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Plant Nutrient Content Does Not Simply Increase with Elevation under the Extreme Environmental Conditions of Ladakh, NW Himalaya

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Abstract

Low temperature is considered the main limiting factor for plant growth and nutrient supply at high elevations. It has been repeatedly reported that an increase in foliar nutrient contents occurs with elevation which is interpreted as the plants' inability to use the absorbed resources for growth. However, although large data sets from various mountainous regions are available, data from elevations exceeding 5000 m elevation are rare, leaving uncertainties on the relevance of these patterns under extreme alpine conditions. To fill this gap, we examined foliar macronutrients (N, P, K, Ca, Mg) content in *Poa attenuata* and *Waldheimia tridactylites* along an elevation gradient of 1600 m in Ladakh, northwestern Himalaya. Species showed rather similar response: N, Ca, and Mg concentration decreased with elevation. However, P concentration decreased with elevation in *Poa* but slightly increased in *Waldheimia*; K concentration was related to elevation in *Poa* only (positively). The surprising decreases of N, and/or N/P and N/K ratios towards higher elevation suggest that nitrogen uptake decreased with elevation and it may limit plant growth. Our results suggest that plants growing at very high elevations tend to be limited by a combination of lower nutrient uptake, possibly because of poorly developed soils, and scarcity of water.

Introduction

Various environmental factors limit the growth and distribution of vascular plants at high elevations. Particularly, both direct and indirect effects of low temperature and snow cover are combined with very short growth season in alpine and subnival zones (Körner, 2003). In spite of numerous studies performed in these regions, there is still uncertainty on which environmental factors chiefly control the distribution of vascular plants at the highest elevation (Klimeš and Doležal, 2010).

Foliar nutrient content may be one of the few (yet indirect) indicators of plant growth limitation at high elevations (Reich et al., 1997; Aerts and Chapin, 2000). For example, plant N to P stoichiometry may track the N to P stoichiometry of the environmental nutrient supply (Sterner and Elser, 2002). In theory, when plant tissue nutrients increase with elevation, growth limitation caused by temperature could be expected (Morecroft et al., 1992); otherwise, increased nutrients would not be reflected into the growth pattern, because the plants at higher elevations are predisposed to grow only a little amount (Diggle, 1997). This is the pattern more often reported in the literature (Woodward, 1986; Körner, 1989) and could be supported by reports of rather high nutrient contents in alpine plants (Körner, 2003). Alternatively, a decrease in nutrient content with elevation would indicate a limitation by nutrients in the system (Köhler et al., 2006; Macek et al., 2009). With increasing elevation, low soil temperatures associated with low rates of soil microbial activity were repeatedly considered as the main limiting factor for plant growth and nutrient supply (cf. Körner, 1989).

Most of the existing evidence indicates that plant growth at higher elevations is limited by temperature, which is reflected in a positive relationship between foliar nutrient content and elevation, both between species and within species (Körner, 1989). These patterns, at least for foliar N and P contents, are supported by abundant pieces of evidence (Körner and Cochrane, 1985; Körner et al., 1986; Woodward, 1986; Morecroft et al., 1992; Bowman et al., 1999; Weih and Karlsson, 2001; Frangi et al., 2005; for the review see also Körner, 1989). However, in these studies, mostly conducted in temperate zones, lowland and alpine habitats were usually compared with each other. Moreover, to the best of our knowledge the highest elevation considered until now never exceeded 5000 m. Finally, the nutritional status of plants from extremely dry mountains has attracted little attention so far. Nevertheless, plants reach their uppermost distribution limit in semi-desert mountains of the subtropical zone (Miehe, 1991; Press et al., 2000; Klimeš, 2003; Körner, 2003; Azócar et al., 2007; Macek et al., 2009; Klimeš and Doležal, 2010) and little is known if these general patterns would also hold under these very constrained habitats.

In Ladakh, a region with very low precipitation (80 mm $year^{-1}$; town of Leh in Jammu Kashmir state of India has an elevation of 3500 m; Miehe, 1990) and snow line around 6400 m elevation, the uppermost distribution limit of vascular plants reaches ~6000 m

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elevation (Klimeš and Doležal, 2010). Ladakh is therefore suitable for studying the nutritional status of plants growing at their upper elevation limit. Here, the plants' nutritional status is likely influenced by extremely cold temperature (night soil temperatures at 6000 m elevation are frequently below zero during the whole season) but also high water stress. It is therefore unclear whether foliar nutrients could also increase with elevation in these habitats. Environmental conditions become more severe with elevation and affect both plant growth and nutrient uptake, which may be reflected by plant nutrient content. It is possible to assume that, under these extreme conditions, the general trend of increasing foliar nutrient content with increasing elevation may not hold, as the plant nutrient uptake becomes one of multiple growth-limiting processes. To test this hypothesis, we measured foliar content of major plant macronutrients (N, P, K, Ca, Mg) in two prominent species of the Ladakh flora, collected along a large elevation gradient.

Material and Methods

SPECIES AND STUDY SITES

For this study we chose two species with an elevation distribution range greater than 1000 m, *Poa attenuata* Trin. (Poaceae) and *Waldheimia tridactylites* Kar. & Kir. (Asteraceae), which are dominant at both alpine and subnival zones of the Ladakh vegetation. We investigated 10 sites in the mountainous region of northwestern Himalaya (Ladakh, Jammu, and Kashmir State, India) where these species normally occur. Seven sites were located along the northwest–southeast Ladakh Range (the majority of soils were on gneiss), and three additional sites were selected in neighboring Nubra Valley (Karakoram Range; granite). A subset of several microsites was selected within each site in order to collect both species at different elevations. A total of 90 and 104 samples were collected for *Poa* and *Waldheimia*, respectively. The sites ranged from 32°56′N to 34°40′N and 77°00′E to 78°28′E, with elevation gradient from 4400 to 6000 m elevation. A mid-season soil volumetric water content along the whole gradient ranged from 4 to 10% (mean ± S.D.: 5.6 ± 1.3; $n = 84$; 12 cm depth).

NUTRIENT ANALYSIS AND STATISTICAL TREATMENT

Fresh, non-damaged and fully developed leaves of plants at a comparable phenological stage were collected around the peak of the growing season, and sun-dried *in situ*. No, or very weak, effect of collection date to nutrient concentration was observed, further confirming the phenology did not play a major role in obtained results (results not shown). After transport to the laboratory the leaves were oven dried (60 °C) until constant weight, ground and analyzed for content of the following macronutrients: nitrogen, phosphorus, potassium, calcium, and magnesium (N, P, K, Ca, and Mg, respectively). Dry leaf biomass was mineralized in 12 mL flasks. About 0.7–0.9 mg of dry weight (DW) were mineralized with 0.2 mL of 98% H_2SO_4 (240 °C, 6 h) for N analyses, 1.5–2.0 mg DW with 0.15 mL of 60% $HClO_4$ (170 °C, 3 h) for P, and 2.0–4.5 mg DW with 0.15 mL of 65% HNO_3 (140 °C, 30 min) for cation analyses. N and P content were analyzed colorimetrically using an autoanalyzer (FIA star 5010 Analyzer, Foss Tecator AB, Höganäs, Sweden) and the cations by atomic absorption spectrometry (SpectrAA 640, Varian Techtron, Melbourne, Australia).

Data were analyzed using different generalized linear models. Alternative models of linear and polynomial (second-order) regressions were fitted to analyze the relationship between elevation and tissue nutrient concentration; model selection followed the Akaike information criterion (Sakamoto et al., 1986).

Results

Foliar nutrient concentration changed significantly with elevation (Table 1); generally, nutrient concentration tended to decrease with increasing elevation. *Waldheimia* foliar N decreased linearly with increasing elevation. Although *Poa* foliar N concentration decreased with increasing elevation as well, this relation was not linear and foliar N tended to increase slightly again at the upper end of the elevation gradient (Fig. 1). A decreasing nutrient concentration with elevation was found also for Ca and Mg for both species. While foliar K increased with elevation in *Poa*, no significant relationship with elevation occurred for K concentration in *Waldheimia*. In contrast, P was positively correlated with elevation in *Waldheimia*. There was no elevation trend in *Poa* for N/P ratios, but there was a strong negative correlation of N/P with elevation in *Waldheimia* (Fig. 1). The N/K ratio decreased with elevation in both *Poa* ($R^2 = 0.25$; $r = -0.50$; $p < 0.001$) and *Waldheimia* ($R^2 = 0.11$; $r = -0.33$; $p < 0.001$).

Generally, except for Ca, the mean foliar nutrient concentrations in both species (Table 1) were similar to the average values normally detected in other alpine species. However, foliar N concentration in *Poa* from the lowest elevations (~4600 m elevation) was rather high, reaching greater than 5% (Fig. 1). N to P ratios also varied between the species: mean N/P in *Poa* was equal to 18, while it was equal to 12 in *Waldheimia*. The very high Ca concentration in *Waldheimia* leaves (2.1% DW) was explained by the presence of fine $CaCO_3$ crystals (cystoliths) in foliar tissues, which was revealed microscopically (data not shown).

Discussion

Our study indicated that there are no consistent patterns of changes in foliar nutrient concentrations with increases in

TABLE 1

Mean ± S.E. nutrient content (%) in leaves of *Poa attenuata* ($n = 90$) and *Waldheimia tridactylites* ($n = 104$) of alpine and subnival belts in Ladakh, NW Himalaya. On right side of each column is an indication of the direction of relation to altitude (▲ for increase, ▼ for decrease, and — for no change). Differences between nutrient contents of the two species are shown (F values). (n.s. = $p > 0.05$; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$).

	Poa		*Waldheimia*		*F*
N	2.55 ± 0.10	▼***	2.02 ± 0.05	▼***	8.11**
P	0.16 ± 0.01	▼***	0.19 ± 0.01	▲**	22.3***
K	1.82 ± 0.09	▲**	1.76 ± 0.04	— n.s.	0.39
Ca	0.68 ± 0.03	▼*	2.09 ± 0.14	▼***	83.5***
Mg	0.20 ± 0.01	▼*	0.26 ± 0.01	▼***	20.2***
N/P	18.0 ± 0.71	— n.s.	12.2 ± 0.53	▼***	44.6***

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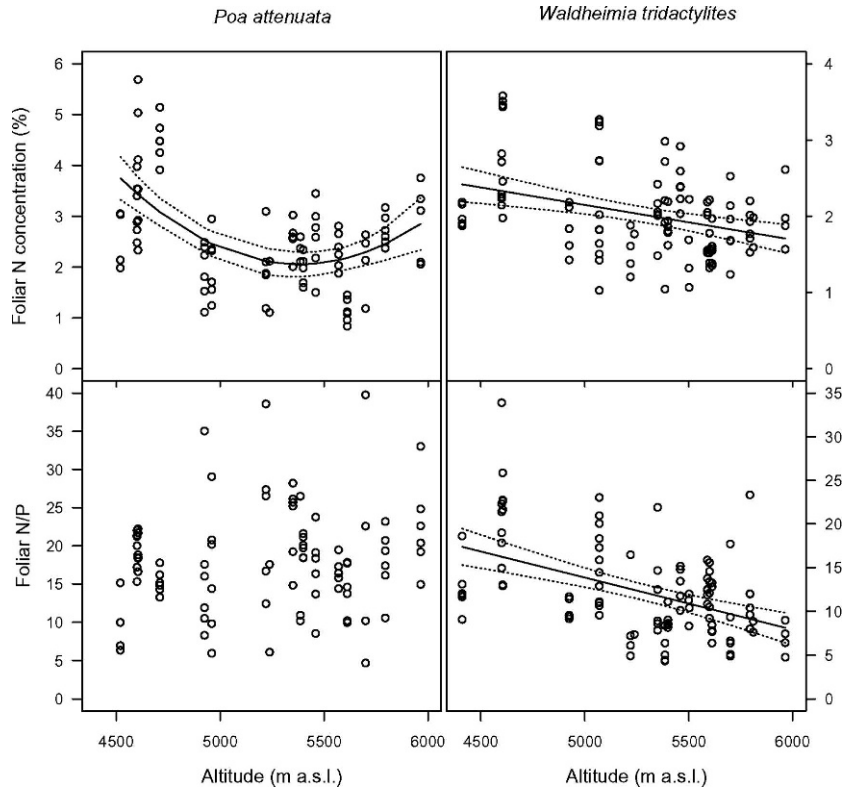


FIGURE 1. Foliar nitrogen concentration (%) and N to P ratio in leaves of *Poa attenuata* and *Waldheimia tridactylites* along altitudinal gradient in Ladakh, NW Himalaya. Solid lines represent significant regression ($p < 0.001$) with 95% confidential interval (dashed lines). Variability explained by models was $R^2 = 0.30$, $R^2 = 0.13$, and $R^2 = 0.23$ for *Poa* N, *Waldheimia* N, and *Waldheimia* N to P ratio, respectively.

elevation. These patterns contradict the generally accepted trends for mountain plants advocating for temperature limitations as the main constraint for plant growth in these ecosystems (Körner, 2011). In our study region, if the growth of the study plants were mainly limited by low temperatures at high elevations, there would be weaker nutrient dilution caused by slower growth, resulting in greater foliar nutrient accumulation. Also other factors can result in greater foliar N content at higher elevations, such as physiological acclimation to lower air temperature with respect to optimal N use (Weih and Karlsson, 2001). However, the leaf tissue concentrations of N and other nutrients in both species mostly decreased with increasing elevation. Our results are similar to some recent studies. Köhler et al. (2006) documented a decrease in foliar N, P, K, and Ca concentrations with increasing elevation in several plant species from the Canary Islands and Macek et al. (2009) documented a decrease in foliar P concentration with increasing elevation in different woody species at the tree line of the high Andes.

Our results may, therefore, seemingly contradict the original hypothesis of Körner (1989), who stated that the concentration of leaf nutrients of plants from (sub)alpine zones increase with increasing elevation. However, Körner's hypothesis is partially supported for *Poa* within the upper part of elevation gradient (see below). Therefore, our results suggest that the theory explaining trends in foliar nutrient concentrations for alpine conditions may not hold for high elevations in our study system. Most likely, the general trend is reversed in our studied species due to the special environmental conditions in Ladakh. Particularly, we hypothesize that a combination of poorly developed soils with little microbial activity restricted by temperature and scarce water availability are imposing a nutrient and drought stress on plants.

Ladakh substrates are geologically younger with rather less developed soils and soil biota (Mani, 1978; Klimeš, 2003). Hence, processes common in older substrates (e.g. N supply from N_2 fixation or N mineralization of organic matter) are possibly less substantial there. In the subnival zone, frequent frosts during the growth season limit soil microbial processes (Schimel et al., 2007), which ultimately leads to nutrient scarcity. Since poor development of soils and/or soil biota often corresponds to nutrient limitation (Holzmann and Haselwandter, 1988; Vitousek, 2004), these factors could contribute to a decrease of foliar nutrient concentration with increasing elevation. Low water supply can affect plant mineral nutrition (Marschner, 1995; Hu and Schmidhalter, 2005). Generally, drought reduces the diffusion rate of nutrients in the soil to the absorbing root surface as well as the nutrient uptake rate by roots and transport to shoots (Hu and Schmidhalter, 2005). Low precipitation together with permafrost proximity (meaning very low soil temperatures) at highest elevations likely limits further nutrient uptake (cf. Karlsson and Nordell, 1996).

Although general leaf N concentration trends in both species were decreasing with increasing elevation, there were some noticeable anomalies in *Poa*: foliar N (and P) concentrations were slightly increasing at the upper elevation limit again. This asymmetrical U-shaped dependence could have a rather plausible explanation: at the upper elevation edge of the *Poa* range (5800–6000 m elevation), other factors, *e.g.* low temperatures, start to influence *Poa* growth, conforming partially to Körner's hypothesis (Körner, 1989). Nitrogen could be considered the most limiting mineral nutrient for alpine plant productivity (Körner, 2003). Even though nitrogen concentrations found for both *Poa attenuata* and *Waldheimia tridactylites* at higher elevations were somewhat lower compared to other alpine plants (Körner, 1989, 2003; Bowman et al., 2003), they should not be considered insufficient for plant growth (Marschner, 1995; Körner, 2003; Wright et al., 2004; Macek and Rejmánková, 2007). Koerselman and Meuleman (1996) suggested mass ratio of $N/P > 16$ indicated a P limitation of plant growth, and $N/P < 14$, indicated a N limitation of growth. On the other hand, several authors have questioned the accuracy of foliar concentration as indicators of the

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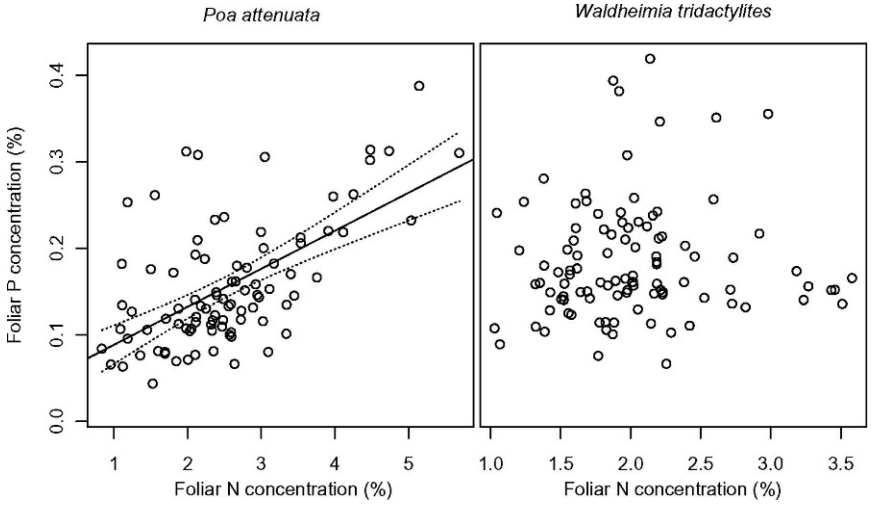


FIGURE 2. Relationships between foliar N and P concentrations for *Poa attenuata* and *Waldheimia tridactylites* along altitudinal gradient in Ladakh, NW Himalaya. Full line represents significant regression ($R^2 = 0.628$, $p < 0.001$) with 95% confidential interval (dashed lines).

limitation of these elements plant growth (e.g. Bowman et al., 2003). While we certainly agree that attention should be given to the interpretation of patterns, we also believe that these indicators have an important value in testing general theory and defining new hypotheses. Different root systems (thick short roots of *Waldheimia*, versus extensive and dense root system of *Poa*) and/or species-specific differences in nutrient use efficiency might affect N to P ratio of the studied species. *Poa* had N/P ratios mostly above 16 (i.e., it may be slightly P-limited), while *Waldheimia* had the N/P ratios that suggested it was more N-limited, especially at higher elevations. It is therefore possible that *Poa*, having more fine roots, could be less dependent on mycorrhiza than *Waldheimia*. Since mycorrhizal infection usually decreases towards the highest elevations (Haselwandter and Read, 1980), decreases in soil N with increasing elevation may affect *Waldheimia* to a larger extent than *Poa*, as indicated by the decrease of foliar N and changes in its N to P stoichiometry. Such disproportional uptake of one nutrient is also reflected in the non-correlation of P and N (Bowman et al., 2003); on the other hand, balanced growth of *Poa* is further supported by positive correlation of P and N (Fig. 2). Limitation by N (or rather N and P co-limitation) is a common feature in pristine ecosystems (Britton and Fisher, 2007) and has also been reported from other regions of Himalaya (Singh and Sundriyal, 2005).

Besides higher foliar Ca concentration in *Waldheimia* leaves (likely caused by $CaCO_3$ precipitation), foliar concentrations of K, Ca, and Mg in *Poa* and *Waldheimia* across all elevations were within a normal range (cf. Marschner, 1995). Although there have been some slight differences in the observed leaf nutrient concentration trends, generally both *Poa* and *Waldheimia* responded similarly along the elevation gradient, i.e. decreased their foliar nutrients. This is consistent with the original hypothesis of Körner (1989), that the trends should be similar among species as well as within species.

Conclusions

The general trend of increasing foliar nutrient concentration with elevation did not occur for our study plants growing at their uppermost distribution limit in dry mountains. The decreases in foliar nutrients we observed with increasing elevation could be explained by a combination of multiple biotic and abiotic constraints, i.e. lower nutrient availability due to poorly developed soils and soil biota, and lower nutrient uptake due to very low temperatures and limited water supply under these extreme conditions. Furthermore, the decreases of foliar N concentration and/or N/P and N/K ratios toward high elevations together with rather lower N concentrations in both species at higher elevations (compared to other alpine taxa) suggest relatively higher N importance for plant growth under such conditions as compared to other nutrients.

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