concentrations in senesced leaf tissue (i.e., resorption patterns were similar between measures). There was a non-significant relationship between N_{prof} and green leaf N:P ($P > 0.05$), and a significant decreasing, asymptotic relationship between P_{prof} and green leaf N:P ($R^2 = 0.65$, $P = 0.016$, $df = 1,6$) (Fig. 2).

H. arbutifolia on and off serpentine soils

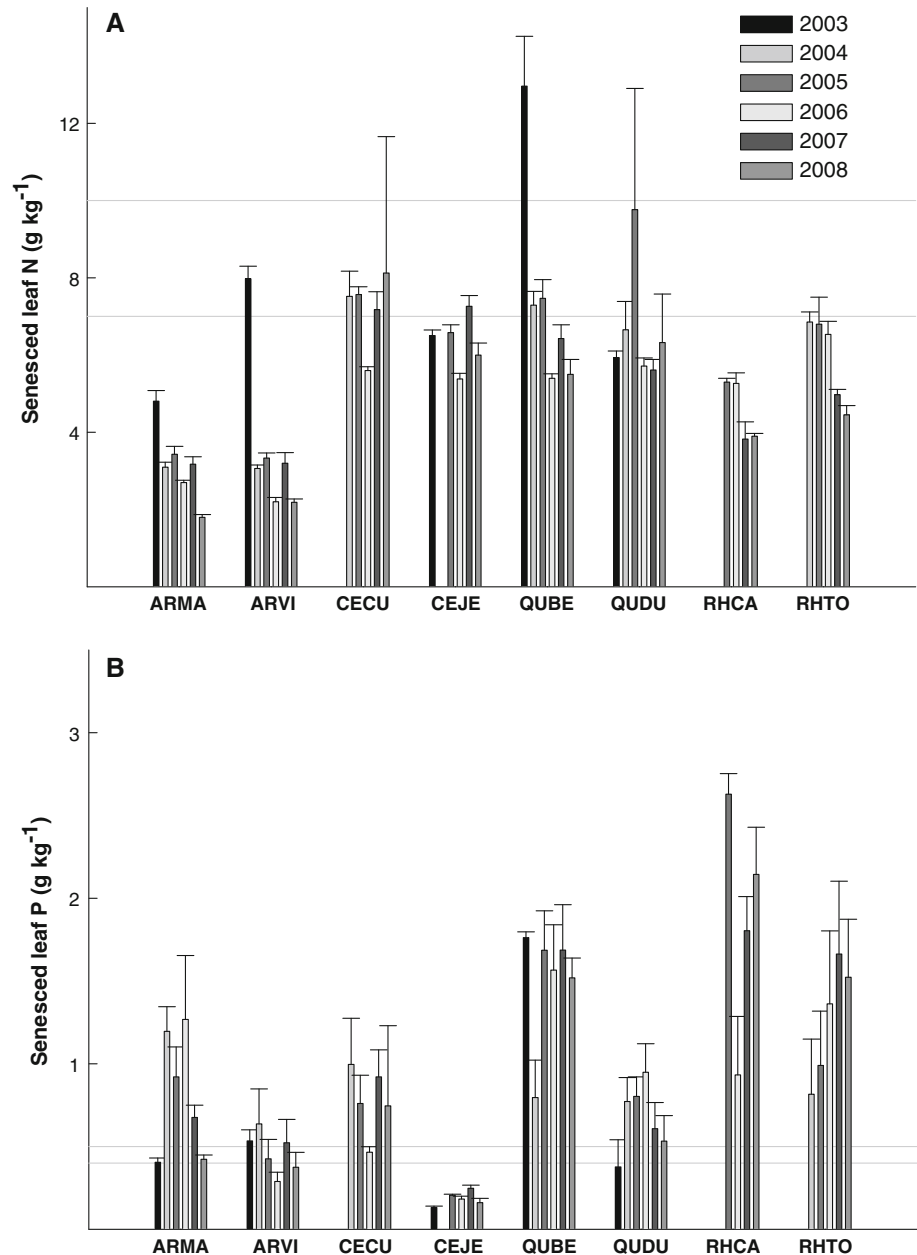
There were no significant differences in N_{prof} between *H. arbutifolia* shrubs growing on and off serpentine soils ($P > 0.05$), and N_{prof} was below the complete resorption range for both non-serpentine and serpentine individuals in

Table 2 Nutrient resorption proficiency for dominant and sub-dominant woody species found on and off serpentine soils

Species	Leaf habit	Functional group	Years sampled	N (g kg ⁻¹)			P (g kg ⁻¹)			CV		Plasticity			
				Mean ± SE	n	Min. Max.	Mean ± SE	n	Min. Max.	Max-min	N	Max-min	P		
Non-serpentine communities															
<i>A. californica</i>	Deciduous	Tree	2004–2008	5.5 ± 0.4	17	3.3	9.8	33.3	1.6 ± 0.2	17	0.5	3.5	58.9	6.5	3.0
<i>A. manzanita</i>	Evergreen	Shrub	2003–2008	3.1 ± 0.2	20	1.7	5.1	31.1	0.8 ± 0.1	20	0.4	2.0	55.0	3.4	1.6
<i>C. betuloides</i>	Deciduous	Shrub	2004–2008	11.2 ± 1.0	17	6.5	21.7	37.9	0.7 ± 0.1	17	0.4	1.5	46.6	15.2	1.1
<i>C. cuneatus</i>	Evergreen	Shrub	2004–2008	7.3 ± 0.8	17	4.2	18.7	44.5	0.8 ± 0.1	17	0.2	2.2	66.0	14.5	2.0
<i>H. arbutifolia</i>	Evergreen	Shrub	2003–2008	3.8 ± 0.3	20	2.3	7.9	29.9	1.6 ± 0.2	20	0.3	3.5	54.5	5.6	3.2
<i>Q. berberidifolia</i>	Evergreen	Shrub	2003–2008	7.4 ± 0.6	20	4.6	15.4	36.7	1.5 ± 0.1	20	0.3	2.4	30.8	10.8	2.0
<i>Q. chrysolepis</i>	Evergreen	Tree	2004–2005	12.2 ± 0.6	6	10.5	13.8	11.2	1.0 ± 0.1	7	0.7	1.1	16.1	3.3	0.4
<i>Q. douglasii</i>	Deciduous	Tree	2003–2008	7.8 ± 0.6	20	5.3	16.0	35.3	1.9 ± 0.2	20	0.6	3.6	48.6	10.7	3.0
<i>Q. kelloggii</i>	Deciduous	Tree	2003–2008	6.1 ± 0.7	20	3.4	17.8	54.2	1.6 ± 0.2	20	0.4	4.3	62.2	14.4	3.9
<i>Q. lobata</i>	Deciduous	Tree	2003–2008	10.0 ± 0.9	21	5.0	20.2	40.3	1.8 ± 0.2	21	0.9	4.0	50.8	15.2	3.1
<i>Q. wislizenii</i>	Evergreen	Tree	2004–2005, 2008	5.9 ± 0.3	10	4.4	7.6	17.7	0.9 ± 0.1	10	0.6	1.6	39.0	3.2	1.0
<i>R. californica</i>	Evergreen	Shrub	2005–2008	4.5 ± 0.2	14	2.5	5.8	19.5	1.9 ± 0.2	14	0.4	2.9	38.8	3.3	2.5
<i>U. californica</i>	Evergreen	Shrub	2003–2008	6.8 ± 0.5	20	5.1	14.8	35.3	0.7 ± 0.0	20	0.5	1.1	23.5	9.7	0.6
Serpentine communities															
<i>A. viscida</i>	Evergreen	Shrub	2003–2008	3.1 ± 0.3	34	1.7	8.5	53.5	0.4 ± 0.0	34	0.1	1.2	65.4	6.8	1.1
<i>C. jepsonii</i>	Evergreen	Shrub	2003, 2005–2008	6.4 ± 0.2	31	4.7	8.4	14.4	0.2 ± 0.0	31	0.1	0.3	31.7	3.7	0.2
<i>G. congdonii</i>	Evergreen	Shrub	2003, 2005–2008	5.4 ± 0.8	31	3.1	28.2	79.7	0.4 ± 0.0	31	0.2	0.9	37.4	25.1	0.7
<i>H. arbutifolia</i>	Evergreen	Shrub	2004–2008	4.6 ± 0.4	21	2.7	10.6	38.9	0.9 ± 0.1	21	0.3	2.2	71.1	7.9	1.9
<i>Q. durata</i>	Evergreen	Shrub	2003–2008	6.6 ± 0.6	35	4.1	25.3	55.9	0.7 ± 0.1	32	0.2	1.4	60.5	21.2	1.2
<i>R. crocea</i>	Evergreen	Shrub	2007	5.7 ± 0.6	3	5.1	6.8	16.7	0.4 ± 0.0	3	0.4	0.5	13.8	1.7	0.1
<i>R. tomentella</i>	Evergreen	Shrub	2004–2008	5.4 ± 0.3	20	3.6	7.5	21.0	1.4 ± 0.2	20	0.2	3.3	60.4	3.9	3.1

Data are averaged across years

Fig. 1 Senesced leaf a N and b P of congeners found off and on serpentine soil. Data are mean \pm SE ($n = 3-8$). ARMA, *A. manzanita*; ARVI, *A. viscida*; CECU, *C. cuneatus*; CEJE, *C. jepsonii*; QUBE, *Q. berberidifolia*; QUDU, *Q. durata*; RHCA, *R. californica*; RHTO, *R. tomentella*. In both panels, the upper reference line indicates the incomplete resorption range, the lower reference line indicates the complete resorption range, and between the upper and lower reference lines indicates the intermediate resorption range (sensu Killingbeck 1996)



all years (Fig. 3a). However, P_{prof} was marginally significant ($P = 0.048$), with senescent leaf P concentrations 1.6-fold greater in non-serpentine than serpentine individuals, when averaged across years (Fig. 3b). Despite these differences, P_{prof} was above the complete resorption range for individuals growing off and on serpentine soils, except for 2007, when mean P_{prof} was at the limit of the complete resorption range for the serpentine individuals.

Leaf habit and resorption in non-serpentine *Quercus* congeners

Deciduous *Quercus* species had 1.3-fold higher senescent leaf N concentrations than evergreen species ($P = 0.03$; Fig. 4a),

averaged across years. None of the deciduous species attained complete N_{prof} , although two of the three sampled evergreen species (*Q. berberidifolia* and *Q. wislizenii*) had N_{prof} values below or near the complete resorption range. There were no significant differences in P_{prof} between deciduous and evergreen species ($P > 0.05$; Fig. 4b). All of the sampled species had P_{prof} values above the complete resorption range ($<0.5 \text{ g kg}^{-1}$ for deciduous species and $<0.4 \text{ g kg}^{-1}$ for evergreen species, sensu Killingbeck 1996).

Correlations between climate and resorption

Mean annual temperature was very consistent throughout the course of the study, while seasonal mean temperatures

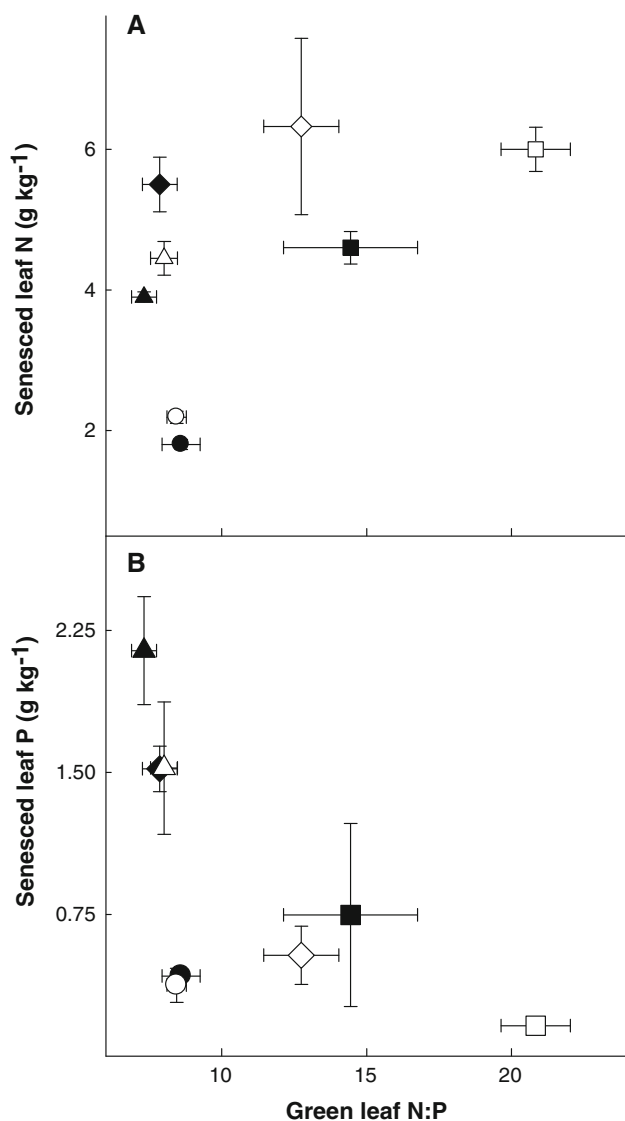


Fig. 2 Relationships between senesced leaf **a** N and **b** P and green leaf N:P. Although both relationships were asymptotic in nature, only the relationship between senesced leaf P and green leaf N:P was significant. Data are mean \pm SE ($n = 3-8$). *Black symbols* are non-serpentine species, *white symbols* are serpentine species. *Arctostaphylos* congeners are *circles*, *Ceanothus* congeners are *squares*, *Quercus* congeners are *diamonds*, and *Rhamnus* congeners are *triangles*

were slightly more variable (Table 3). In contrast, total precipitation varied greater than twofold over the 6 years of the study, with large variation in seasonal precipitation across years (Table 3). Of all the seasonal and annual climate variables, N_{prof} in our focal congeners only was correlated with second quarter mean temperature ($R = -0.28$, $P = 0.0001$) and fourth quarter precipitation ($R = 0.29$, $P < 0.0001$). All other correlations between climate and N_{prof} were not significant ($P > 0.0025$ following Bonferroni correction). None of the climate variables were significantly correlated with P_{prof} in our focal congeners ($P > 0.0025$ following Bonferroni correction).

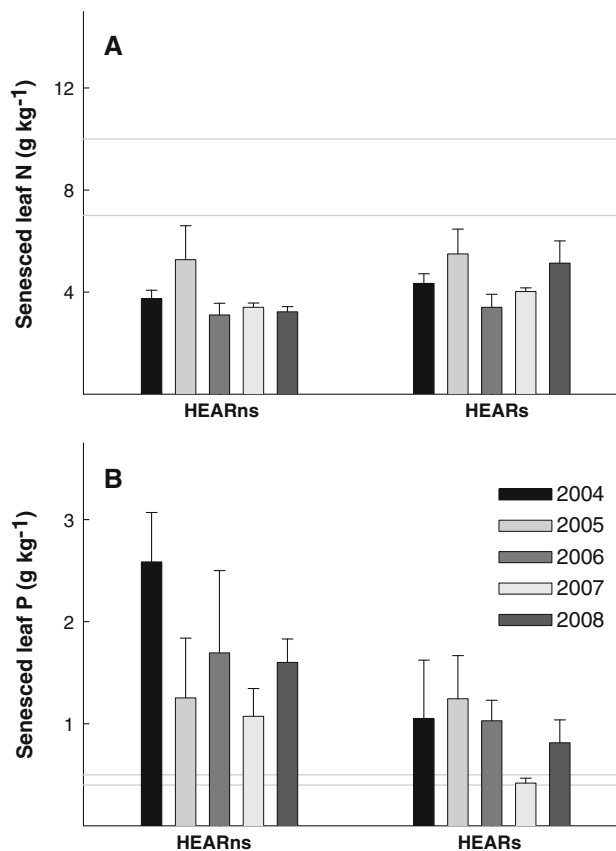


Fig. 3 Senesced leaf **a** N and **b** P of *H. arbutifolia* growing off (HEARns) and on (HEARs) serpentine soil. Data are mean \pm SE ($n = 3-8$). *Reference lines* indicate the complete, intermediate, and incomplete resorption ranges as described for Fig. 1

Discussion

As hypothesized, species found on serpentine soils had greater P_{prof} than species found off serpentine soils. This hypothesis was supported by community-level, congener, and *H. arbutifolia* comparisons and is consistent with the large difference in P availability between these soils. Comparing our data to published values (Killingbeck 1996), species found on serpentine soils were more likely to completely resorb P than their non-serpentine counterparts. Additionally, the significant correlation between P_{eff} and P_{prof} , and the decreasing, asymptotic relationship between P_{prof} and green leaf N:P indicate the tight controls between plant P status and P_{prof} . Together, these data suggest that the low phosphorus, serpentine soils have been a consistent selective force for greater P resorption in species endemic to them. Contrary to our initial hypothesis, however, most species on both soil types were nearly equally N proficient, with half of the non-serpentine species and all serpentine species exhibiting complete N resorption. Previous data indicate that shrub species growing on serpentine at McLaughlin are strongly N

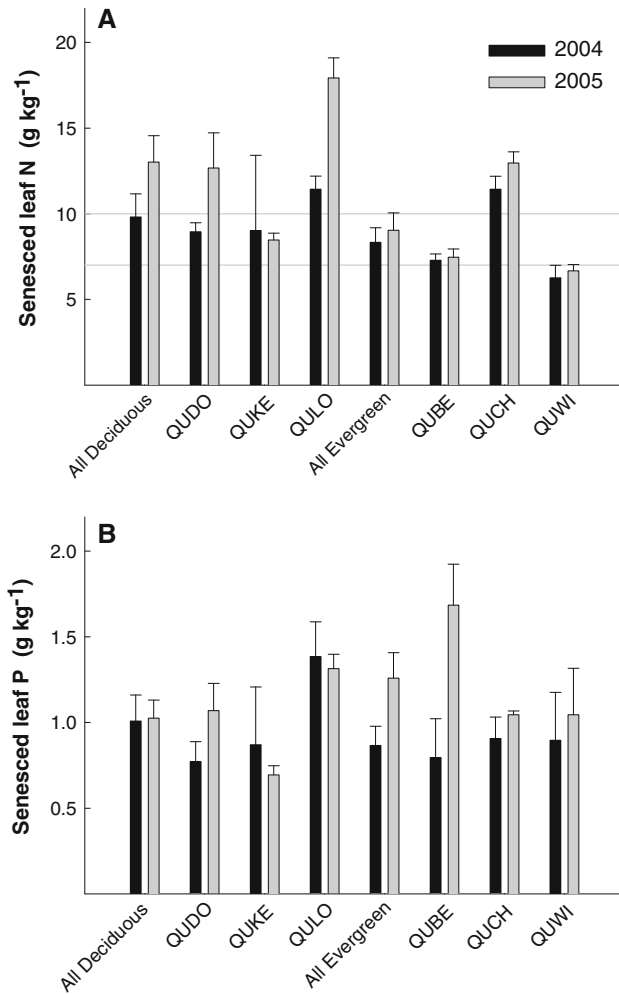


Fig. 4 Senesced leaf **a** N and **b** P of mean values for deciduous and evergreen *Quercus* congeners growing in non-serpentine soil, as well as individual species means. Data are mean \pm SE ($n = 3-9$). QUBE, *Q. berberidifolia*; QUCH, *Q. chrysolepis*; QUDO, *Q. douglasii*; QUKE, *Q. kelloggii*; QULO, *Q. lobata*; QUWI, *Q. wislizenii*. Reference lines for N_{prof} indicate the complete, intermediate, and incomplete resorption ranges as described for Fig. 1. Reference lines are not presented for P_{prof} , as ranges differ between deciduous and evergreen species (Killingbeck 1996)

limited (O'Dell et al. 2006), and thus for them proficient N resorption is likely a key N conservation mechanism. However, total soil N was low in both non-serpentine and serpentine soils, with the higher total soil N in serpentine soils balanced by a higher soil C:N ratio. Under these conditions, plant-available N may be lower due to increased microbial N limitation (Hobbie 1992). Together, the soil chemical analyses suggest that low soil N in both soil types should be a strong selective force for proficient N resorption in the dominant woody species of both serpentine and non-serpentine communities.

Variation in nutrient resorption among functional groups

In partial support of our hypothesis, evergreen *Quercus* congeners were more proficient at resorbing N than deciduous *Quercus* congeners, but we detected no differences in P_{prof} between these functional groups within the genus. These data are similar to predictions based on the meta-analysis conducted by Yuan and Chen (2009), in which evergreen species were more N proficient than deciduous species. However, both the meta-analyses by Killingbeck (1996) and Yuan and Chen (2009) detected significantly greater P_{prof} in evergreen compared to deciduous species, which contrasts with our observations. The lack of difference in P_{prof} between deciduous and evergreen *Quercus* congeners is surprising, given the previously observed strong differences among these functional groups. Obviously, our *Quercus* dataset was smaller than those included in the previous works and are based on only two field seasons of data, which could account for the unexpected patterns. However, we posit that our data may suggest a role for phylogeny in driving resorption processes, as the previous analyses did not take into account phylogeny or only accounted for differences among gymnosperms and angiosperms. It is possible that similar resorption patterns among the deciduous and evergreen

Table 3 Seasonal and annual climate data (temperature and precipitation) for the 6 years of the study

Years	Temperature ($^{\circ}\text{C}$)					Precipitation (mm)				
	Winter	Spring	Summer	Fall	Average	Winter	Spring	Summer	Fall	Total
2003	9.83	14.80	24.26	11.20	15.02	244.35	169.93	3.56	494.28	912.11
2004	9.19	16.67	23.17	11.13	15.04	437.39	32.00	1.02	449.83	920.24
2005	9.06	13.83	24.00	11.87	14.69	401.57	219.20	0.00	441.20	1,061.97
2006	6.87	16.69	24.04	11.04	14.66	518.16	202.44	0.00	229.87	950.47
2007	9.52	17.15	22.3	11.07	15.01	278.64	48.01	7.11	180.85	514.60
2008	7.76	16.74	24.41	12.41	15.33	459.00	10.16	0.25	228.60	699.01

Data were from the Morgan Valley meteorological station at the University of California's Donald and Sylvia McLaughlin Natural Reserve

oaks in our study were due to their shared evolutionary history and the similar selective forces under which they evolved in this Mediterranean-type habitat. A lack of correlation between leaf habit and resorption proficiency has been observed in other deciduous and evergreen species in the Fagaceae (Hevia et al. 1999). In their study, N_{prof} did not differ among deciduous and evergreen Chilean *Notofagus* species, and although the species differed in P_{prof} , these differences were not related to leaf habit. Recent work comparing leaf chemical composition of deciduous and evergreen species using phylogenetically independent contrasts suggests family of origin is a stronger influence than leaf habit (Villar et al. 2006).

Interestingly, we know from greenhouse work that both *Ceanothus* species can form symbiotic associations with N-fixing *Frankia* (O'Dell et al. 2006). However, under field conditions, both species showed complete (or near complete) N resorption, similar to the *Rhamnus* congeners, which are also members of the Rhamnaceae but are not N-fixing (Swensen 1996; Richardson et al. 2000). Generally, N-fixing plants show poorer N resorption than species that do not fix N, suggesting a trade-off between these two strategies (Killingbeck 1993, 1996; Tateno 2003; Stewart et al. 2008). Our observations are also in contrast with previous work on *Ceanothus americanus* (N-fixing) and *Rhamnus catharticus* (non-N-fixing), in which both species were poor at resorbing N; in this work, the authors suggested similarly low N_{prof} among the congeners indicated that poor resorption evolved in their putatively N-fixing common ancestor (Stewart et al. 2008). However, relationships within the Rhamnaceae and the evolution of actinorhizal symbiosis are still under investigation (Richardson et al. 2000), and it is possible that the common ancestor of these congeners was not capable of fixing N. If so, the proficient N resorption observed in the *Ceanothus* and *Rhamnus* congeners may suggest that the evolution of N-resorption traits may have occurred before the split of these clades, and that their common ancestor was proficient at N resorption. It is also possible that resorption in these N-fixing species may be highly plastic and environment-dependent. Further studies should document the presence or absence of a functional symbiotic relationship between these *Ceanothus* species and *Frankia* symbionts. In contrast to the *Ceanothus* congeners, N-resorption in *Cercocarpus betuloides*, another species capable of N-fixation via symbiosis with *Frankia*, was incomplete, similar to expectations for N-fixing species.

Variation among species and years

One strong theme that emerges from our dataset is the inherent variability in the phenomenon of resorption. The coefficient of variation was >30 for 13 of the 18

community N_{prof} values and for 17 of the 18 community P_{prof} values, with CVs as high as 79.7 and 71.1 for N_{prof} and P_{prof} , respectively (Table 2). In general, this plasticity was not correlated with either seasonal or annual temperature or precipitation in our focal congener pairs. Although senesced leaf N was negatively correlated with mean spring temperature and positively correlated with total fall precipitation, in general these correlations were weak. It is surprising resorption plasticity was not more strongly correlated with climate among the congeners, as previous studies at both local (e.g., Aerts et al. 2007) and global (e.g., Yuan and Chen 2009) scales have observed significant relationships between resorption patterns and climate. One factor not accounted for in our study was plasticity at the individual level, which may be as great or greater than interannual variability (Nordell and Karlsson 1995). We are currently planning future studies that will account for individual plasticity in our study system.

Our plasticity data indicate large variation between the minimum and maximum values observed for each species, as well as large annual variation. Combining these points of reference, a clear picture of the difference between the concepts of potential resorption (the amount of nutrients that can be physiologically resorbed) and realized resorption (the amount of nutrients resorbed in any given year) begins to emerge (potential and realized resorption definitions; sensu Killingbeck 2004). If we consider the minimum values observed in each species, we can see that at least some individuals were able to reduce N or P to minimal levels. These minimum values, as observed from multiple field seasons, indicate the maximum potential resorption for these species at this site, whereas the plasticity in N and P resorption indicate the effects of environmental factors on resorption for these species at this site. Given the ability of most species to reduce both N and P to minimal values, but also the large annual variability in resorption, we propose that environmental effects have a greater impact on resorption proficiency than genetic factors. Future work will focus on testing this hypothesis, with repeated sampling of individuals over multiple years.

Conclusions

Through repeated, multi-year sampling, which accounted for phylogeny, we detected strong environmental effects on realized and potential resorption, as evidenced by large inter-annual variability (i.e., realized resorption effects) as well as differences in P_{prof} between soil types (i.e., potential resorption effects). As suggested by previous work, resorption proficiency can be very sensitive to soil nutrient limitations. Species found on serpentine (i.e., low P soils) were more P-proficient than their non-serpentine

counterparts, and most species, regardless of soil type, were highly N-proficient, suggesting N-limitation for both serpentine and non-serpentine species in these Mediterranean-type habitats.

Clearly, one factor leading to an incomplete understanding of the resorption process is the lack of multiyear datasets for most species studied. In his initial review of resorption proficiency, Killingbeck (1996) cites only three papers including multi-year data and states that inter-annual variability is a “constant feature” of resorption studies. However, more than 10 years later, multi-year data for this process are very rare. For example, in their recent meta-analysis of senesced leaf nutrient concentrations, only $\approx 5\%$ of the studies included had more than 1 year of resorption data and of these most represent only 2–3 field seasons (Yuan and Chen 2009). Yet, it is clear that many species do not consistently reach minimal (i.e., potential) resorption values. Without a clear understanding of potential resorption for species, we will not fully understand the evolutionary drivers of this process. Moreover, assessing environmental effects on realized resorption will require multiple long-term datasets.

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