Alpine Landscape Variation in Foliar Nitrogen and Phosphorus Concentrations and the Relation to Soil Nitrogen and Phosphorus Availability

Authors: Bowman, William D., Bahn, Leslie, and Damm, Mary

Source: Arctic, Antarctic, and Alpine Research, 35(2) : 144-149

Published By: Institute of Arctic and Alpine Research (INSTAAR), University of Colorado

URL: https://doi.org/10.1657/1523-0430(2003)035[0144:ALVIFN]2.0.CO;2

Arctic, Antarctic, and Alpine Research, Vol. 35, No. 2, 2003, pp. 144–149

Alpine Landscape Variation in Foliar Nitrogen and Phosphorus Concentrations and the Relation to Soil Nitrogen and Phosphorus Availability

*William D. Bowman,**
Leslie Bahn,† and
Mary Damm‡

*Mountain Research Station,
Institute of Arctic and Alpine Research
and Department of Environmental,
Population, and Organismic Biology,
University of Colorado, Boulder,
Colorado 80309-0334, U.S.A.
bowman@spot.colorado.edu
†Earth and Environmental Sciences,
Columbia University, P.O. Box 1000,
Palisades, New York 10964, U.S.A.
‡University of Colorado Museum,
Museum Field Studies Program, Boulder,
Colorado 80309-0218, U.S.A.

Abstract

We tested the hypothesis that foliar nitrogen and phosphorus concentrations are correlated with estimates of soil nutrient supply, a common assumption in studies of plant nutrient relations. This hypothesis was tested in an alpine ecosystem characterized by a wide range of soil nutrient availabilities using 3 herbaceous plants with widespread distributions. Rates of soil N and P supply were estimated using ion exchange resin bags deployed during the first half of the growing season, when the majority of plant nutrient uptake occurs. Measurements were made at 3 to 5 landscape positions (vegetation types) at 3 sites: a valley bottom that was glaciated until 12,000 yr ago and 2 ridgetop sites, 1 with deposits of Tertiary age and 1 that was not glaciated during the Pleistocene. Foliar N and P concentrations generally were not correlated with rates of soil N and P supply. We present several hypotheses to explain the lack of a correlation between soil N and P supply and foliar N and P concentrations, most notably the probable buffering between soil nutrient supply and foliar nutrient concentrations by belowground nutrient storage in plants and the use of organic N by plants. Foliar N:P ratios reflected the specific nutrient limitation of production for 1 of the 3 study species. Rates of soil N supply were associated with landscape position, indicating that microclimatic and/or plant species effects were the most important controls over spatial variation in N supply. Rates of P supply differed significantly among valley and ridge locations, but not with landscape position. Soil age and eolian deposition of dust probably differ between these collection sites and may explain the differences in soil P supply. These results suggest that caution should be used in estimating soil fertility and specific nutrient limitations of growth based on foliar nutrient concentrations in herbaceous communities.

Introduction

Variation in the supply of nutrients to plants in terrestrial ecosystems may result from numerous factors, including variation in microclimate; soil type, texture, and age; and plant effects on the quality of soil organic matter (Jenny, 1980; Burke, 1989; Hobbie, 1992; Vitousek et al., 1993). Individual plant species may respond to variation in nutrient supply by varying growth rates if that nutrient is limiting, resulting in relatively invariant foliar nutrient concentrations across environmental gradients. Alternatively, plants may take up nutrients in excess of the amount needed for growth, a process sometimes referred to as "luxury consumption" (Chapin, 1980), or nutrient uptake may not be diluted by growth owing to morphological constraints on the amount of vegetative development that can occur (e.g., Diggle, 1997; Bret-Harte et al., 2001). The latter two possibilities would result in a positive correlation between nutrient supply and foliar concentrations and would permit the use of foliar nutrient measurements as a proxy for soil nutrient supply, which is a common assumption in studies of plant nutrient relations (e.g., Aerts, 1996).

The relationship between soil nutrient supply and foliar concentration of a single nutrient may be influenced by the ratios of 2 or more potentially limiting nutrients. Nitrogen (N) and phosphorus (P) are the most common nutrients limiting growth of plants in terrestrial ecosystems (Vitousek and Howarth, 1991). Measurement of the foliar ratios of their concentrations has been suggested as a method for estimating which of the nutrients limits plant growth (Vitousek et al., 1988; Aerts et al., 1992, Koerselman and Meuleman, 1996; Aerts and Chapin, 2000), and several studies have demonstrated a good empirical relationship between N and P availability and foliar and root N:P ratios (e.g., Walbridge, 1991; Vitousek et al., 1995; Carreira et al., 1997). The use of foliar N:P ratios to determine N and P limitation of production assumes that luxury consumption of the nonlimiting nutrient will occur and/or that the capacity of the plant to increase growth will match the rate of increased supply of the limiting nutrient.

In this paper we examine the relationship between landscape variation in N and P supply and foliar N and P concentrations in 3 widespread alpine plant species. Topographic heterogeneity is substantial in the alpine and determines variation in winter snow accumulation. Variation in snow depth in turn is correlated with variation in soil microclimate, the amount of vegetative cover, plant community types, and nutrient cycling (Walker et al., 1993; Stanton et al., 1994; Fisk et al., 1998). Fertilization experiments indicate that N and P supply are important constraints on primary production in the alpine and that luxury consumption occurs in some species in response to greater N and P supply (Bowman et al., 1993, 1995; Bowman, 1994; Lipson et al., 1996). Limited comparisons between alpine plant communities differing in fertility indicate that a positive correlation may exist between foliar nutrient concentrations and soil N and P supply (Bowman et al., 1993; Bowman, 1994). Thus, we hypothesized that foliar N and P concentrations would correlate positively with N and P supply, respectively. We also examined whether the foliar N:P ratios varied across the alpine landscape within a species and among our study species, and how well this ratio reflected the specific nutrient limitation of production in our study species.

We examined the correlations between soil N and P supply and foliar N and P concentrations in ridge and valley locations to determine

1523-0430/03 $7.00

whether geomorphological factors influence these relationships. Our valley site was glaciated until approximately 12,000 yr BP, while the ridge sites were not glaciated during the Pleistocene but have surficial deposits of potentially different ages (Madole, 1982). Valley- versus ridge-site differences may reflect differences in soil ages and/or eolian dust deposition. Thus, N and P biogeochemistry may be significantly different at these sites, independent of variation in microtopography.

Materials and Methods

STUDY SITES

We selected 3 sites on or adjacent to Niwot Ridge, Colorado, to examine the relationship between soil N and P supply and foliar N and P concentrations. A site within the Green Lakes Valley, north of Green Lake 4 and south of Niwot Ridge at 3550 m a.s.l., was selected to represent a valley bottom. This site (hereafter referred to as the "valley site") was glaciated until 12,000 yr BP (Harbor, 1984; Caine, 2001) and has the youngest soils of our study sites. We also used 2 ridgetop sites on Niwot Ridge. One (hereafter referred to as the "D1 site") is near the D1 climate station at 3700 m a.s.l. and is covered with diamicton, a deposit of poorly sorted materials containing a range of particle sizes (Madole, 1982). Although these deposits were formerly attributed to a morainal deposit from the early Pleistocene, it is likely that they are derived from alluvial and colluvial deposits of Tertiary age (Madole, 1982). The third site (hereafter referred to as the "Saddle site") was east of the Saddle research site on Niwot Ridge, at 3500 m a.s.l.. This site contains soils that have not been subject to glacial disturbance. The ages of the soils at the 2 Niwot Ridge sites are uncertain, but are probably early Pleistocene or older, and have been subject to significant periglacial mixing (Burns, 1980). Burns (1980) described the soils of Niwot Ridge and the Green Lakes Valley as Cryochrepts and Cryumbrepts, derived from Precambrian granites.

PLANT AND SOIL COLLECTION AND ANALYSIS

At each study site, estimates of soil N and P supply and plant collections were made during the 1999 growing season within 1-m^2 plots in 3 to 5 plant communities, representing repeated landscape units (Walker et al., 1993). Fellfields occur in windswept areas with minimal winter snow cover and are dominated by cushion plants, dry meadows have low snow cover and are dominated by *Kobresia myosuroides* (Vill.) Fiori & Paol., and moist meadows have snowpacks between 0.5 and 2 m of winter snow and are dominated by *Deschampsia caespitosa* (L.) P. Beauv. and *Acomastylis rossii* (R Br.). Wet meadows have variable snow cover, are characterized by flat topography and poor soil drainage, and are dominated by *Carex* species. Snowbeds receive the highest snow cover (2 to 5 m) and are dominated by *Sibbaldia procumbens* (L.). Within each of the 3 study sites, 2 to 7 separate plant and soil collections were made within each of the community types, for a total of 45 sampling locations. Snowbed and fellfield sites were not present in the valley-bottom site.

Rates of soil N and P supply were estimated using ion exchange resin bags (Binkley and Matson, 1983), which provide an index of plant-available inorganic nutrients (Binkley and Vitousek, 1989) and combine the effects of both the production and movement of the nutrients in the soil. Mixed-bed ion exchange resins (J. T. Baker, IONAC NM-60 H^+/OH^-) were placed in fine mesh nylon bags, surrounded by a plastic cylinder (4.9 cm^2, ca. 25 mm height) to maintain a rigid structure in the soil. Four bags were placed in the soil within 1-m^2 plots at each of the collection locations. The bags were inserted into the soil at a depth of 7 cm, the zone of maximum root density, by removing a plug of intact soil and sod and inserting the resin bags into the soil at the edge of the hole in such a manner that the column of soil above the bag remained undisturbed. The resin bags were deployed within each community at the start of the growing season (early to late June, as soon as snow melted from the sites) and were removed after 23 to 34 d, the period of time when the majority of plant nutrient acquisition occurs (Theodose et al., 1996; Jaeger et al., 1999). A subset of resin bags was used as blanks. Within 4 h of collection in the field the resin bags were brought back to the lab, composited into a single sample per collection location, and extracted with 2 N KCl. The extractant was analyzed for NH_4^+, NO_3^-, and PO_4^{2-} using a Lachat colorimetric autoanalyzer (Milwaukee, Wisconsin, U.S.A.). The rates of inorganic N and P supply were estimated as the amount of nutrient per bag d^{-1}. Although nitrification of NH_4^+ on the resins has been suggested to be negligible (Binkley, 1984), we chose to report only total inorganic N as the sum of $NH_4^+ + NO_3^-$ to avoid any problems associated with microbial transformations during the 3- to 4-wk period that the resins were in the field.

At each collection location, 2 to 4 leaves from 4 plants of each of 3 widespread alpine species were collected and composited. The species were *Acomastylis rossii*, *Artemisia scopulorum* Gray, and *Bistorta bistortoides* (Pursh) Small, all perennial herbs. Leaves were collected from plants at the same phenological stage, approximately 3 wk after leaf emergence. Although these species are found in each of the communities sampled, not all of them were present at some of the collection locations. Thus, replication within a community type within a site varied from 1 to 7. The leaf material was dried to constant mass at 70°C, ground, digested, and analyzed for P and total Kjehldahl N using a Lachat autoanalyzer.

STATISTICAL ANALYSES

The relationships between soil N and P supply and foliar N and P concentrations in the 3 study species were examined using Pearson correlation analysis. Variations in soil N and P supplies related to landscape position (vegetation type) and site (valley, D1, and Saddle) were analyzed using analysis of variance, with landscape position and sampling site as class variables. Tukey's *a posteriori* test for differences among the means was used if a significant result was found for the analysis of variance. A two-way analysis of variance was run for the dry, moist, and wet meadows at all 3 sampling sites to determine whether significant interactions between landscape position and sampling site influenced N and P supply. Because fellfield and snowbed communities were not present in the Green Lakes Valley, it was not possible to analyze the interaction term between landscape position and sampling site for all landscape positions. In addition, the relationship between foliar N and P concentrations within each species was analyzed using Pearson correlation analysis, and the variation in N:P ratios associated with landscape position for each species was analyzed using analysis of variance.

Results

Rates of soil N and P supply varied greatly among collecting locations, approximately 10-fold for inorganic N (6.7 to 68.9 μg N bag^{-1} d^{-1}), and 100-fold for P (0.017 to 2.37 μg P bag^{-1} d^{-1}). Rates of N supply were significantly related to vegetation type (landscape position), with significantly higher rates in moist and wet meadows and snowbeds relative to dry meadows and fellfields ($F = 14.59$, $P < 0.001$, Fig. 1a). Sampling sites (valley bottom, ridgetop) did not significantly influence rates of N supply ($F = 1.261$, $P = 0.294$, Fig. 1a), but rates of P supply were significantly related to sampling site ($F = 3.74$, $P < 0.05$, Fig. 1b). Rates of P supply were higher on the diamicton on Niwot Ridge than at the valley site and were intermediate in the unglaciated soils on the eastern part of Niwot Ridge. Landscape position did not influence rates of P supply ($F = 1.307$, $P = 0.284$). There were no significant

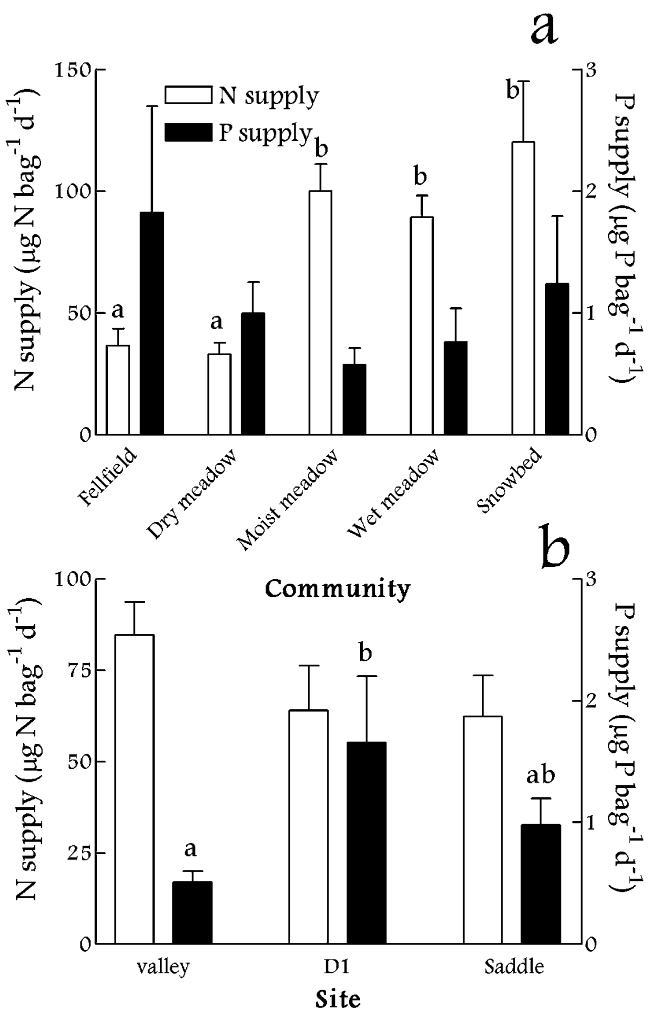

FIGURE 1. Variation in N and P supply on Niwot Ridge and the Green Lakes Valley, Colorado, estimated using ion exchange resin bags, at the landscape scale as indicated by vegetation types (averaged across all sampling sites) (a), and at different sampling sites (averaged across all vegetation types) (b), representing a valley glaciated 12,000 yr BP (valley), a ridge site covered by a Tertiary age diamicton (D1), and unglaciated soils on the eastern part of the ridge (Saddle). Letters indicate significant differences as determined by a Tukey's multiple range test.

interactions between landscape position and sampling site influencing N and P supply rates.

Variation in foliar N and P concentrations for the 3 herb species was less than that for soil N and P supply. There was a significant positive correlation between N supply and foliar N concentrations only for *Acomastylis* (Fig. 2a), and the slope of the relationship was relatively shallow. Similarly, foliar N varied significantly in relation to landscape position only for *Acomastylis* ($F = 3.75$, $P < 0.01$, data not shown). Foliar P concentrations were not related to soil P supply when analyzed using both linear and logarithmic scales (Fig. 2b), nor were foliar P concentrations related to the sampling sites, despite significant variation in P supply.

Foliar N and P concentrations were significantly correlated for *Acomastylis* and *Bistorta* but not for *Artemisia* (Fig. 3). *Artemisia* had greater N:P ratios than the other 2 species ($F = 15.06$, $P < 0.001$; mean ± s.e.: 12.91 ± 0.31 for *Acomastylis*, 17.78 ± 1.04 for *Artemisia*, and 14.54 ± 0.40 for *Bistorta*). Landscape position was not a significant source of variation for N:P ratios in any of the species, but sampling site was significantly related to N:P ratios in *Acomastylis*, with the valley site exhibiting higher ratios than the sites on Niwot Ridge (data not shown).

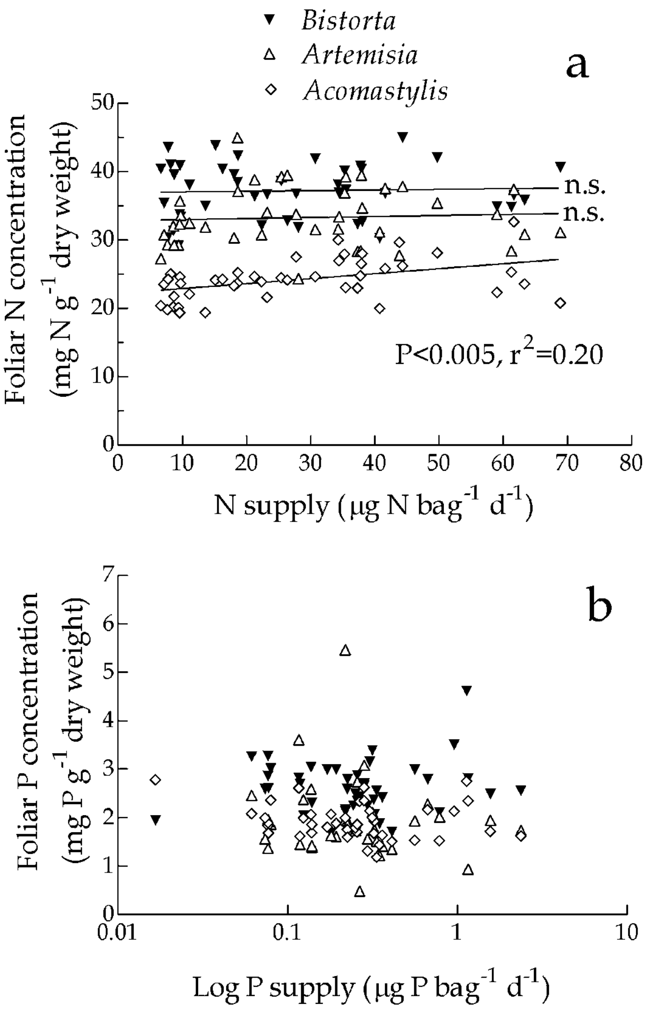

FIGURE 2. Relationships between estimates of (a) soil N supply and foliar N concentrations and (b) the log soil P supply and foliar P concentrations, for 3 widespread alpine species, Bistorta bistortoides *(▼),* Artemisia scopulorum *(△), and* Acomastylis rossii *(◇). Correlations were not significant except for Acomastylis N concentrations and soil N supply. Correlations between foliar P concentrations and P supply on a linear scale were also not significant.*

Discussion

Foliar N and P concentrations of the 3 study species were poor indicators of soil N and P supply, as estimated by ion exchange resin bags. Only foliar N in *Acomastylis* was correlated with soil N supply, but the amount of variability explained was relatively small (20%). This was unexpected, as previous experiments have demonstrated luxury consumption of N and P in some alpine species after fertilization, and differences in foliar nutrient concentrations have been found for single species occurring in communities characterized by different fertilities (Bowman, 1994; Bowman et al., 1993, 1995). The relatively slow growth of alpine plants (Diggle, 1997; Körner, 1999) along with the ability of the rooting systems to sequester a large fraction of added N in labeling experiments (Theodose et al., 1996; Jaeger et al., 1999) indicate that these plants are likely to show a correlation between soil nutrient supply and foliar nutrient concentrations.

Why didn't foliar N and P concentrations reflect variation in soil N and P supplies? Several factors may have influenced the relationship

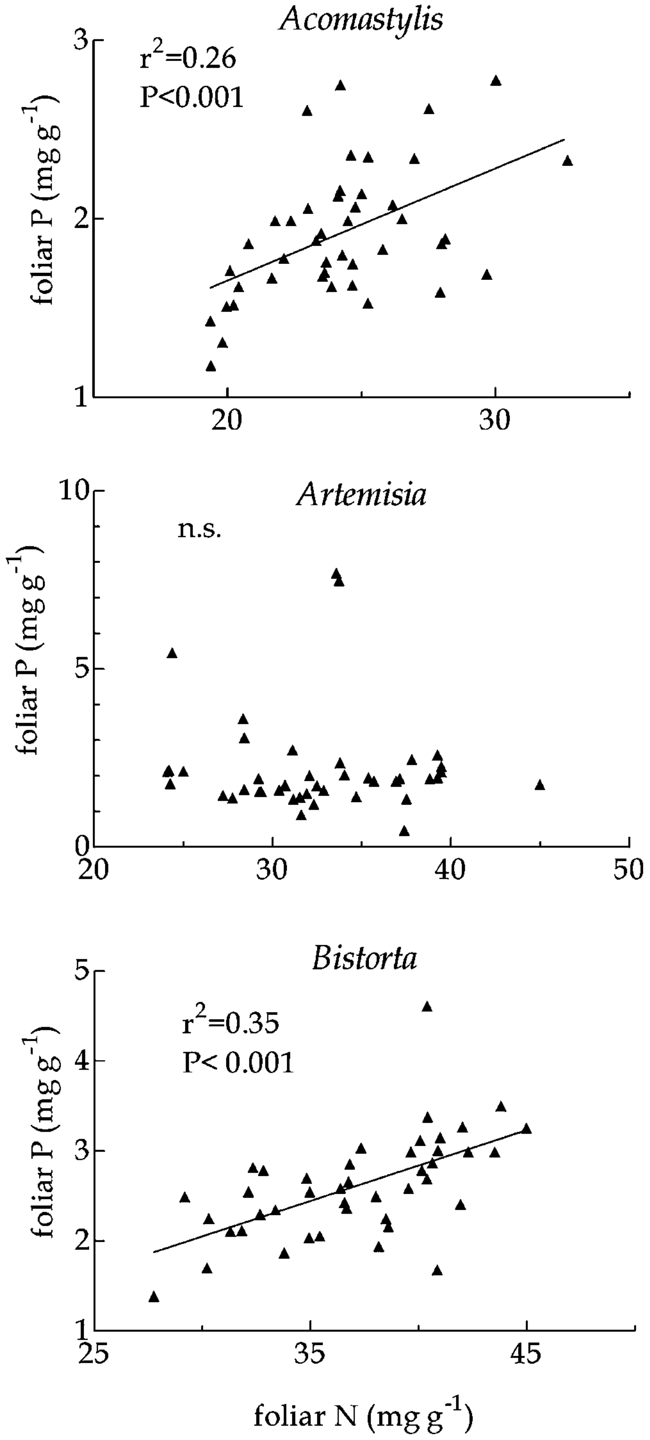

FIGURE 3. Relationships between foliar N concentrations and foliar P concentrations for 3 widespread alpine species, Bistorta bistortoides*,* Artemisia scopulorum*, and* Acomastylis rossii*. Data were analyzed using Pearson correlation analysis. Note that different scales are used for axes among the species.*

between our estimates of soil N and P supply and foliar N and P concentrations. First, luxury consumption may occur only at relatively high rates of nutrient supply, with higher foliar nutrient concentrations occurring only after belowground storage pools become saturated. Alpine plants are relatively slow growing, and many rely on nutrient storage in belowground tissues for much of their growth demand (Monson et al., 2001). For example, approximately 60% of the current year's N requirement in *Bistorta* is met using belowground reserves (Jaeger and Monson, 1992; Lipson et al., 1996). Belowground storage of nutrients may act to buffer foliar nutrient concentrations from background variation in soil nutrient supply. Lipson et al. (1996) found that rhizome N concentrations accounted for all of the luxury consumption in fertilized relative to control *Bistorta* plants, and that after fertilization 100% of the plant demand was met using stored reserves. Belowground nutrient storage may also minimize potential nutrient losses to herbivores. Second, foliar nutrient concentrations may respond to variation in the ratios of supply of soil nutrients, particularly N:P, rather than variation in the supply of a single nutrient. Our results, however, failed to show significant correlations between N:P supply ratios and variation in either foliar N and P concentrations (data not shown).

A third factor influencing the correlation between inorganic N supply and foliar concentrations is the potential reliance of plants on organic N to meet nutritional demands. Small amino acids such as glycine are relatively abundant in alpine soils and may be an important source of N for plants (Raab et al., 1996, 1999; Miller and Bowman, 2003). Although uptake of glycine appears to occur in most of the alpine plants examined (Miller and Bowman, 2003), there does not appear to be preferential uptake of glycine over inorganic forms of N. There does appear to be differing availability of glycine among alpine communities (Miller 2002), so this factor could contribute to the lack of correlation between inorganic N supply and foliar N concentrations.

Last, it is possible that resin bags may not accurately estimate soil N and P supply. However, the landscape variation we obtained in rates of N and P supply correlates well with variation in N uptake by the total plant community (Bowman, 1994; Fisk et al., 1998), and our resin bag results probably provided a good index of the variability in N supply among our sampling locations. A similar conclusion regarding the use of resin bags to estimate spatial variation in N and P supply was found in the Arctic by Giblin et al. (1994). Thus, we have no reason to suspect errant values for N and P estimates from our resin bags. Although other factors may have influenced the lack of correlation between soil N and P supply and foliar concentrations, we suggest that the most likely reason is the belowground storage of these nutrients by the plants, which buffers variation in leaves in response to variation at low rates of N and P supply, and the potential for organic N use by plants.

The foliar N:P ratios of *Bistorta* and *Acomastylis* suggest that growth of these species is either N or N and P colimited, while *Artemisia* had N:P ratios that suggest that its growth is P limited (Lajtha and Klein, 1988; Koerselman and Meuleman, 1996; Aerts and Chapin, 2000). However, long-term (11-yr) fertilization with high levels of P, N, and N + P (Bowman et al., 1993) failed to increase the cover of *Acomastylis* and *Artemisia*, while *Bistorta* increased significantly in N and N + P plots (Suding and Bowman, unpublished data). Thus, foliar N:P ratios did not provide a good proxy to determine the nutrient limiting growth in these species. This is not surprising given the lack of correspondence between soil N and P supply and foliar N and P concentrations. Alpine plants generally exhibit relatively high foliar N and P concentrations compared with congeneric lowland plants (Körner, 1989; Bowman et al., 1999), and N and P are likely to be positively correlated owing to their combined role in leaf metabolic processes, primarily photosynthesis. The positive correlation between foliar N and P in *Acomastylis* and *Bistorta* suggests that the uptake of these nutrients may be regulated in part by the concentration of both nutrients, rather than by the supply of an individual nutrient. This suggestion is supported by our finding of little change in N:P foliar ratios in our species among landscape and sampling sites, and by the results of Vitousek et al. (1995), who found little variation in foliar N:P ratios in a single tree species among sites with different N and P availabilities.

Variation in the supply of N was related to landscape position, indicating that associated microclimatic (site temperature, moisture, hydrology) or plant species controls are important in determining the rate of N supply. This is consistent with previous work in the alpine that has suggested that at the landscape scale, soil moisture is the most important control on rates of N cycling (Fisk et al., 1998). Significant plant species control on soil N transformations has been found within moist meadow alpine communities (Steltzer and Bowman, 1998), but the contribution of plant species effects to landscape variation in N cycling has not been fully explored in the alpine.

The supply of P was not related to landscape variation but instead was influenced more by site. The highest rates of P supply were found in soils on Niwot Ridge in a Tertiary age deposit, the lowest rates were found in the youngest soils in the Green Lakes Valley, and intermediate rates were found in unglaciated soils on the eastern part of Niwot Ridge. A more thorough analysis of these soils using the Hedley fractionation technique (Cross and Schlesinger, 1995) found a similar trend for indices of plant-available P, although the ranking was saddle < valley < D1 (Townsend et al., unpublished data). The variation in P supply is somewhat consistent with the Walker and Syers (1976) model of P biogeochemistry change during pedogenesis, although other factors could have influenced our result. Eolian deposition of dust contributes significantly to the geochemistry of alpine soils in the Colorado Front Range (Litaor, 1987), and it is possible that differences in the rates of dust deposition among our collection sites contributed to these differences in P supply. Additional measurements of soil age and rates of dust deposition are required to determine the contribution of these factors to the observed differences in P supply, but it is clear that geochemical differences in the soils are more important for determining plant P supply than microclimatic variation associated with landscape variation in topography.

In summary, our research failed to show a strong correlation between foliar N and P concentrations and soil N and P supply. This result suggests that foliar nutrient concentrations should be used with caution as a means of estimating soil nutrient supply in herbaceous species. Likewise, N:P ratios were useful for suggesting a N or P limitation of growth for only 1 of the 3 study species. Finally, microclimatic controls appeared to be most important in determining N supply, while variation in soil geochemistry appeared to best explain variation in P supply at our alpine collection sites.

Acknowledgments

We are grateful for the assistance of Chris Seibold for analyses of the resin extracts and to Trevor Popp for the foliar nutrient analyses. Field logistics were provided by the University of Colorado Mountain Research Station. Amy Miller, Tim Seastedt, Katie Suding, and Alan Townsend provided helpful comments and suggestions on earlier drafts of this manuscript. Funding for this research was provided by the Andrew W. Mellon Foundation and the National Science Foundation through a Research Experiences for Undergraduates site grant and support for the Niwot Ridge Long-Term Ecological Research program.

References Cited

Aerts, R., 1996: Nutrient resorption from senescing leaves of perennials: Are there general patterns? *Journal of Ecology,* 84: 597–608.

Aerts, R., and Chapin F. S., III, 2000: The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Advances in Ecological Research,* 30: 1–67.

Aerts, R., Wallén, B., and Malmer, N., 1992: Growth-limiting nutrients in *Sphagnum*-dominated bogs subject to low and high atmospheric nitrogen supply. *Journal of Ecology,* 80: 131–140.

Binkley, D., 1984: Ion exchange resin bags: factors affecting estimates of nitrogen availability. *Soil Science Society of America Journal,* 48: 1181–1184.

Binkley, D., and Matson, P. A., 1983: Ion exchange resin bag method for assessing forest soil nitrogen availability. *Soil Science Society of America Journal,* 47: 1050–1052.

Binkley, D., and Vitousek, P. M., 1989: Soil nutrient availability. *In* Pearcy, R. W., Ehleringer, J. R., Mooney, H. A., and Rundel, P. W. (eds.), *Plant Physiological Ecology: Field Methods and Instrumentation.* London: Chapman and Hall, 75–96.

Bowman, W. D., 1994: Accumulation and use of nitrogen and phosphorus by following fertilization in two alpine tundra communities. *Oikos,* 70: 261–270.

Bowman, W. D., Theodose, T. A., Schardt, J. C., and Conant, R. T., 1993: Constraints of nutrient availability on primary production in two alpine tundra communities. *Ecology,* 74: 2085–2097.

Bowman, W. D., Theodose, T. A., and Fisk, M. C., 1995: Physiological and production responses of plant growth forms to increases in limiting resources in alpine tundra: implications for differential community response to environmental change. *Oecologia* 101: 217–227.

Bowman, W. D., Keller, A., and Nelson, M., 1999: Altitudinal variation in leaf gas exchange, nitrogen and phosphorus concentrations, and leaf mass per area in populations of *Frasera speciosa. Arctic, Antarctic, and Alpine Research,* 31: 191–195.

Bret-Harte, M. S., Shaver, G. R., Zoerner, J. P., Johnstone, J. F., Wagner, J. L., Chavez, A. S., Gunkelman, R. F., Lippert, S. C., and Laundre, J. A., 2001: Developmental plasticity allows *Betula nana* to dominate tundra subjected to an altered environment. *Ecology,* 82: 18–32.

Burke, I. C., 1989: Control of nitrogen mineralization in a sagebrush steppe landscape. *Ecology,* 70: 1115–1126.

Burns, S. F., 1980: Alpine soil distribution and development, Indian Peaks, Colorado Front Range. Ph.D. dissertation, University of Colorado, Boulder. 360 pp.

Caine, N., 2001: Geomorphic systems. *In* Bowman, W. D., and Seastedt, T. R. (eds.), *Structure and Function of an Alpine Ecosystem.* New York: Oxford University Press, 45–74.

Carreira, J. A., Lajtha, K., and Niell, F. X., 1997: Phosphorus transformations along a soil/vegetation series of fire-prone, dolomitic, semi-arid shrublands of southern Spain—Soil P and Mediterranean shrubland dynamic. *Biogeochemistry,* 39: 87–120.

Chapin, F. S., III, 1980: The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics,* 11: 233–260.

Cross, A. F., and Schlesinger, W. H., 1995: A literature review and evaluation of the Hedley fractionation—Applications to the biogeochemical cycle of soil-phosphorus in natural ecosystems. *Geoderma,* 64: 197–214.

Diggle, P. K., 1997: Extreme preformation in alpine *Polygonum viviparum*: An architectural and developmental analysis. *American Journal of Botany,* 84: 154–169.

Fisk, M. C., Schmidt, S., and Seastedt, T.R., 1998: Topographic patterns of above- and belowground production and nitrogen cycling in alpine tundra. *Ecology,* 79: 2253–2266.

Giblin, A. E., Laundre, J. A., Nadelhoffer, K. J., and Shaver, G. R., 1994: Measuring nutrient availability in arctic soils using ion-exchange resins—a field test. *Soil Science Society of America Journal,* 58: 1154–1162.

Harbor, J., 1984: Terrestrial and lacustrine evidence for Holocene climatic/geomorphic change in the Blue Lake and Green Lakes valleys of the Colorado Front Range. M.A. thesis, University of Colorado, Boulder. 205 pp.

Hobbie, S. E., 1992: Effects of plant species on nutrient cycling. *Trends in Ecology and Evolution,* 7: 336–339.

Jaeger, C. H., and Monson, R. K., 1992: The adaptive significance of nitrogen storage in *Bistorta bistortoides*, an alpine herb. *Oecologia,* 92: 578–585.

Jaeger, C. H., Monson, R. K., Fisk, M. C., and Schmidt, S. K., 1999: Seasonal partitioning of nitrogen by plants and soil microorganisms in an alpine ecosystem. *Ecology,* 80: 1883–1891.

Jenny, H., 1980: *The Soil Resource.* Berlin: Springer-Verlag.

Koerselman, W., and Meuleman, A. F. M., 1996: The vegetation N:P ratio: a new tool to detect the nature of nutrient limitation. *Journal of Applied Ecology,* 33: 1441–1450.

Körner, Ch., 1989: The nutritional status of plants from high altitudes. *Oecologia,* 81: 379–391.

Körner, Ch., 1999: *Alpine Plant Life—Functional Plant Ecology of High Mountain Ecosystems.* Berlin: Springer. 338 pp.

Lajtha, K., and Klein, M., 1988: The effect of varying nitrogen and phosphorus availability on nutrient use by *Larrea tridentata*, a desert evergreen shrub. *Oecologia,* 75: 348–353.

Lipson, D. A., Bowman, W. D., and Monson, R. K., 1996: Luxury uptake and storage of nitrogen in the rhizomatous alpine herb, *Bistorta bistortoides*. *Ecology,* 77: 1277–1285.

Litaor, M. I., 1987: The influence of eolian dust on the genesis of alpine soils in the Front Range, Colorado. *Soil Science Society of America Journal,* 51: 142–147.

Madole, R. F., 1982: Possible origins of till-like deposits near the summits of the Front Range in north-central Colorado. U.S. Geological Survey Professional Paper 1243. 31 pp.

Miller, A. E., 2002: Uptake of organic and inorganic nitrogen by alpine tundra plants. Ph.D. thesis, University of Colorado, Boulder. 104 pp.

Miller, A. E., and Bowman, W. D., 2003: Alpine species show species-level differences in the uptake of organic and inorganic nitrogen. *Plant and Soil,* 250: 283–292.

Monson, R. K., Mullen, R., and Bowman, W. D., 2001: Plant nutrient relations. *In* Bowman, W. D., and Seastedt, T. R. (eds.), *Structure and Function of an Alpine Ecosystem.* New York: Oxford University Press, 198–221.

Raab, T. K., Lipson, D. A., and Monson, R. K., 1996: Non-mycorrhizal uptake of amino acids by roots of the alpine sedge *Kobresia myosuroides*: implications for the alpine nitrogen cycle. *Oecologia,* 108: 488–494.

Raab, T. K., Lipson, D. A., and Monson, R. K., 1999: Soil amino acid utilization among species of the Cyperaceae: plant and soil processes. *Ecology,* 80: 2408–2419.

Stanton, M. L., Rejmánek, M., and Galen, C., 1994: Changes in vegetation and soil fertility along a predictable snowmelt gradient in the Mosquito Range, Colorado, U.S.A. *Arctic and Alpine Research,* 26: 364–374.

Steltzer, H., and Bowman, W. D., 1998: Differential influence of plant species on soil N transformations within moist meadow alpine tundra. *Ecosystems,* 1: 464–474.

Theodose, T. A., Jaeger, C. H., III, Bowman, W. D., and Schardt, J. C., 1996: Uptake and allocation of 15N in alpine plants: implications for the importance of competitive ability in predicting community structure in a stressful environment. *Oikos,* 75: 59–66.

Vitousek, P. M., and Howarth, R. W., 1991: Nitrogen limitation on land and in the sea: How can it occur? *Biogeochemistry,* 13: 87–115.

Vitousek, P. M., Fahey, T., Johnson, D. W., and Swift, M. J., 1988: Element interactions in forest ecosystems—succession, allometry and input-output budgets. *Biogeochemistry,* 5: 7–34.

Vitousek, P. M., Walker, L. R., Whiteaker, L. D., and Matson P. A., 1993: Nutrient limitations to plant growth during primary succession in Hawaii—Volcanoes National Park. *Biogeochemistry,* 23: 197–215.

Vitousek, P. M., Turner, D. R., and Kitayama, K., 1995: Foliar nutrients during long-term soil development in Hawaiian montane rain-forest. *Ecology,* 76: 712–720.

Walbridge, M. R., 1991: Phosphorus availability in acid organic soils of the lower North Carolina coastal plain. *Ecology,* 72: 2083–2100.

Walker, T. W., and Syers, J. K., 1976: The fate of phosphorus during pedogenesis. *Geoderma,* 15: 1–19.

Walker, D. A., Halfpenny, J. C., Walker, M. D., and Wessman, C. A., 1993: Long-term studies of snow-vegetation interactions. *BioScience,* 43: 287–301.

Ms submitted January 2002
Revised ms submitted July 2002