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# Soil Acidity, Content of Carbonates, and Available Phosphorus Are the Soil Factors Best Correlated with Alpine Vegetation: Evidence from Troms, North Norway

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## Abstract

We investigate which bedrock-derived soil nutrients are most important for the floristic composition and diversity of alpine, exposed, rocky habitats in North Norway, and whether the widely used pH parameter is a good estimate of soil chemical conditions in the middle alpine belt. Vegetation at 17 sites was recorded using the grid frequency method. Differences in the diversity of vascular plants, bryophytes, and lichens on the different substrates were compared using Shannon's diversity index. Local soil consisted of weathered material from one of five bedrock categories: carbonate rocks, calcareous mica schist, noncalcareous mica schist, mafic rocks, and felsic rocks. Particle size, loss on ignition, pH, and levels of calcium, magnesium, potassium, phosphorus, and nitrogen were measured in soil samples. Canonical Correspondence Analysis showed that soil pH and bedrock derived phosphorus in the soil influence the floristic composition. Randomization tests further indicated that the floristic variation explained by bedrock derived phosphorus was not correlated with soil pH. Thus, the pH measure should be used with caution for the characterization of soil conditions. Vegetation growing directly in soil derived from carbonate rocks is distinct from communities on other calcareous soils. Species at such sites should be referred to as carbonate specialists rather than lime demanding.

## Introduction

The classic "rich" to "poor" edaphic gradient is of primary importance to floristic composition, together with the snow-cover gradient (Vestergren, 1902; Fries, 1913; Nordhagen, 1937; Dahl, 1957; Walker et al., 2001a). It is usually related to the shift from alkaline or circumneutral, calcareous substrates derived from carbonates, to acid, siliceous substrates derived from felsic rocks.

Most classifications of alpine and arctic vegetation use calcareous versus siliceous substrate as a factor for subdividing plant communities. A number of widespread, as well as rare, alpine species are considered to indicate or demand calcium (Hultén, 1968; Gjærevoll, 1990; Ellenberg et al., 1991; Virtanen and Eurola, 1997; Schmidtlein and Ewald, 2003). According to the phytosociological system, the alliance usually occurring on siliceous substrates is denoted Loiseleurio–Diapension (Daniëls, 1982); and on calcareous substrates, Caricion nardinae (Nordhagen, 1955). Also, Walker (2000) uses the gradient from acidic to alkaline substrate as a main factor for the classification of arctic tundra. However, there has been less focus on other soil parameters than acidity that could be important to plants, and soil pH is often the only one discussed to assess soil-plant relationships in the mountains of Europe and North America, as well as in the Arctic (e.g. Dahl, 1957; Lunde, 1962; Elvebakk, 1982; Edlund and Alt, 1989; Gough et al., 2000; Walker et al., 2001b). One exception is Walker et al. (1994), who included measurements of the cations $Ca^{++}$, $Mg^{++}$, and $K^{+}$. The bedrock in mountain ranges such as the Rocky Mountains, the European Alps, the Himalaya, or the former Caledonian mountain range of Scandinavia harbor igneous, sedimentary, and metasedimentary rocks (Kruckeberg, 2002). Hence, the mineralogical variation is more complex than expressed by the carbonate/silica proportion. Even in silicate rocks, trace amounts of Ca can contribute significantly to the soil chemistry regime, especially when fresh surfaces are exposed, as after glaciations, or in areas with pronounced frost shattering and cryoturbation of soil (Clow et al., 1997; White et al., 1999). In addition, other minerals than carbonates are subjected to chemical weathering; potassium ions, for example, are mainly produced by dissolution from micas, and biotite in particular (Pozzuoli et al., 1992). This mineral is widespread in most mica schists. Could variation in the amount of potassium leaching from different bedrocks modify floristic composition?

In general, the availability of nutrients is important to the local distribution of plants (Tyler, 1992; Baddeley et al., 1994; Elvebakk, 1997; Theodose and Bowman, 1997). Wielgolaski (1975) concluded that the availability of nitrogen (N) and phosphorus (P) are limiting factors for plant growth in the Fennoscandian mountains. Both these components are mainly recycled through the decomposition of organic matter. Bedrock does not provide any significant input of nitrogen, but the cycle of phosphorus has a continuous input from weathering of the minerals apatite or phosphorite. Could also the availability of bedrock-derived phosphorus influence the occurrence of certain species?

Here, we address these questions for middle-alpine ridges (*sensu* Moen, 1998) in North Norway. The study sites were ridges left as exposed bedrock after the retreat of the Weichselian ice sheet (15,000–17,000 yr BP), with no overlying moraine, and subjected to chemical weathering and frost shattering since then. The substrate for vegetation at such sites is mainly the weathered material derived from the local bedrock accumulating in cracks and minor depressions in the bedrock surface. The litter produced

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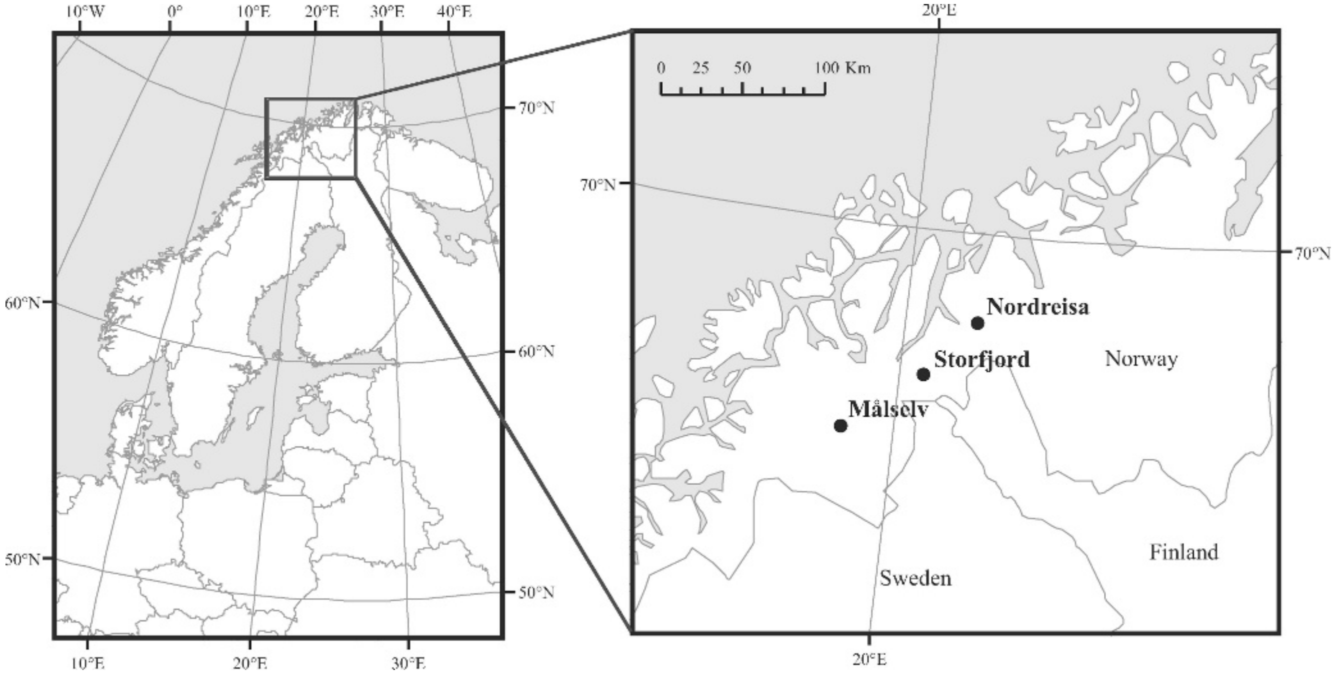

**FIGURE 1. Maps of Northern Europe and Troms County, with the location of the three municipalities where the study took place.**

by the sparse vegetation is mainly blown off. This substrate lacks horizons, and is similar to what Edlund and Alt (1989) described from the Queen Elizabeth Islands of Arctic Canada, except that our study area has only discontinuous permafrost. Here, we aim at revealing the relationship between bedrock-derived elements and alpine vegetation. At the chosen sites, the effect of other common soil processes such as humification and the hydrological regime are minimal. The nutrient availability to the plants is largely conditioned by the weathering of the bedrock, and not through the recycling of decomposing litter. We recorded the vegetation on five different bedrock categories, namely carbonate rocks, calcareous mica schists, noncalcareous mica schists, mafic rocks, and felsic rocks, and assessed its relationship with the chemical composition of the bedrock-derived material. Data on the availability of Ca, Mg, K, P, and N, as well as pH, loss on ignition (LOI), and particle size, were obtained from soils derived from the five bedrock categories and correlated with corresponding vegetation data of vascular plants, bryophytes, and lichens.

The main objectives of the study were to (1) reveal if and how plant species composition and diversity are related to soil chemical factors, other than the classic calcareous/noncalcareous pH gradient; and (2) assess the adequacy of the widely used pH parameter to explain to the composition of alpine flora.

## Material and Methods

Nomenclature of vascular plants follows the seventh edition of Lid and Lid (Elven, 2005), except that *Luzula arcuata* and *L. confusa* are treated as a collective species here. Bryophytes and lichen species are named according to Frisvoll et al. (1995) and Santesson (2004), respectively. Collected specimens were deposited at Tromsø University Museum (TROM).

### *STUDY AREAS AND GEOCHEMICAL FEATURES*

The three study areas are located in the middle alpine belt (here from 800 to 1205 m a.s.l.) of the North Norwegian Caledonides, which are the remnants of the Caledonian mountain range (Fig. 1). The sites are equally located along the coast/inland climatic gradient (Werner Johannesen, 1974; Aune, 1981), in the transition between the oceanic and continental vegetation sections (Moen, 1998).

On the basis of mineralogical composition and chemical weathering rate, the bedrock of the study areas was classified into five categories: (1) Carbonate rocks (Carb), which include limestone and dolomite, usually metamorphosed into marble. Prevailing minerals are calcite and dolomite. (2) Calcareous mica schist (CMS). Calcite and/or dolomite are important minerals in this group as well, but mica schists are characterized by the micas muscovite and/or biotite in addition to quartz. Feldspars and chlorite occur in varying amounts. (3) Noncalcareous mica schist (N-CMS). This is similar to the preceding group, but lacking calcite. Less soluble calcium silicates may be present. (4) Mafic rocks (Mafic). This generally denotes rocks with a high content of magnesium and iron. Amphibolite and gabbro are widespread in the study area, often intruding the surrounding metasedimentary rocks. The main minerals are plagioclase feldspars, pyroxenes, and amphiboles. (5) Felsic rocks (Felsic). This is a common name for light colored rocks enriched with quartz. Feldspars (both plagioclase and potassium feldspar) and micas occur in varying amounts. Granite, gneiss, quartzite, and arkose are examples of felsic rocks, which often are hard and resistant to weathering and erosion.

Dry, exposed ridges were selected as study sites. A ridge is here defined as a well-drained convex landform of bedrock above the tree line, which accumulates a minimal amount of snow during winter. Dead plant debris is blown away from such sites, leaving a sparse and discontinuous mineral soil derived from the local bedrock as the substrate for vegetation. For the study sites to be as uniform as possible, they were selected on the following criteria: moderate cryoturbation, pronounced wind deflation, minimal admixture of allochthonous sediments such as ablation moraine, minimal thickness or nonexistence of a humic layer, no stagnant surface water, and horizontal or subhorizontal inclination. The bedrock categories and elevations of the selected sites were not correlated (Fig. 2).

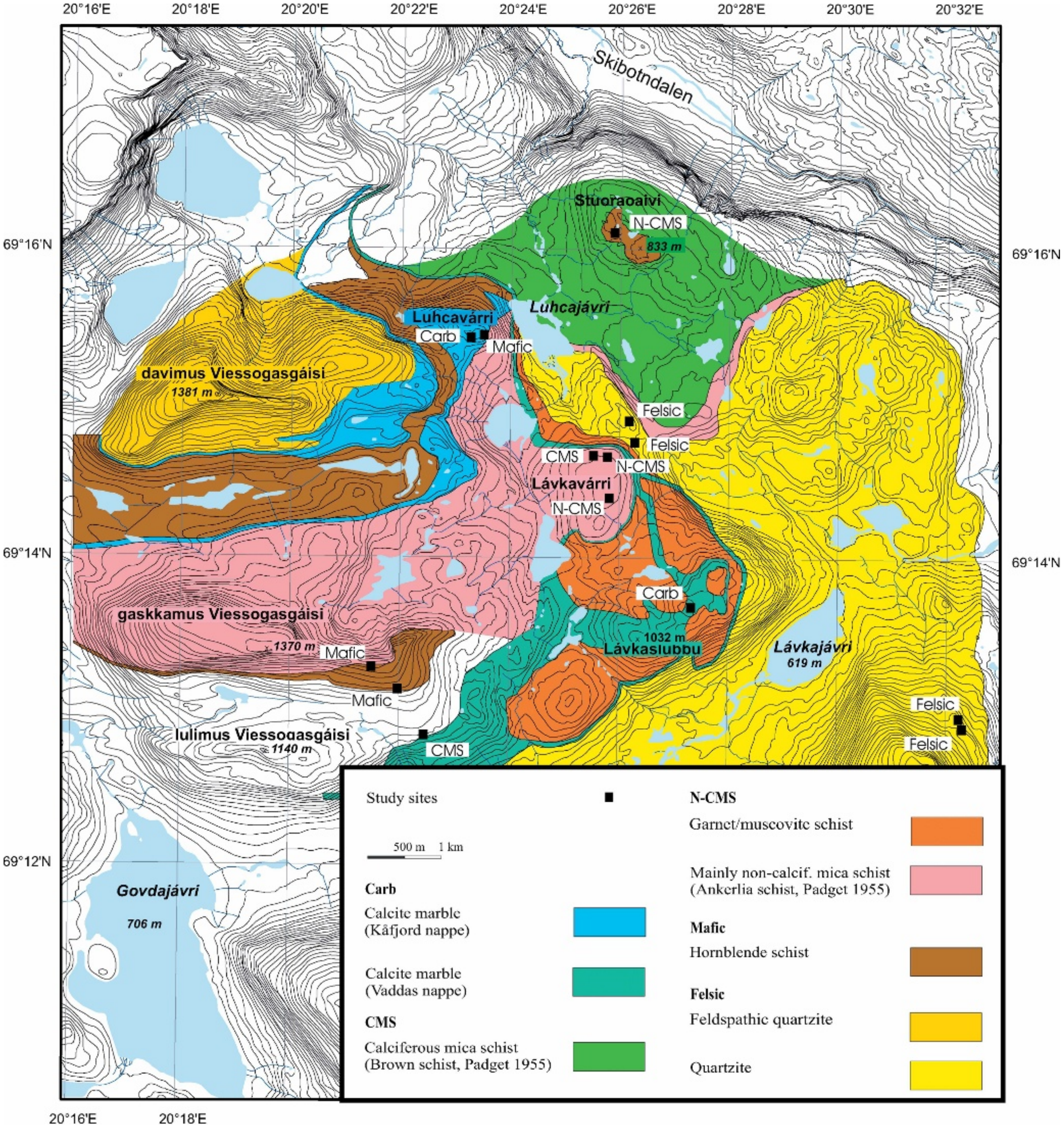

**FIGURE 2. Geological map of the study area in Storfjord, SW of Skibotndalen valley. The 14 study sites in this area are shown as black quadrates. The western study site at Mount Luhčavárri is situated on a lens of hornblende schist, too small to appear on the map. The equidistance is 20 m. For further information of adjacent areas and lithostratigraphy, see Zwaan (1988). Carb = carbonate rocks, CMS = calcareous mica schist, N-CMS = noncalcareous mica schist, Mafic = mafic rocks, and Felsic = felsic rocks.**

## *FIELD SAMPLING AND LABORATORY PROCEDURES*

Vegetation and soil sampling was performed at 17 sites in three study areas: (1) Two sites on the mountain Gråhøgda (1200–1267 m a.s.l.), Målselv, with predominantly carbonates and calcareous mica schist. (2) Fourteen sites in the mountains between the valley of Kitdalen and the valley of Skibotndalen (830–1205 m a.s.l.), Storfjord. The local distribution of bedrock in Storfjord is drafted in Figure 2, supplemented by Zwaan (personal communication, 1996), Padget (1955), and our own field observations. (3) One site on the mountain Pihkahistama/Javroaivit (909 m a.s.l.), Nordreisa, with calcareous mica schist.

For floristic analysis, 85 sampling units were analyzed, 5 at each site. The units consisted of five 50 × 50 cm quadrates: a central one and one placed at each corner of the central one. In each of the quadrates, species frequency was recorded using the grid-frequency method, with a sampling frame subdivided into 16 squares. Saxicolous and crustose lichens were not recorded. Three samples of the bedrock-derived substrate were collected at each study site. The texture of the weathered material is partly caused by the physical properties of the parent bedrock. Marbles disintegrate into gravel formed by the original crystals of calcite or dolomite, while mica schists, especially the calcareous kind, often produce a more fine-grained material of mica and calcite. The material weathered from felsic and mafic rocks is often a product of frost shattering, containing a variety of grain sizes. More important, however, subsequent cryoturbation produces a considerable amount of fine material in the bedrock-derived soils, independent of bedrock category. The soil occurring at our study sites can be classified as leptosols according to the FAO soil classification system (FAO, 1998), and the thickness varied between 0 and 10 cm. It was sampled across its entire depth, where available. Pebbles were removed, along with loose plant litter. The samples were then put to dry at 30°C, stored in paper bags.

In addition to pH and LOI, the amounts of the elements calcium, magnesium, potassium, phosphorus, and nitrogen were measured. Nitrogen analysis was carried out using the Kjeldahl method (Farstad et al., 1985), which gives the total nitrogen content. The amount of the elements P, K, Mg, and Ca available to plants was estimated using the so called Acetate-Lactate (AL) method (based on the quantity of elements extractable with a solution of acetic acid [0.4 M] and ammonium lactate [0.1 M]). The method is described in Egner et al. (1960) and Houba et al. (1997). Two particle size fractions were separated using sieving, namely the fraction of fine particles, i.e. clay and silt ($\leq$0.06 mm), and the fraction of coarser particles, i.e. sand and gravel ($>$0.06 mm). These particle size limits follow the standard of the U.S. Department of Agriculture (USDA) presented in Gee and Bauder (1986). From the two fractions a ratio was calculated reflecting the dominance of fine particles in the soil. This soil texture ratio (STR) is likely to reflect the moisture retention capability of the soil (Arya and Paris, 1981). For each site and soil variable, the averages of the values measured in the three soil samples were used in the analysis.

### *NUMERICAL ANALYSIS*

In order to relate species diversity to the selected bedrock categories, the Shannon diversity index (*H*) was calculated for vascular plants, bryophytes, lichens, and for the entire data set, for each of the five bedrock categories. This commonly used index accounts for both abundance and evenness of the species present to express species diversity in a community:

$$H = -\sum_{i=1}^{s} p_i \ln p_i \tag{1}$$

where $s$ = the number of species, $p_i$ = the proportion of individuals or the abundance of the $i^{\text{th}}$ species expressed as a proportion of the total cover, and ln = the natural logarithm. Due to the low number of sampling sites, testing for statistically significant differences in species diversity between bedrock categories was not meaningful.

To visualize the differences and similarities in the floristic composition of the different sites, we used nonmetric multidimensional scaling (NMDS; Kruskal, 1964) in combination with the Bray-Curtis dissimilarity index to quantify the ecological distance between sites (Bray and Curtis, 1957). NMDS is a robust form of unconstrained ordination which has the potential of revealing gradient structures in the data if the calculated similarity between plots reflects their position along the gradients. The Bray-Curtis dissimilarity index, standardized to unit maximum for each species and to unit sample total, has shown to be an index with this property (Faith et al., 1987). NMDS requires that the dimensionality of the data is specified in advance. As the aim of the NMDS here is to visualize the variation in the floristic data, we used NMDS in two dimensions. Namely, it can be presented as a plot where the pairwise distances between the sites are ranked similarly to the distances calculated from the floristic data. In other words, NMDS maximizes the correlation between rank order of the distances between sites in ordination spaces and the rank order of the dissimilarities calculated for the sites from the species data.

As a statistic of goodness of fit, the discrepancy between the distances in the ordination space and the dissimilarities calculated from the species data is quantified, and termed stress. Algorithms for NMDS rely on iterative processes, and therefore we repeated the procedure with multiple random start configurations aiming to find a constellation of the sites that produces the lowest stress. This constellation does not depend on the environmental data. To facilitate the interpretation of the NMDS, environmental variables were plotted as arrows on top of the NMDS plot. The direction of an arrow indicates the direction of the gradient and its length indicates the correlation with the NMDS plot. The significance of these correlations was quantified using permutations tests. These tests verify that the correlations are not found when the soil variables are randomly permuted.

To test the importance of the relationships between the measured bedrock-related soil variables and the floristic composition of the sites, we constrained the ordination using the soil data in a Canonical Correspondence Analysis (CCA). While the NMDS showed the major gradients in the floristic data, the CCA optimizes the fit of the sites relative to the environmental variables (ter Braak and Prentice, 1988). Rather than showing all the variation in the data, as with the NMDS, the CCA quantifies how much of the variation in the species data can be accounted for by the measured environmental gradients. The contributions of the different soil variables to the CCA model were inspected separately. This was done using permutation tests that quantified if the effect of a variable was still significant after the variation caused by the other variables had been removed (Legendre and Legendre, 1998).

Results from one outlier site on mafic rocks were omitted from the statistical analyses, as soil conditions appeared to be locally influenced by an adjacent marble outcrop. The software package R with the MASS (Venables and Ripley, 2002) and vegan (Oksanen, 2005) packages, were used for the statistical analysis and modeling.

## Results

### *SOIL CONDITIONS*

pH was higher in soil derived from carbonates (mean pH 7.4) and calcareous mica schist (mean pH 6.6) than in soil from the noncalcareous bedrocks (Table 1). Felsic soil had the lowest pH with a mean of 4.9.

Calcium and magnesium are the main cations of carbonate minerals. They showed very high values in soils from the carbonate-containing bedrock types. In soil from carbonate rocks, the mean value of Ca was $4.3 \times 10^4$ parts per million (ppm), and that of Mg was 948 ppm (one of the marbles was dolomitic). The average Ca and Mg values in soil derived from calcareous mica schist were 7448 and 354 ppm, respectively. In comparison, average Ca and Mg values of felsic soils were 51 ppm and 2 ppm, respectively. For the statistical analysis, the concentrations of Ca and Mg were transformed using the natural logarithm.

TABLE 1

**Descriptive statistics for soil parameters in the weathered material of different bedrock types. Carb = carbonate rocks, CMS = calcareous mica schist, N-CMS = noncalcareous mica schist, Mafic = mafic rocks, and Felsic = felsic rocks, LOI = loss on ignition, STR = soil texture ration (% clay and silt) / (% sand and gravel).**

| | | pH | Ca (ppm) | Mg (ppm) | K (ppm) | P (ppm) | N (% dry matter) | LOI (% dry matter) | STR |
|---|---|---|---|---|---|---|---|---|---|
| Carb | Mean | 7.4 | $4.3 \times 10^4$ | 948 | 16 | 1.7 | 0.2 | 5.0 | 0.17 |
| $n = 3$ | Min | 7.0 | 2807 | 27 | 13 | 0.6 | 0.2 | 4.0 | 0.14 |
| | Max | 7.7 | $12 \times 10^4$ | 2346 | 19 | 3.6 | 0.2 | 6.0 | 0.20 |
| CMS | Mean | 6.6 | 7448 | 354 | 35 | 1.1 | 0.2 | 6.8 | 0.53 |
| $n = 4$ | Min | 6.2 | 2560 | 91 | 15 | 0.5 | 0.1 | 3.0 | 0.30 |
| | Max | 7.7 | $2.1 \times 10^4$ | 808 | 66 | 2.1 | 0.5 | 13.0 | 0.89 |
| N-CMS | Mean | 5.0 | 125 | 36 | 31 | 3.1 | 0.1 | 3.3 | 0.38 |
| $n = 3$ | Min | 4.9 | 63 | 5 | 26 | 2.2 | 0.1 | 2.0 | 0.31 |
| | Max | 5.2 | 211 | 88 | 39 | 4.5 | 0.1 | 4.0 | 0.45 |
| Mafic | Mean | 5.2 | 112 | 14 | 16 | 7.9 | 0.1 | 3.0 | 0.20 |
| $n = 2$ | Min | 4.9 | 91 | 12 | 11 | 4.5 | 0.1 | 2.0 | 0.14 |
| | Max | 5.4 | 133 | 16 | 20 | 11.3 | 0.1 | 4.0 | 0.26 |
| Felsic | Mean | 4.9 | 51 | 2 | 12 | 2.3 | 0.1 | 2.3 | 0.29 |
| $n = 4$ | Min | 4.6 | 42 | 2 | 9 | 0.8 | 0.0 | 2.0 | 0.18 |
| | Max | 5.1 | 61 | 3 | 15 | 6.2 | 0.1 | 3.0 | 0.39 |

The phosphorus content was generally low. In soil from carbonate rock, all mica schists, and felsic rocks, none of the mean values exceeded 3.5 ppm. However, the values in soil derived from mafic rocks were higher, with a mean of 6.9 ppm and maximum, 11.3 ppm. Mean potassium values were highest in soil from calcareous and noncalcareous mica schists; values being 35 and 31 ppm, respectively. Both soil from carbonates, mafic and felsic rocks had low K values with means between 11 and 16 ppm. The organic admixture in the soil samples, as quantified by nitrogen content and LOI, hardly differed between soil samples of different bedrock origin. Ranges of mean total nitrogen content and LOI were 0.1–0.2% and 2.3–6.8%, respectively (Table 1).

### *PLANT DIVERSITY*

Dry, exposed ridges in the middle-alpine belt have a low cover of vascular plants (5–30%). The overall species richness of vascular plant, bryophyte, and lichen species is low to moderate at most of the analyzed sites, varying from 16 to 52 species.

One general pattern of carbonate ridges is that the diversity of vascular plants, bryophytes, and lichens is low (Fig. 3, Table 2). Nevertheless, on felsic and mafic substrates the diversity of vascular plants is even lower than on carbonate rocks. The diversity of vascular plants is considerably higher on calcareous mica schist, and somewhat higher on noncalcareous mica schist, than on the other substrates. The diversity of bryophytes shows little variation except being slightly lower on carbonates than on all other bedrock categories. Lichen diversity is higher than the diversity of vascular plants and bryophytes on all bedrock categories, and on mafic rocks in particular. The exception is on calcareous mica schist, where the diversity of vascular plants is highest.

### *SOIL–PLANT RELATIONS*

In most cases, the vegetation of plots on the same bedrock types tended to be more similar than on different bedrock types, as indicated by the NMDS in two dimensions (stress = 5.7%; Fig. 4). pH, P, ln(Ca), and ln(Mg) showed a significant correlation with the NMDS ordination configuration ($p_{\mathrm{pH}} < 0.001$, $p_{\mathrm{P}} = 0.033$, and $p_{\ln(\mathrm{Ca})} < 0.001$, $p_{\ln(\mathrm{Mg})} = 0.004$). There was weak statistical evidence that N and K were correlated with the NMDS configuration ($p_{\mathrm{N}} = 0.079$ and $p_{\mathrm{K}} = 0.075$), while LOI, altitude, and soil texture ratio did not appear correlated with it ($p_{\mathrm{LOI}} = 0.12$, $p_{\mathrm{alt}} = 0.81$, and $p_{\mathrm{STR}} = 0.259$, respectively). Since ln(Ca) and ln(Mg) were highly correlated with pH ($R^2 = 0.95$ and $R^2 = 0.84$, respectively), however, only pH was included in the CCA.

Three environmental variables quantifying bedrock related soil chemistry were included in the CCA model, namely phosphorus and potassium concentrations as well as pH (Fig. 5). The first CCA axis was strongly related to pH, while the second and third axes were most correlated with phosphorus and potassium, respectively (Table 3). It was clear that pH and P were the variables that contributed most to the model (pseudo-$F_{\mathrm{pH}} = 3.4$, $p_{\mathrm{pH}} < 0.005$, and pseudo-$F_{\mathrm{P}} = 2.3$, $p_{\mathrm{P}} = 0.005$, respectively), while the significance of the contribution of K was less clear (pseudo-$F = 1.9$, $p = 0.04$). We tested conditioning the model using the environmental variables altitude, N, and soil texture ratio, which are not or indirectly related to the chemical composition of the bedrock. Including the conditions did not reduce the constrained inertia by more than 7% and permutation tests showed that they did not improve the model significantly ($p < 0.005$ in the three cases). This indicates that the effects attributed to pH and phosphorus are highly unlikely to have been due to variation in N, altitude, or soil texture.

## Discussion

This study confirms that there are important chemical and physical differences between soils produced by weathering of different bedrocks. At least on alpine ridges with bedrock-derived soil, these differences seem to have an influence on vegetation and floristic composition. Especially interesting is the importance of phosphorus availability, as this variation is not correlated with pH.

### *PHOSPHORUS AVAILABILITY*

The availability of phosphate may be a limiting factor in arctic and alpine communities due to slow decomposition rates

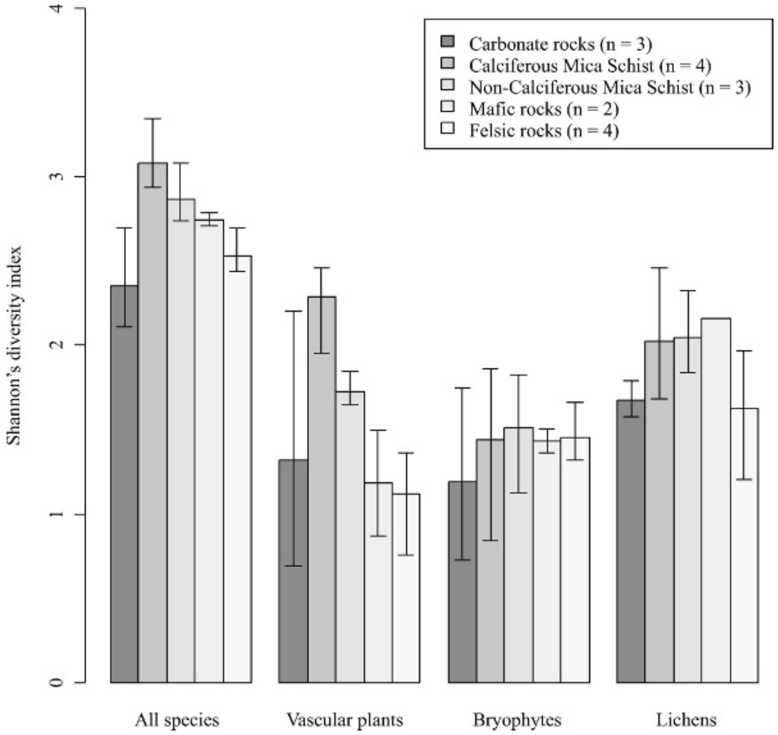

**FIGURE 3. Shannon diversity indices showing the diversity of vascular plants, bryophytes, and lichens as well as the total diversity on the five bedrock categories. The whiskers indicate minimum and maximum values.**

(Wielgolaski, 1975; Wielgolaski et al., 1981; Crawford, 1989; Shaver and Kummerow, 1992; Hobbie et al., 2005). Ultimately the element phosphorus is derived from the mineral apatite, but in most systems the phosphorus available to plants is recycled from decomposing litter. At exposed mountain ridges this may not be the case, as most dead litter is removed. This suggests that the local availability of phosphorus could be lower than elsewhere in alpine systems. Our data confirm this assumption; the sites were unusually poor in phosphorus with a mean value of 2.7 ppm. In comparison, Haselwandter et al. (1983) found a mean plant-available phosphorus concentration in soils in the nival zone of the Alps of 14.6 ppm, and Walker (1985) found a mean value of 8.0 ppm in different Alaskan tundra habitats. It needs to be noted however, that some of this difference could be due to different extraction methods (Otabbong et al., 2004). Furthermore, the variation in the small amounts of available phosphorus was correlated neither with nitrogen content ($r = -0.16$) nor with LOI ($r = -0.17$), confirming that decomposing organic matter was not the source of phosphate compounds at the study sites.

The only other available source of phosphorus is the bedrock. The cycle of phosphorus is slow and can be considered as unidirectional from the weathering of rocks to sediments and sea deposits (Holtan et al., 1988). The phosphate mineral apatite occurs in igneous and metamorphic rocks (Walker and Syers, 1976; Holtan et al., 1988). Thus, it is plausible that mafic rocks and certain other silicate rocks leach more phosphate than other local bedrocks. As the availability of phosphorus is inhibited by high soil pH (Holtan et al., 1988; Tyler, 1992), this topic can be more readily observed at the noncalcareous sites. Among the sites on mafic rocks, felsic rocks, and noncalcareous mica schist there seemed to be a varying availability of phosphorus that was not correlated with soil pH (Fig. 5). The mean values of P in soil derived of mafic rocks were higher than elsewhere. Both mafic sites and one felsic site had high scores on the phosphorus axis. The remaining noncalcareous sites with comparable pH levels showed lower scores on the phosphorus axis in the CCA (Fig. 5). This suggests that bedrock derived phosphorus in certain noncalcareous soils could be significant to vegetation when there is limited availability of phosphorus from organic matter. What seems to characterize the wind-exposed ridges, where most phosphorus originates from bedrock, is a higher diversity and abundance of lichens (Fig. 3), as well as a higher abundance of certain vascular plant species (Table 2). Further studies, however, should address to what extent the vegetation itself, and the lichens in particular, facilitate the weathering of the minerals and subsequent release of phosphorus (Wilson, 1995). This facilitation could occur, for example, through the release of organic acids.

### *THE ROLE OF PH AND CALCIUM*

pH was the measured soil parameter proving to be most important to the floristic composition. Calcium, which was abundant in carbonate-containing substrates, was highly correlated with pH, which is a commonplace observation. Meanwhile, there seemed to be a difference between the gravelly marble soils producing basic soil conditions, and the more composite soil derived from calcareous mica schist, producing a circumneutral pH. The soils of carbonate rocks had extremely high values of calcium (Table 1), sometimes in combination with high values of magnesium, due to dolomitic admixture. Available calcium and magnesium levels in soil weathered from calcareous mica schist were also considerable, but with few exceptions lower than those in soil weathered from carbonates.

Phosphorus and potassium concentrations in the latter soils were generally low. The high amount of carbonate/bicarbonate ions produces a high pH, which may be of importance to the root absorption of nutrients (Tyler, 1992). Especially, the absorption of phosphate is inhibited by basic soil conditions (Holtan et al., 1988). On the other hand, several alpine species growing on carbonate rocks are referred to as ‘‘lime-demanding’’ (Gjærevoll, 1990). This is probably an inadequate expression, as no plant species has the extreme calcium demand corresponding to the amount of Ca ions available in carbonate soils (Table 1).

TABLE 2

Mean frequency of the recorded species on the different bedrock types. The species could have a frequency score ranging between 0 and 16. Carb = carbonate rocks, CMS = calcareous mica schist, N-CMS = noncalcareous mica schist, Mafic = mafic rocks, and Felsic = felsic rocks.

| Species name | Carb | CMS | N-CMS | Mafic | Felsic |
|---|---|---|---|---|---|
| *n* | 3 | 4 | 3 | 2 | 4 |
| **Vascular plants** | | | | | |
| *Arctous alpinus* | 0.0 | 0.0 | 0.3 | 0.0 | 0.1 |
| *Arenaria humifusa* | 0.2 | 0.1 | 0.0 | 0.0 | 0.0 |
| *Astragalus alpinus* | 0.0 | 4.6 | 0.0 | 0.0 | 0.0 |
| *Beckwithia glacialis* | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 |
| *Betula nana* | 0.0 | 0.0 | 0.1 | 0.0 | 0.4 |
| *Bistorta vivipara* | 1.7 | 8.0 | 0.1 | 0.0 | 0.0 |
| *Campanula uniflora* | 0.3 | 1.1 | 0.0 | 0.0 | 0.0 |
| *Carex bigelowii* | 0.0 | 0.0 | 0.0 | 1.7 | 0.3 |
| *Carex capillaris* | 0.0 | 0.2 | 0.0 | 0.0 | 0.0 |
| *Carex fuliginosa* ssp. *misandra* | 0.4 | 0.5 | 0.0 | 0.0 | 0.0 |
| *Carex glacialis* | 1.8 | 0.6 | 0.0 | 0.0 | 0.0 |
| *Carex nardina* | 0.0 | 2.5 | 0.0 | 0.0 | 0.0 |
| *Carex rupestris* | 6.4 | 10.6 | 2.2 | 0.0 | 0.0 |
| *Cassiope tetragona* | 0.0 | 1.0 | 0.4 | 0.0 | 0.4 |
| *Cerastium alpinum* | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Diapensia lapponica* | 0.0 | 3.5 | 3.1 | 0.0 | 5.9 |
| *Dryas octopetala* | 10.4 | 9.0 | 4.3 | 0.5 | 0.3 |
| *Empetrum hermaphroditum* | 0.0 | 0.3 | 0.2 | 0.0 | 0.1 |
| *Euphrasia wettsteinii* | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 |
| *Festuca ovina* | 0.0 | 0.1 | 1.1 | 0.2 | 0.0 |
| *Festuca vivipara* | 0.0 | 0.3 | 0.0 | 0.4 | 0.0 |
| *Harrimanella hypnoides* | 0.0 | 0.2 | 0.0 | 0.0 | 0.0 |
| *Hierochloë alpina* | 0.0 | 0.0 | 0.3 | 0.0 | 0.0 |
| *Huperzia selago* | 0.0 | 0.1 | 0.1 | 0.0 | 0.0 |
| *Juncus biglumis* | 0.3 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Juncus trifidus* | 0.0 | 0.1 | 1.5 | 0.0 | 1.2 |
| *Loiseleuria procumbens* | 0.0 | 0.1 | 0.0 | 0.0 | 0.7 |
| *Luzula arcuata* coll. | 0.2 | 0.2 | 1.5 | 2.2 | 1.4 |
| *Luzula spicata* | 0.0 | 0.6 | 0.0 | 0.0 | 0.0 |
| *Minuartia stricta* | 0.9 | 0.1 | 0.0 | 0.0 | 0.0 |
| *Oxytropis lapponica* | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 |
| *Pedicularis flammea* | 0.0 | 0.2 | 0.0 | 0.0 | 0.0 |
| *Pedicularis hirsuta* | 0.0 | 0.2 | 0.0 | 0.0 | 0.2 |
| *Rhododendron lapponicum* | 0.0 | 2.2 | 0.0 | 0.0 | 0.0 |
| *Salix herbacea* | 0.0 | 0.9 | 8.1 | 9.9 | 5.3 |
| *Salix polaris* | 0.1 | 0.2 | 0.0 | 0.0 | 0.0 |
| *Salix reticulata* | 0.1 | 0.6 | 0.0 | 0.0 | 0.0 |
| *Saxifraga aizoides* | 1.4 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Saxifraga oppositifolia* | 10.5 | 6.5 | 0.1 | 0.0 | 0.1 |
| *Silene acaulis* | 1.7 | 1.9 | 0.5 | 1.1 | 0.0 |
| *Thalictrum alpinum* | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 |
| *Tofieldia pusilla* | 0.0 | 0.6 | 0.0 | 0.1 | 0.0 |
| *Vaccinium uliginosum* | 0.0 | 2.4 | 0.0 | 0.0 | 0.0 |
| *Vaccinium vitis-idaea* | 0.0 | 0.9 | 1.9 | 0.0 | 0.0 |
| **Bryophytes** | | | | | |
| *Andreaea rupestris* | 0.0 | 0.0 | 0.0 | 0.0 | 1.1 |
| *Anthelia juratzkana* | 0.0 | 2.0 | 0.8 | 0.0 | 4.0 |
| *Aulacomnium turgidum* | 0.1 | 0.2 | 0.0 | 0.0 | 0.0 |
| *Conostomum tetragonum* | 0.0 | 0.2 | 0.5 | 0.9 | 0.0 |
| *Dicranum fuscescens* | 0.0 | 1.1 | 0.7 | 0.0 | 0.0 |
| *Dicranum scoparium* | 0.5 | 0.3 | 0.0 | 0.0 | 0.0 |
| *Distichium capillaceum* | 0.1 | 0.6 | 0.0 | 0.0 | 0.0 |
| *Ditrichum flexicaule* | 5.3 | 1.5 | 0.6 | 0.4 | 0.0 |
| *Encalypta* sp. | 0.2 | 0.1 | 0.0 | 0.0 | 0.0 |
| *Grimmia incurva* | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 |
| *Gymnomitrion corallioides* | 0.0 | 1.2 | 11.7 | 14.4 | 5.7 |
| *Hylocomium splendens* | 0.5 | 0.0 | 0.0 | 0.1 | 0.0 |
| *Hypnum revolutum* | 0.7 | 0.2 | 0.0 | 0.0 | 0.0 |
| *Marsupella* spp. | 0.0 | 0.0 | 0.4 | 0.2 | 0.2 |
| *Mnium thomsonii* | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 |
| *Nardia* sp. | 0.0 | 0.0 | 0.0 | 0.2 | 0.0 |
| *Oligotrichum hercynicum* | 0.5 | 0.4 | 0.6 | 0.0 | 0.4 |
| *Pleurocladula albescens* | 0.0 | 0.0 | 0.1 | 0.0 | 0.1 |
| *Pohlia cruda* | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 |
| *Pohlia nutans* | 0.0 | 0.2 | 0.7 | 2.5 | 1.0 |
| *Polytrichastrum alpinum* | 0.0 | 2.6 | 6.2 | 4.9 | 1.3 |
| *Polytrichastrum sexangulare* | 0.0 | 0.0 | 0.0 | 0.4 | 0.9 |
| *Polytrichum piliferum* | 0.0 | 0.1 | 1.7 | 12.5 | 0.7 |
| *Psilopilum laevigatum* | 0.0 | 0.0 | 0.2 | 0.0 | 0.0 |
| *Ptilidium ciliare* | 0.0 | 0.4 | 0.1 | 0.0 | 0.0 |
| *Racomitrium lanuginosum* | 0.0 | 5.2 | 1.1 | 0.4 | 2.3 |
| *Rhytidium rugosum* | 0.4 | 0.1 | 0.0 | 0.0 | 0.0 |
| *Tetraplodon pallidus* | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 |
| *Timmia* sp. | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Tortella fragilis* | 0.1 | 0.5 | 0.0 | 0.0 | 0.0 |
| **Lichens** | | | | | |
| *Alectoria nigricans* | 0.3 | 0.6 | 2.7 | 2.4 | 3.4 |
| *Alectoria ochroleuca* | 0.1 | 2.1 | 3.6 | 0.1 | 4.4 |
| *Arthrorhaphis alpina* | 0.1 | 0.0 | 0.0 | 0.3 | 0.1 |
| *Bryocaulon divergens* | 0.7 | 3.1 | 1.9 | 2.6 | 2.5 |
| *Caloplaca cerina* | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 |
| *Candelariella aurella* | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Candelariella placodizans* | 0.0 | 0.0 | 0.0 | 0.3 | 0.0 |
| *Catolechia wahlenbergii* | 0.0 | 0.0 | 0.0 | 0.1 | 0.1 |
| *Cetraria aculeata* | 0.0 | 0.1 | 1.2 | 1.0 | 0.7 |
| *Cetraria islandica* | 0.3 | 0.6 | 0.1 | 0.0 | 0.4 |
| *Cetrariella delisei* | 0.0 | 0.1 | 0.1 | 0.4 | 0.1 |
| *Cladonia gracilis* | 0.1 | 0.1 | 0.2 | 0.2 | 0.0 |
| *Cladonia mitis* | 0.0 | 0.0 | 0.0 | 0.1 | 0.0 |
| *Cladonia pleurota* | 0.0 | 0.6 | 2.7 | 10.8 | 0.2 |
| *Cladonia pocillum* | 0.0 | 0.2 | 0.0 | 0.0 | 0.0 |
| *Cladonia stricta* | 0.0 | 0.0 | 0.0 | 0.2 | 0.0 |
| *Cladonia uncialis* | 0.0 | 0.5 | 0.2 | 0.2 | 0.0 |
| *Flavocetraria cucullata* | 0.1 | 0.8 | 0.3 | 1.1 | 0.5 |
| *Flavocetraria nivalis* | 2.1 | 7.9 | 4.1 | 3.8 | 1.3 |
| *Fulgensia bracteata* | 0.1 | 0.9 | 0.0 | 0.0 | 0.0 |
| *Gyalecta foveolaris* | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Hypogymnia physodes* | 0.0 | 1.0 | 0.2 | 0.0 | 0.0 |
| *Hypogymnia vittata* | 0.0 | 0.3 | 0.0 | 0.6 | 0.0 |
| *Lecanora epibryon* | 2.9 | 2.7 | 0.1 | 0.0 | 0.0 |
| *Lecidea ramulosa* | 0.0 | 0.7 | 0.0 | 0.0 | 0.0 |
| *Micarea assimilata* | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 |
| *Nephroma expallidum* | 0.0 | 0.2 | 0.0 | 0.0 | 0.0 |
| *Ochrolechia grimmiae* | 0.0 | 0.4 | 0.1 | 0.0 | 1.0 |
| *Ochrolechia upsaliensis* | 0.3 | 0.8 | 0.0 | 0.0 | 0.0 |
| *Ochrolechia/Pertusaria* spp. | 10.7 | 11.5 | 15.0 | 12.6 | 9.1 |
| *Parmelia saxatilis* | 0.0 | 0.0 | 0.1 | 0.7 | 0.2 |
| *Peltigera kristinssonii* | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 |
| *Peltigera venosa* | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Pertusaria oculata* | 0.9 | 0.2 | 0.0 | 0.0 | 0.0 |
| *Pseudephebe pubescens* | 0.0 | 0.2 | 6.7 | 11.0 | 6.3 |
| *Psoroma hypnorum* | 0.0 | 0.1 | 0.3 | 0.0 | 0.0 |
| *Solorina crocea* | 0.0 | 0.0 | 0.8 | 5.9 | 0.0 |
| *Solorina saccata* | 0.1 | 0.1 | 0.0 | 0.0 | 0.0 |
| *Sphaerophorus globosus* | 0.1 | 3.2 | 5.2 | 7.1 | 2.9 |
| *Stereocaulon* sp. | 0.0 | 0.0 | 0.0 | 1.8 | 0.0 |
| *Thamnolia vermicularis* | 3.5 | 5.1 | 1.9 | 1.8 | 0.9 |
| *Vulpicida juniperinus* | 2.0 | 0.9 | 0.1 | 0.0 | 0.0 |

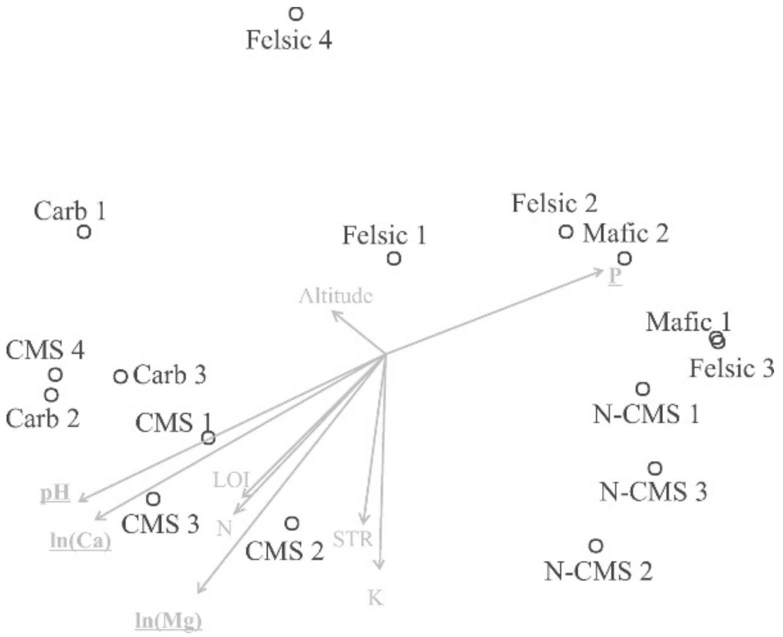

**FIGURE 4. Nonmetric multidimensional scaling of the sites based on the floristic data and the Bray Curtis dissimilarity to quantify the ecological distance between the sites. Environmental variables were overlaid on the result as arrows. The length of each arrow indicates the strength of the correlation between the variable and the nonmetric multidimensional scaling (NMDS), and its direction indicates the orientation of the gradient. Variables that were significantly correlated with the NMDS constellation are underlined (confidence level = 0.05). Carb = carbonate rocks, CMS = calcareous mica schist, N-CMS = noncalcareous mica schist, Mafic = mafic rocks, and Felsic = felsic rocks, LOI = loss on ignition, STR = soil texture ration (% clay and silt / % sand and gravel).**

It would be more suitable to refer to these species as carbonate specialists, since they appear adapted to the actual nutrient stress at such sites.

The impression in the field was that middle-alpine marble ridges had a low species diversity and supported plant individuals with a poor vegetative development. Ridges of calcareous mica schist had a higher diversity with well-developed specimens, e.g. *Astragalus alpinus* and *Rhododendron lapponicum*, which is typically absent on ridges of carbonate rocks. This was confirmed by the analyses of floristic data. The Shannon diversity index was low at carbonate sites and higher at calcareous mica schist sites, especially for vascular plants. In the CCA plot, sites on carbonate rocks and one site on calcareous mica schist occurred in the upper left corner (Fig. 5). These are species-poor sites occupied by

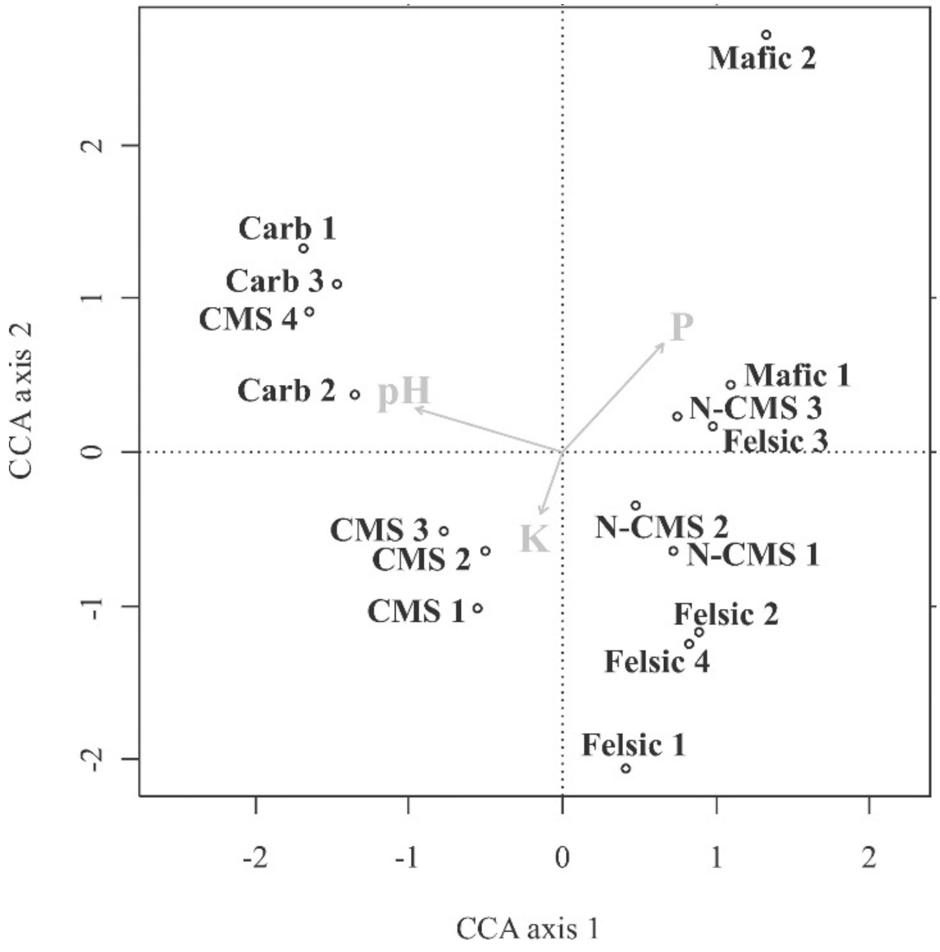

**FIGURE 5. Canonical correspondence analysis plot, showing the sites and the four variables related to soil chemistry. Carb = carbonate rocks, CMS = calcareous mica schist, N-CMS = noncalcareous mica schist, Mafic = mafic rocks, and Felsic = felsic rocks.**

TABLE 3

**Canonical correspondence analysis of the species data using selected edaphic variables. Scores of the different environmental variables along the first three axes of the analysis, pseudo-*F* values and associated *p*-values produced by a permutation test comparing the complete model with a model excluding the variable in question.**

| Variable | CCA-axis 1 | CCA-axis 2 | CCA-axis 3 | pseudo-*F* (*p*) |
|---|---|---|---|---|
| pH | −0.96 | −0.28 | −0.0061 | 3.42 (<0.005) |
| P | 0.66 | −0.71 | −0.26 | 2.25 (0.005) |
| K | −0.14 | −0.40 | −0.90 | 1.88 (0.035) |
| % of constrained inertia explained* | 53 | 26 | 22 | |

* Percentage of total inertia that is constrained = 41.

carbonate specialists. The species-rich sites on calcareous mica schist occurred as a distinct group lower and more centrally in the CCA plot. In known classifications of alpine and arctic areas, vegetation of exposed ridges on calcareous substrate is treated as one vegetation unit (often denoted Caricion nardinae or Kobresieto–Dryadion, in the classic phytosociological system). Our findings suggest, however, that the vegetation on ridges of carbonate rocks with basic soil pH is different from the vegetation on ridges of calcareous mica schists. Vegetation growing directly in soil originating from weathering of carbonate rocks is not rare in middle- and high-alpine environments or in the High Arctic (Scholander, 1934, Rønning, 1965, Edlund and Alt, 1989), and should probably be treated as a separate vegetation unit.

### *POTASSIUM AND MAGNESIUM*

The CCA indicated a relationship between floristic composition and the availability of potassium, although this relationship was less clear than that with pH and phosphorous. It is possible that a survey on a larger scale including more sites can throw more light on the relationship between flora and potassium availability.

Soil weathered from mafic rocks, which is the most magnesium rich bedrock category included in this study, had low magnesium values, indicating that the large amount of magnesium bonded in the dark minerals (pyroxenes and amphiboles) is not subject to extensive chemical weathering. Another interesting topic, which was not treated here, is the difference between dolomitic and calcitic carbonates. Both minerals are easily weathered, but calcite is less resistant than dolomite. On the other hand, dolomite carries, per definition, a larger proportion of magnesium carbonate in its mineral structure. This accounts for a great input of Mg to the soil. To assess the importance of Mg in different carbonate soils, it would be necessary to perform a comparative study, including several sites on dolomitic as well as calcitic carbonates.

## Conclusions

The present study has revealed the following patterns in the relationships between middle-alpine ridge vegetation and soil chemistry:

(1) Next to soil pH, which is correlated with carbonate mineral content, the availability of phosphorus is the soil factor most correlated with the primary floristic gradients, explaining a considerable amount of the floristic variation.

(2) The amount of calcium available in soil weathered from carbonate rocks exceeds the physiological requirement of the plant species present. This may also be the case in soil derived from calcareous mica schist, which, on the other hand, provides sufficient amounts of potassium. An excess of carbonate minerals leads to increased soil pH, which influences the availability of phosphorus, and possibly other nutrients, negatively. It may be more adequate to denote species growing on such substrates as carbonate specialists instead of "lime-demanding," which is widely used today. The vegetation composed of these carbonate specialists has low diversity and is different from the more diverse and vital vegetation of the alliance Caricion nardinae occurring on calcareous mica schist.

(3) Soil weathered from mafic rocks contains more phosphorus than soil derived from other bedrocks included in the present study. Variation in floristic composition, not explained by the calcium content, is associated with the availability of phosphorus. This variation is not correlated with pH, which demonstrates that this widely used parameter for soil conditions should be used with caution.

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