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Inefficient nitrogen resorption in genets of the actinorhizal nitrogen fixing shrub *Comptonia peregrina*: physiological ineptitude or evolutionary tradeoff?

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Abstract. Nutrient resorption was measured in an actinorhizal nitrogen-fixing shrub, *Comptonia peregrina*, for five years in the understory of a deciduous oak forest in Rhode Island, USA. Mean resorption of nitrogen was extremely inefficient (11%) compared to most deciduous species (50% +), yet resorption of phosphorus was efficient (53%) and comparable to other species. Of the seven additional nutrients studied, only copper (6%) and zinc (10%) were resorbed from senescing leaves. Resorption of nitrogen (5%–20%) and phosphorus (40%–71%) varied significantly among years. Copper was resorbed from leaves in three years and accreted into leaves in two years. Five-year resorption means differed among individual genets by as much as a factor of 2.5 for nitrogen, and 1.3 for phosphorus. Resorption of nitrogen, copper, and zinc were highly correlated, yet resorption of phosphorus remained autonomous from other nutrients. The ecophysiological tradeoffs in *Comptonia* which have resulted in the cooccurence of actinorhizal nitrogen fixation, inefficient nitrogen resorption, and efficient phosphorus resorption suggest that plant nutrient status does have an impact on resorption efficiency and that the evolution of nutrient conservation strategies is nutrient-specific.

Key words: Actinorhizal plants – Evolutionary tradeoffs – Nitrogen fixation – Nutrient resorption – Phosphorus

Plant species in the genus *Alnus* harbor the nitrogen-fixing microsymbiont *Frankia* (Schwintzer and Tjepkema 1990) and therefore have a source of nitrogen (N) not available to plants lacking N-fixing symbionts. *Alnus* species appear to be abnormally inefficient at resorbing N from senescing leaves (Stachurski and Zimka 1975; Dawson and Funk 1981; Rodriguez-Barrueco et al. 1984; Côté and Dawson 1986; Côté et al. 1989) and produce litter containing unusually high amounts of N (Turner et al. 1976; Gorham et al. 1979).

An intuitively appealing hypothesis which offers an explanation for the relationship above is that foliar N is not conserved during senescence because it is readily available through biochemical fixation. The implication is that N is not a limiting resource in *Alnus* and therefore is not conserved. The significance of this potential relationship bears on the more general question of whether resorption is a function of nutrient availability. This question remains unresolved and controversial because of the existence of papers which both support (Small 1972; Stachurski and Zimka 1975; Ralhan and Singh 1987) and dispute (Staff 1982; Birk and Vitousek 1986; Chapin and Moilanen 1991) the hypothesis that nutrient availability or plant nutrient status are closely related to nutrient resorption. Species with N-fixing symbionts provide a unique opportunity to address this issue because availability of N is regulated internally and is therefore more predictable than availability of other nutrients such as phosphorus (P).

Two additional hypotheses suggest alternative explanations for inefficient resorption of N in *Alnus*. First, it is possible that species of *Alnus*, and actinorhizal nitrogen fixing species in general, are simply inept at resorbing all nutrients from senescing foliage. Second, abundant amounts of cytokinins and delayed senescence, both potentially induced by high levels of N in *Alnus*, have been suggested as causes for inefficient resorption of N (Dawson and Funk 1981). By inference, both hypotheses suggest that no nutrient, including those efficiently resorbed by most plants, would be efficiently resorbed by species hosting actinorhizal N-fixers.

One such N-fixing species, *Comptonia peregrina* (L.) Coult., was chosen in 1984 for a long-term, multi-nutrient study on the dynamics of resorption. *Comptonia peregrina* forms root nodules which are capable of fixing atmospheric N (Ziegler and Huser 1963) and which are colonized by an actinomycete symbiont (Callaham et al. 1978). This symbiont, *Frankia*, is the organism responsible for fixing N in *Comptonia*, *Alnus*, and a variety of other genera (Schwintzer and Tjepkema 1990). *Comptonia peregrina* is a small, shade-intolerant clonal shrub that grows along woodland margins or in the understory of nutrient-poor, open-canopy forests in eastern North America (Stokes 1981; Dawson 1990). Its seeds are long-lived and respond to disturbance (Del Tredici 1977).

In 1984, net fluxes of nine nutrients were measured in the senescing foliage of individual genets (clones) of *Comptonia peregrina*. The four nutrients that were conserved through resorption in that year were then followed in four subsequent years. The fundamental goal of the study was to discern the long-term resorption patterns of nutrients whose availability would (i.e. N), and would not (e.g. P) be directly controlled by the N-fixing capabilities of the *Comptonia–Frankia* complex. The specific questions that were addressed focused on the resorption dynamics of *Comptonia* and included: 1) Is the resorption of N in *Comptonia* similar to that in most other deciduous species? 2) Is the resorption of N fundamentally different from that of other nutrients resorbed by *Comptonia*, or is the resorption of all nutrients unilaterally inefficient? 3) Does nutrient resorption vary significantly among years, and if so, do all nutrients follow similar patterns of change? 4) Do individual genets differ in their ability to resorb nutrients from senescing leaves?

Materials and methods

Five genets of *Comptonia peregrina* (sweet fern; to be referred to as *Comptonia*) were studied in the research reserve of the University of Rhode Island W. Alton Jones Campus in West Greenwich, RI during 1984, 1985, 1987, 1988, and 1989. The study site was an eastern deciduous forest dominated by *Quercus alba* and *Q. borealis* (white oak and northern red oak) in the overstory, and *Gaylussacia baccata* (black huckleberry), *Q. ilicifolia* (black scrub oak), and *Vaccinium vacillans* (lowbush blueberry) in the understory. The relatively open canopy (40–60% closure; Killingbeck and Costigan 1988) allowed the shade-intolerant *Comptonia* to grow in the understory. The soils are stony, well drained sandy loams derived from glacial till (Rector 1981) and the climate is humid mesothermal (Thornthwaite 1948).

Each of the five genets consisted of densely clustered, interconnected ramets that formed a genet no more than 1.0 m in diameter. All genets grew within an area approximately 50 × 100 m, and each was distinctly separate from all other *Comptonia* genets. The genets being studied were presumably nodulated and capable of fixing N because the excavated root systems of eight nearby *Comptonia* genets all were nodulated.

In each of the five study years, approximately 75–125 presenescent, green leaves were collected from each genet at the end of the growing season before the onset of senescence. All leaves were collected on a single day in each year between 13–24 September. Leaves were collected from all sections of each genet and were passed through a LI-COR Model 3100 area meter in the laboratory to determine surface area.

Senesced leaves were collected from the same genets during the same five years. Approximately 75–125 freshly fallen leaves were taken from the ground immediately under each genet and/or were picked directly from branches throughout the canopy of each genet. Because timing of maximum senescence and abscission varied among years, collection dates varied between 27 October–25 November. All collections were made on a single date in a given year except in 1989 when each genet was sampled on one of three dates between 27 October–10 November. Surface areas were measured in all years except 1985, when the senesced leaves were so curled and brittle that accurate areas could not be obtained.

In 1989, ten additional *Comptonia* genets were sampled within the W. Alton Jones research reserve, but at a site >600 m from the primary five *Comptonia* genets. These ten genets served to increase sample size in a given year to 1) enable more realistic correlation analysis among resorption efficiencies of all nutrients resorbed, and 2) enable a more accurate assessment of the range of resorption variability in *Comptonia*. Presenescent leaves were collected on 13 September, and senesced leaves were collected on three dates between 27 October and 10 November. Sampling procedures followed those for the primary five genets.

Leaves were oven-dried at 60° or 70° C to constant mass, weighed, and ground in a Wiley mill to pass a 40-mesh screen. Cations were extracted from 1.0-g leaf samples that were dry-ashed at 500° C for 3 h and dissolved in 5.0 N nitric acid. Calcium (Ca), magnesium (Mg), potassium (K), sodium (Na), copper (Cu), iron (Fe), manganese (Mn), and zinc (Zn) were measured in these extracts with a Varian 1475 atomic absorption spectrophotometer. Nitrogen (N) and phosphate-phosphorus (P) were extracted from 0.25-g leaf samples with a sulfuric acid – hydrogen peroxide wet digestion technique (Thomas et al. 1967) and measured with a Technicon AutoAnalyzer.

On 12 October 1988, leaves from five previously unsampled *Comptonia* genets were collected from the study site to determine whether leaching losses could account for significant losses of nutrients from leaves during senescence. Leaves from one genet at a time were spread on a mesh net stretched over a 27 cm diameter container lined with a plastic bag to collect leachate. In succession, 38–70 leaves from each genet (358–397 cm^2 of leaves per genet) were sprinkled with approximately 1140 ml of distilled water to simulate a 2-cm rainfall. Leachate was collected, filtered, and analyzed with the Technicon AutoAnalyzer and Varian atomic absorption spectrophotometer for the elements (N, P, Cu, Zn) that were resorbed by *Comptonia* in previous years. Measurable amounts of these four elements were not detected in the leachate. Therefore, decreases in foliar N, P, Cu, and Zn during senescence were predominantly due to resorption, not leaching.

Resorption was calculated as the difference in nutrient content ($\mu g\ cm^{-2}$) between presenescent and senesced leaves divided by presenescent content, the quantity multiplied by 100 ($R\% = [\text{P CONTENT} - \text{S CONTENT}/\text{P CONTENT}] \times 100$). The resulting percentage represents efflux from senescing leaves into perennial tissues. Temporal changes in foliar nutrient content rather than foliar nutrient concentration ($\mu g\ g^{-1}$) were used to estimate resorption. Because changes in leaf mass during senescence can raise or lower the concentration of a nutrient even when there is no net influx or efflux of that nutrient, resorption estimates based solely on concentration changes may be erroneous.

In 1985, it was not possible to estimate resorption from temporal changes in nutrient content ($\mu g\ cm^{-2}$) because accurate surface areas were not available for senesced leaves. To see whether it would be legitimate to estimate resorption in 1985 with nutrient concentration change data, I compared resorption estimates calculated with concentration data to those calculated with content data in the study years before and after 1984. In 1984, 1987, and 1989, resorption estimates calculated with concentration data did not differ from estimates calculated with content data for any of the elements resorbed by *Comptonia* ($P > 0.05$; *t*-test; N, P, Cu, Zn). Only in 1988 was there a significant difference between estimates ($P < 0.05$; *t*-test), and that was just for one element, Cu. Based on this analysis, temporal changes in nutrient concentration 1) were used to estimate resorption in 1985 and 2) appear to accurately reflect net nutrient movements during senescence in this species, at this site, in this time frame. This does not suggest or imply, however, that nutrient resorption estimates calculated with concentration data are generally appropriate.

Statistical analyses were performed primarily with SYSTAT software (Wilkinson 1989) on a Macintosh computer. Probabilities of differences between pairs of means were generated with *t*-tests. Probabilities of differences among multiple means were generated with analysis of variance (ANOVA) when Bartlett's test indicated homogeneity of group variances. When the assumption of homogeneity of group variances was not met, the Kruskal-Wallis nonparametric statistic was used to determine the probability of differences among means. Multiple means comparisons were made with the Tukey HSD test or Duncan's Multiple Range Test (SAS software was used to process the Duncan's statistic on an IBM mainframe [SAS Institute Inc. 1985]).

Results

In 1984, levels of Ca, Mg, Na, Fe, and Mn increased 9–80% in the senescing leaves of *Comptonia* (Fig. 1). Foliar

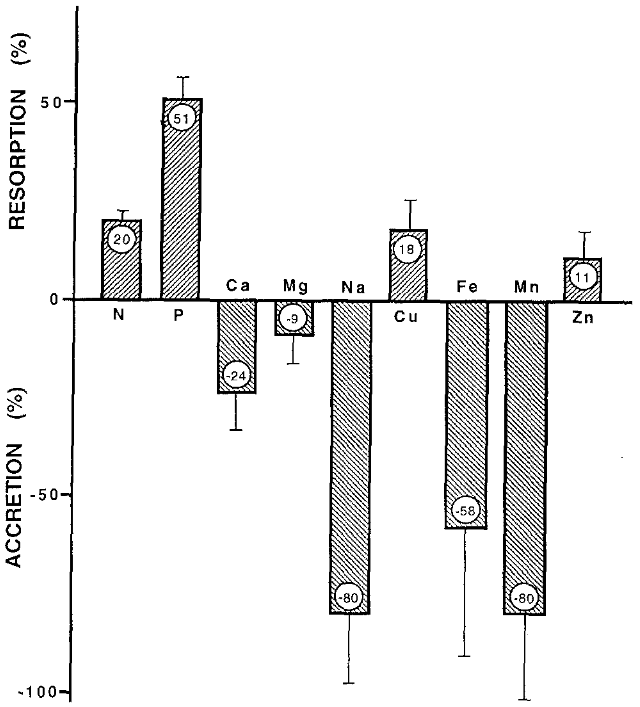

Fig. 1. Mean resorption and accretion of nitrogen (N), phosphorus (P), calcium (Ca), magnesium (Mg), sodium (Na), copper (Cu), iron (Fe), manganese (Mn), and zinc (Zn) in the senescing leaves of five *Comptonia peregrina* genets in 1984. Vertical bars represent one standard error of the mean; $n = 5$

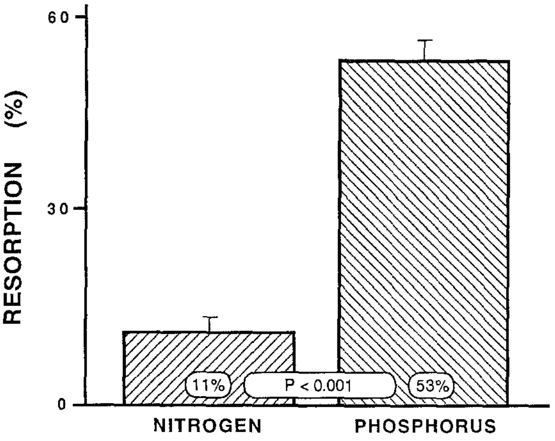

Fig. 2. Mean resorption of nitrogen and phosphorus in *Comptonia peregrina* genets during five years of study. Statistical difference between means is indicated by a *t*-test probability. Vertical bars represent one standard error of the mean; $n = 25$

accretion of Na, Fe, and Mn were particularly high (58–80%) and represent a significant change in leaf chemistry. Concomitant with this net flux of cations into senescing *Comptonia* leaves was a net efflux of N, P, Cu, and Zn (Fig. 1). Because the focus of this longitudinal study was the process of resorption, the five elements that were accreted in 1984 were not measured in subsequent years. The remainder of this paper will therefore focus on the resorption of foliar N, P, Cu, and Zn in *Comptonia.*

Table 1. Mean concentration (% or $\mu g\ g^{-1}$) and content ($\mu g\ cm^{-2}$) of nitrogen, phosphorus, copper, and zinc in the presenescent and senesced leaves of five *Comptonia peregrina* genets during five years of study. Standard error of the mean follows the ± signs, and $n = 25$ throughout except for content in senesced leaves where $n = 20$ because leaf surface areas could not be measured accurately in 1985

		Presenescent leaves	Senesced leaves
Nitrogen	%	2.02 ±0.04	1.76 ±0.05
	$\mu g\ cm^{-2}$	164 ±3	142 ±6
Phosphorus	%	0.076 ±0.002	0.035 ±0.002
	$\mu g\ cm^{-2}$	6.1 ±0.1	2.6 ±0.2
Copper	$\mu g\ g^{-1}$	2.6 ±0.2	2.3 ±0.1
	$\mu g\ cm^{-2}$	0.021 ±0.001	0.019 ±0.001
Zinc	$\mu g\ g^{-1}$	20.3 ±1.2	17.7 ±1.0
	$\mu g\ cm^{-2}$	0.160 ±0.010	0.15 ±0.01

During the five study years, a mean of 5.6% (SE = 4.8) of the Cu, and 9.6% (SE = 3.8) of the Zn in *Comptonia* leaves were resorbed during senescence. Mean resorption of N during this same period was 11% (SE = 2.1) and resorption of P was 53% (SE = 2.9; Fig. 2). This five-fold difference between resorption of N and P was statistically significant ($P < 0.001$; *t*-test) as were the comparisons between N and P resorption in each of the five study years independent of the other years ($P < 0.01$; *t*-tests).

Green, presenescent leaves of *Comptonia* contained approximately 2% N, 0.08% P, 3 $\mu g\ g^{-1}$ Cu, and 20 $\mu g\ g^{-1}$ Zn (Table 1). Senesced leaves contained only 1.8% N, 0.04% P, 2 $\mu g\ g^{-1}$ Cu, and 18 $\mu g\ g^{-1}$ Zn. On a mass per unit area basis, presenescent *Comptonia* leaves contained more than 160 $\mu g\ cm^{-2}$ N and less than 1 $\mu g\ cm^{-2}$ Cu and Zn (Table 1). Nutrient content in senesced leaves ranged from 142 $\mu g\ cm^{-2}$ N to 0.02 $\mu g\ cm^{-2}$ Cu. Resorption values calculated from data in Table 1 will differ slightly from values reported throughout this paper because of numeric information lost during rounding. This is especially true for Cu and Zn because of the inherently low numeric values of their concentration and content in *Comptonia* leaves.

Resorption of N varied from a high of slightly more than 20% in 1988 to a low of 5% in 1989 (Fig. 3). Analysis of variance indicated that N resorption varied among years ($P = 0.009$), yet the Tukey HSD test failed to classify N resorption as statistically different between any specific pairs of years. Although the combination of a significant ANOVA coupled with a multiple means comparison indicating a lack of significance between pairs of means is relatively rare and quite incongruous, it is statistically possible (P. Fleury and J. Heltshe, personal communication). The less conservative Duncan's multiple means comparison indicated that N resorption varied significantly among years. Resorption was significantly higher in 1984 and 1988 than in 1985, 1987, and 1989 ($P < 0.05$). Resorption of P also varied markedly among years ($P < 0.001$; ANOVA) and ranged from 71% in 1988 to 40% in 1985 (Fig. 3). Resorption of P was significantly higher in 1988 than in 1984, 1985, or 1987 ($P < 0.05$; Tukey HSD test).

Resorption of the two trace metals was particularly variable among years (Fig. 3), but variance within years

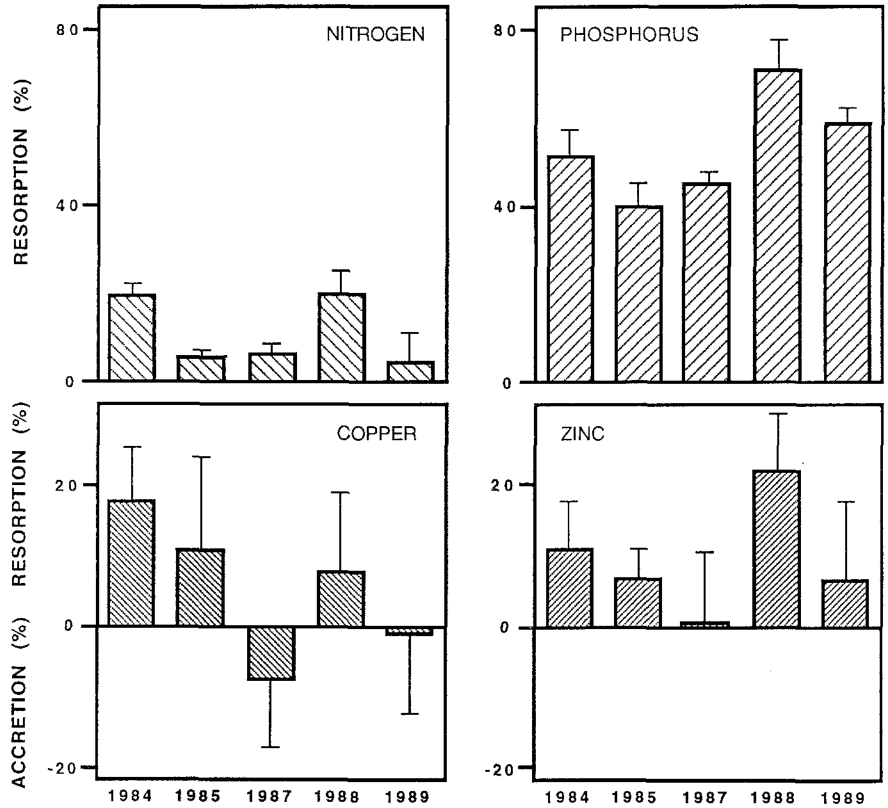

Fig. 3. Mean resorption and accretion of nitrogen, phosphorus, copper, and zinc in five *Comptonia peregrina* genets in each of the five years of study. Vertical bars represent one standard error of the mean; $n=5$

was so high that differences in Cu and Zn resorption among years were not statistically significant ($P>0.05$; ANOVA). Copper was the only element studied in which mean temporal changes during senescence varied from effluxes in some years (i.e. resorption in 1984, 1985, and 1988) to influxes in others (i.e. accretion in 1987 and 1989). Mean values for change in foliar Cu during senescence ranged from 18% resorption in 1984 to more than 1% accretion in 1989. Yearly mean net fluxes in foliar Zn were always effluxes and varied from 22% in 1988 to less than 1% in 1987.

Mean resorption of N over the five years of study differed by as much as a factor of 2.5 among individual genets of *Comptonia* (Fig. 4). Variance around the mean of each genet was high indicating substantial changes in resorption among years for each genet. For example, the two genets that had the highest N resorption in 1985 (SF2 and SF3) also were the only two genets to accrete N in 1989. Mean resorption of P differed by a factor of only 1.3 among genets and was less variable than N resorption (Fig. 4). Phosphorus was always resorbed, and never accreted in individual genets.

Variation in foliar flux of Cu and Zn was also considerable among genets. For example, even though mean net fluxes of foliar Zn were effluxes in every year (Fig. 3), one or more genets accreted Zn in every year. However, whether a specific genet resorbed or accreted Zn was not entirely consistent among years. Net changes of foliar Zn in genet SF3 were 36% accretion, 33% resorption, and 35% accretion in the years 1987, 1988, and 1989, respectively. Changes in foliar Cu also varied between resorption and accretion among individual genets. In all years there were genets that resorbed Cu, and those that accreted Cu. In 1984, genet SF4 was the least conservative with its Cu (1% accretion) of all genets, yet in 1987 when all other genets accreted Cu into their senescing leaves, SF4 resorbed 22% of its foliar Cu.

Even though differences in resorption of N and Zn among individual genets were not statistically significant when years were used as pseudoreplicates ($P>0.05$;

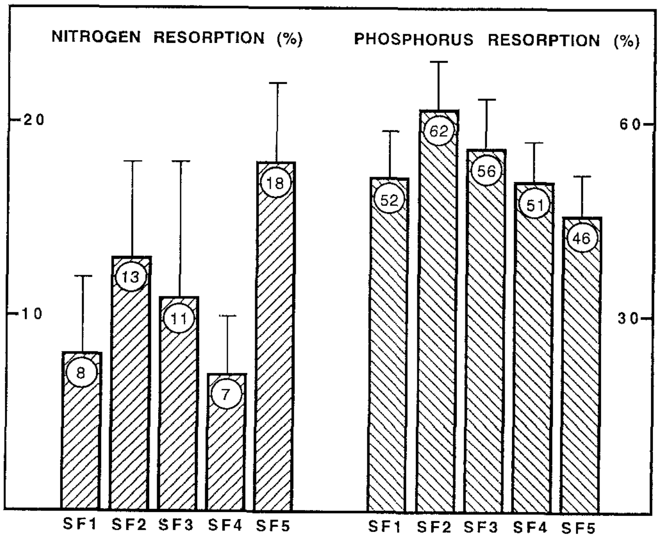

Fig. 4. Mean resorption of nitrogen and phosphorus in individual genets of *Comptonia peregrina* (SF1-SF5) during five years of study. Vertical bars represent one standard error of the mean; $n=5$

ANOVA), genets differed in the concentration of N in their senesced leaves during the study years ($P=0.011$; ANOVA). Genet SF2 produced senesced leaves with lower N concentrations than SF1, SF3, and SF5 ($P<0.05$; Tukey HSD test). It accomplished this with a high degree of consistency among years (Table 2). Genet SF1 had the highest, or second highest concentrations of N in senesced leaves in four of the five study years. Concentrations of Zn in senesced leaves also differed among genets ($P=0.003$; Kruskal-Wallis). Genet SF5 produced senesced leaves with lower Zn concentration than any other genet in four of five years, and had the second lowest Zn concentration in the remaining year (Table 2). Genets SF1 and SF4 had collectively higher Zn concentrations in their senesced leaves than any other genets in four of five years.

In 1989, resorption of N, P, Cu, and Zn in the five primary genets was not statistically different from resorption of the same nutrients in ten additional *Comptonia* genets located >600 m away ($P>0.05$; *t*-test). Correlation analysis using data from all 15 genets sampled in 1989 indicated significant relationships in resorption among N, Cu, and Zn (Fig. 5). Resorption of N was positively correlated with resorption of both Cu ($r=0.884$; $P<0.001$; Pearson product-moment correlation) and Zn ($r=0.706$; $P<0.001$). Resorption of Cu was also positively correlated with resorption of Zn ($r=0.838$; $P<0.001$). Resorption of P, however, was not significantly correlated with resorption of any of the other three nutrients ($P>0.05$).

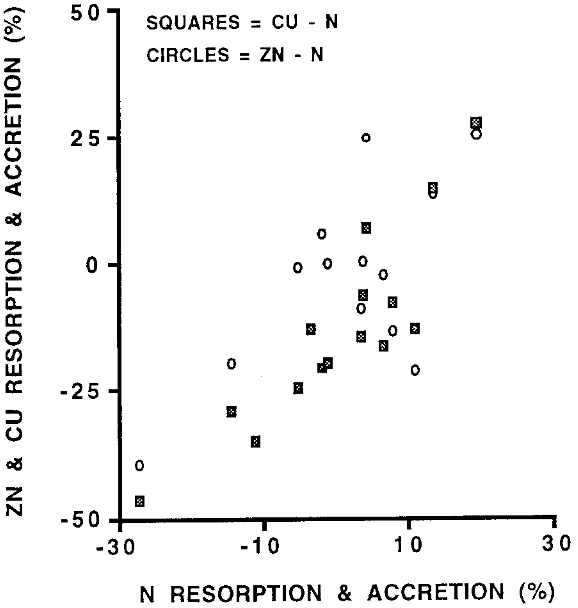

Fig. 5. Resorption and accretion of nitrogen (N) compared with resorption and accretion of copper (Cu) and zinc (Zn) in 15 genets of *Comptonia peregrina* in 1989. Resorption is represented by positive numbers and accretion is represented by negative numbers

Discussion

Inefficient resorption of nitrogen

The vast majority of deciduous plants appear to have the ability to resorb 50% or more of their foliar N before autumnal abscission. Resorption of N averaged 52% for 36 plant species listed by Chapin and Kedrowski (1983) and ranged from 52–81% in 25 species listed by Rippel (1921). Extremely inefficient resorption of N (<25% recovery of foliar N) can occur (Killingbeck 1988; Killingbeck 1992), but the occurrences of such inefficiency have been short-term episodic events, rather than long-term consistent patterns, since the species involved resorbed large amounts of N in some years (Killingbeck et al. 1990; Killingbeck in press). The only plant species in which resorption of N has previously been documented to be consistently low is *Alnus glutinosa* (Dawson and Funk 1981; Rodriguez-Barrueco et al. 1984; Côté and Dawson 1986; Côté et al. 1989), an actinorhizal N fixer (Schwintzer and Tjepkema 1990). Additionally, *Alnus* species in general are known to produce N-rich litter (Turner et al. 1976; Gorham et al. 1979) and therefore may also be inefficient at resorbing N.

Consistent, long-term inefficient resorption of N in *Comptonia peregrina* (Fig. 1, 2), another actinorhizal N fixer, suggests the possibility that actinorhizal N fixers in general do not resorb large amounts of N from their senescing foliage. Further support for this possibility comes from the fact that the actinorhizal species *Myrica pensylvanica* and *Elaeagnus umbellata* also resorb below-normal amounts of N (Killingbeck personal observation, *Myrica* and *Elaeagnus*; Côté et al. 1989, *Elaeagnus*). The only exception to this generality I am aware of is a report of relatively high N resorption (62%) in *Alnus crispa* (Chapin and Kedrowski 1983).

The apparent relatedness of N fixation and N resorption in these actinorhizal species may prove significant to the unresolved question of whether resorption of a nutrient can be related to the availability of that nutrient. If nutrient resorption and availability are not related, then N-rich actinorhizal species such as *Comptonia* would be expected to resorb N as efficiently as other deciduous perennials. Because N resorption in *Comptonia* was consistently inefficient (Fig. 2, 3), we are left to conclude that

Table 2. Rank-order relationships among five *Comptonia peregrina* genets (SF1-SF5) based on differences in nitrogen and zinc concentration in senesced leaves. Statistical significance of differences among genets during five years of study are indicated by ANOVA and Kruskal-Wallis probabilities

	Nitrogen	Zinc
1984	SF1>SF4>SF5>SF3>SF2	SF1>SF4>SF3>SF2=SF5
1985	SF1>SF4=SF5=SF3>SF2	SF4=SF1>SF3>SF2>SF5
1987	SF4>SF1>SF5>SF3>SF2	SF4>SF3>SF1>SF2>SF5
1988	SF1>SF3>SF5>SF4>SF2	SF1>SF4>SF2>SF5>SF3
1989	SF3>SF5>SF1>SF4>SF2	SF1>SF4>SF3>SF2=SF5
1984–89	ANOVA; $P=0.011$	Kruskal-Wallis; $P=0.003$

resorption and availability of N are likely related, or that actinorhizal N fixers such as *Comptonia* are physiologically inept at resorbing nutrients. In light of the fact that resorption of P in *Comptonia* during the five years of the present study was highly efficient (Fig. 2), the latter conclusion can be rejected. Rodriguez-Barrueco et al. (1984) also found a similar, but less extreme, difference between N and P resorption efficiency in *Alnus glutinosa* (14% and 37%, respectively).

An additional hypothesis previously proposed to explain inefficient N resorption in *Alnus glutinosa* suggested that "... high levels of tissue nitrogen in alders, due to symbiotic nitrogen fixation, may in some way directly or indirectly interfere with the processes of autumnal leaf senescence ..." (Dawson and Funk 1981). The implication is that a delay in leaf senescence, possibly mediated by cytokinins (Dawson and Funk 1981), caused low N resorption. Côté and Dawson (1986) refined this general hypothesis by suggesting that observed delays in senescence allowed *Alnus* foliage to be exposed to a hard frost which preempted normal senescence and N resorption. *Comptonia*, like *Alnus*, retains its leaves longer in the autumn than most of its competitors, yet delayed senescence coupled with frost-induced damage in leaves of any species would be expected to preempt the resorption of all nutrients, not just N. The large-scale discrepancy between N and P resorption in *Comptonia* (Fig. 2) and *Alnus glutinosa* (Rodriguez-Barrueco et al. 1984) suggests that delayed senescence is not a primary cause of inefficient N resorption in actinorhizal N fixers.

It seems clear that there has been an evolutionary tradeoff between N fixation and efficient resorption of N in *Comptonia*. Although it is possible that the ability to fix N, and the inability to efficiently resorb N are coincidentally juxtaposed in actinorhizal plants, that possibility seems remote given the fact that consistent, inefficient resorption of N is known to exist only in species which fix N, and that resorption of other nutrients, such as P, is consistent and highly efficient in *Comptonia*.

Variability in resorption among years

The degree to which nutrient resorption varies among years is poorly known because of the paucity of long-term resorption data. In *Comptonia*, resorption of N and P varied markedly among years (Fig. 3). Interyear variance in resorption of N and P was statistically significant in a three-year study of *Populus tremuloides* (Killingbeck et al. 1990), but was not statistically significant in a four-year study of *Quercus ilicifolia* (May and Killingbeck 1992). Variance in resorption of Cu and Zn in *Comptonia* was also evident among years, but extremely high intergenet variance within years precluded statistical significance in interyear comparisons (Fig. 3). Copper resorption did not differ statistically among years in the *Populus* study (Killingbeck et al. 1990; Zn was not resorbed), but did differ significantly among years in the *Quercus* study, as did Zn resorption (May and Killingbeck 1992).

Resorption of a nutrient in any given year can be much lower than a plant's physiological potential to resorb that nutrient (Killingbeck et al. 1990). Therefore, it is possible that the interyear differences in resorption observed in *Comptonia* were due to yearly fluctuations in one or more environmental parameters that reduced resorption efficiencies below their potential maximum in some, or all years. It is also conceivable, but purely speculative, that interyear differences in resorption of N were linked to fluctuations in the synthesis of fixed N. In a study on *Alnus glutinosa* seedlings, foliar N concentrations in nodule-free, non-N fixing plants did not decrease during senescence (Côté et al. 1989). However, because foliar N concentration would remain constant if an efflux of foliar N were accompanied by a proportional efflux of other leaf constituents, net resorption of N may have occurred even though N concentration remained constant. The possibility of a link between N resorption efficiency and rates of N fixation in *Comptonia* remains intriguing enough to warrant testing.

Variability in resorption among genets

"The genetic uniqueness of individuals has important ecological consequences" (Lomnicki 1988), yet for a process such as resorption which occurs only once per year, it is inherently difficult to determine whether resorption differs significantly among individuals (i.e. uniqueness of individuals) because of a lack of statistical variance within one year for an individual. Data from multiple years improve the chances of discerning individual differences, yet environment-induced interyear variance and the vagaries of pseudoreplication (Hurlbert 1984) pose interpretational problems.

During the five years of the *Comptonia* study, resorption varied markedly among individual genets (e.g. Fig. 4), but the patterns in percent resorption among individuals were not consistent from year to year (see Results). There was no individual genet that consistently had the highest or lowest resorption efficiencies for any nutrient throughout the study. However, the relative ability of a genet to reduce N and Zn in its senescing leaves to higher or lower levels than its neighboring genets was highly consistent from year to year (Table 2). The relative importance of this finding regarding patterns of intergenet differences in resorption remains somewhat obscure because the concentration of a nutrient in senesced leaves is not a direct measure of resorption efficiency, and because it is a reflection of both a plant's ability to resorb that nutrient and the concentration of that nutrient in unsenesced foliage. Given the fact that intragenet ramets vary in their resorption abilities (Killingbeck et al. 1990), it seems reasonable to suspect that individual genets may also differ in their resorption abilities. The *Comptonia* data, however, do not provide unequivocal evidence that one genet is inherently better than another when growing in a common environment.

Interrelatedness among resorption efficiencies of different nutrients

A high degree of correlation between the resorption efficiencies of different nutrients in senescing *Comptonia* leaves indicates a coupling in nutrient flux patterns (Fig. 5). Even though during resorption it appears that "the time at which leaves become capable of exporting mobile nutrients may be governed by a separate factor for each nutrient ..." (Hill 1980), resorption and accretion of N, Cu, and Zn in *Comptonia* were highly related. For at least some pairs of nutrients then, patterns in resorption are influenced by 1) similarities in response to ecophysiological factors which control resorption, 2) internutrient cause: effect relationships, or 3) both. The fact that resorption and accretion of N were coupled with that of Cu and Zn in *Comptonia* also supports previous speculation suggesting the possibility of a degree of interrelatedness between trace metals and macronutrient resorption (Killingbeck 1985; Killingbeck 1992).

Conversely, N and P resorption were not linked in *Comptonia* nor in three marsh graminoids studied by Shaver and Melillo (1984). In *Comptonia*, not only were significant correlations between N and P resorption absent in 15 genets studied in 1989, but the ratio of P resorption to N resorption varied from 2.6–12.1 among the five study years. Such pattern divergence indicates a high degree of autonomy in the resorption of these two important macronutrients.

Conclusions

The ecological literature is packed with conflicting conclusions regarding the relationship, or lack thereof, between resorption efficiency and plant nutrient status. Two quotations are offered as examples: 1) "... we found no evidence that N resorption efficiency was related to plant nutrient status." (Chapin and Moilanen 1991), and 2) "Our data show that the amount of nutrient resorbed and the efficiency of the resorption process depend on plant nutrient and water status ..." (Pungnaire and Chapin 1992). The ecophysiological tradeoffs in *Comptonia* which have resulted in the co-occurrence of actinorhizal N fixation, inefficient N resorption, and efficient P resorption suggest that plant nutrient status does have an impact on resorption efficiency and that the evolution of nutrient conservation strategies is nutrient-specific.

It has recently been suggested that nutrient conservation/acquisition processes may form a "shifting, complementary complex of nutrient conservation adaptations" on which selection has acted collectively, rather than individually (Killingbeck and Costigan 1988). If this is true, then it is possible that resorption is always related to plant nutrient status, but that selection for efficient resorption may be preempted by selection for alternative strategies that act to conserve or acquire a nutrient. Resorption may appear to be unrelated to nutrient status in short-term fertilization experiments, and indeed it may be in the proximate sense. However, since resorption is directly related to evolutionary fitness (May and Killingbeck 1992) and serves primarily as a nutrient conservation strategy, the lack of a relationship between resorption and plant nutrient status would be surprising.

In the nutrient poor environments that species such as *Comptonia* and *Alnus* routinely colonize, the evolution of N fixation may have reduced the need for efficient resorption of N while not diminishing the selection potential for resorption of P. Given the fact that N acquisition strategies are likely to be complementary to some degree (Gutschick 1981) and that the controls that regulate demand for N are highly integrative (Gutschick 1981), a theory for the integrated evolution of fixation and resorption in actinorhizal N fixers seems to have some merit. The continued interest in understanding ecological tradeoffs (Aerts 1990; Tilman 1990) and the inherent importance of N fixation (Okon and Hardy 1983) and nutrient resorption (Chapin et al. 1990) make actinorhizal N fixers valuable organisms for further study.

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