ALPINE PLANT COMMUNITIES: A STATISTICAL ASSESSMENT OF THEIR RELATION TO MICROCLIMATOLOGICAL, PEDOLOGICAL, GEOMORPHOLOGICAL, AND OTHER FACTORS

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Abstract: Floristic composition and environmental factors vary widely among plant communities in the alpine belt. Thus far no study has attempted to measure all relevant site conditions in a larger number of alpine communities. Here we show (1) which environmental factors were highly correlated with the floristic composition of the 14 plant communities investigated in the Swiss Alps and (2) which plant communities have similar environmental affinities. In every plant community investigated, the main factors potentially having an impact on plant life were measured and the floristic composition was defined. We used nonmetric multidimensional scaling (NMDS) to determine linkage between plant communities and complex environmental gradients. The first axis of the NMDS corresponds to a climate gradient (temperature/wind speed), and the second axis corresponds to a soil gradient (soil suction/pH/Ca content). With the exception of the Nardus grassland and Carex curvula turf, plant communities belonging to the same phytosociological class are exposed to very similar combinations of environmental factors. Our study shows that the variation between phytosociological classes is much larger than within classes. Still, the variation of environmental factors within individual classes leads to a further differentiation of the floristic composition. Thus, our study reinforces the validity of the phytosociological classification. [Key words: phytosociology, Alps, nonmetric multidimensional scaling NMDS, environmental factors, floristic composition.]

INTRODUCTION

Alpine vegetation near and above the treeline resembles a fine-scale mosaic composed of numerous, generally well delimited plant communities (e.g., Ellenberg,
The phytosociological method of vegetation classification assumes that each community is characterized by a site-specific range of environmental factors leading to differences in species composition (e.g., Dierschke, 1994). Floristic compositions of alpine plant communities and their ecological conditions were described for the first time at the end of the 19th and beginning of the 20th century (e.g., Stebler and Schröter, 1892; Brockmann-Jerosch, 1907; Rübel, 1911–1912). Since then, many phytosociological studies have contributed to classifying alpine vegetation (e.g., Grabherr and Mucina, 1993), and the ecological conditions of alpine plant communities have been described in numerous textbooks (e.g., Favarger and Robert, 1995; Ellenberg, 1996; Mertz, 2000).

Comparative studies that involve measured environmental factors, however, often include only a small number of environmental factors or communities. Previous investigations include micro-climatic studies (e.g., Gigon, 1971; Cernusca, 1976, 1989; Mosimann, 1985; Cernusca and Seeber, 1989a, 1989b) and analyses of soil nutrients and water status (e.g., Rehder, 1970, 1976; Gigon, 1971; Rehder and Schäfer, 1978; Körner et al., 1980, 1989; Galland, 1982; Friis, 1985; Mosimann, 1985; Wieser et al., 1989) for some alpine plant communities. Other studies have investigated the influence of herbivory (e.g., Cernusca, 1989; Dullinger et al., 2003), growing-season length (e.g., Klug-Pümpel, 1982; Wallossek, 1990; Kudo, 1991), solifluction (e.g., Johnson and Billings, 1962), and avalanches (e.g., Erschbamer, 1989) on vegetation.

Although the phytosociological relationships of the dominant plant communities in the Alps are well known, the microclimatological, pedological, and geomorphological factors governing these plant communities are not well documented. To the best of our knowledge, no study so far has attempted to measure all relevant site conditions in a larger number of communities. Thus, the aim of our field survey was to investigate the linkage between environmental conditions and floristic composition of 14 widely distributed, representative, and well-documented plant communities occurring in the alpine belt of the European Alps.

In this study, the main factors influencing plant life, as selected by Kammer and Möhl (2002), were measured or observed in each of the 14 plant communities. These factors are: air temperature, relative air humidity, wind speed, global radiation, UV-B radiation, growing-season length, soil moisture, main soil nutrients, pH, waterlogging, soil movement, denudation, avalanches, herbivory, wind damage, and freezing damage. The 14 plant communities investigated cover the main vegetation types of the area above treeline in the European Alps, including extreme habitats such as wind-exposed communities, scree slopes, and snowbeds. Thus, our study is expected to be representative for most of the different habitats occurring in the European Alps, with the exception of rock-surface, bog, and fen communities.

In this study, we first explored how the floristic composition of the plant communities is related to the different environmental gradients. Our aim was not to assess the variation of environmental factors within each community (this would have required a replicated experimental design) but rather to analyze the more general response curves along environmental gradients. Thus, we discuss the environmental variables that we found to be highly correlated with the floristic composition. Second, we determined how the plant communities belonging to the same
phytosociological class can be characterized by their specific combinations of environmental factors.

RESEARCH AREA

The present study was restricted to plant communities that occur widely throughout the Alps and are clearly defined in phytosociological literature (characteristic species) and habitat characteristics (Landolt and Urbanska, 1989; Grabherr and Mucina, 1993; Ellenberg, 1996). Fourteen plant communities were chosen in the field based on the close correspondence of their floristic composition (characteristic species, dominant species) and site factors (Table 1) with those of plant associations described in the existing phytosociological literature. Syntaxa names and classification follow Grabherr and Mucina (1993).

Field work was carried out in the western part of the Central Swiss Alps at Gemmi Pass and Grimsel Pass (Fig. 1). Grimsel Pass is situated in the crystalline Aare massif. Rankers and Podzols have developed on its siliceous bedrock made of granite and gneiss (Imhof, 1965–1978; Landolt and Urbanska, 1989). Long-term climate data are available from the meteorological station at Grimsel Hospiz (1980 m), roughly 1 km north of Grimsel Pass. The mean annual temperature at Grimsel Hospiz was 1.61°C during the period 1964–2004 (this and all subsequent values are derived from the on-line database of MeteoSwiss, Swiss National Meteorological Service). Northwesterly winds dominate. The mean annual precipitation total is 2130 mm, of which 62% falls as snow. The snow cover is thicker than 10 cm during 226 days of the year, and only 124 days were snow free on average. Maximum winter snow cover ranged between 1.9 m (1964) and 6.9 m (1970).
The substrata of the Gemmi area consist of Mesozoic sedimentary rocks generally rich in carbonates. Rendzinas and alpine Brown Earths have developed on the calcareous bedrock of this area (Imhof, 1965–1978; Landolt and Urbanska, 1989). The climate conditions at Grimsel Hospiz are also representative for the Gemmi area (Imhof, 1965–1978).

### Table 1. Characteristics of the Alpine Plant Communities Studied

<table>
<thead>
<tr>
<th>Abbr.</th>
<th>Community</th>
<th>Area</th>
<th>Alt.</th>
<th>Exp.</th>
<th>Slope</th>
<th>Cover</th>
<th>Characteristic species</th>
</tr>
</thead>
<tbody>
<tr>
<td>thl</td>
<td>Thlaspi repens scree community</td>
<td>Ge</td>
<td>2370</td>
<td>NW</td>
<td>27</td>
<td>32</td>
<td>Cerastium latiolum, Hutchinsia alpina, Linaria alpina, Moehringia ciliata, Thlaspi repens</td>
</tr>
<tr>
<td>leo</td>
<td>Leontodon montanus scree community</td>
<td>Ge</td>
<td>2280</td>
<td>S</td>
<td>23</td>
<td>11</td>
<td>Galium megalospermum, Leontodon montanus, Ranunculus parrasiifolius, Trietum distichophylllum, Viola cenisia</td>
</tr>
<tr>
<td>polG</td>
<td>Polytrichum sexangulare snowbed community Polytrichetum sexangularis</td>
<td>Gr</td>
<td>2182</td>
<td>–</td>
<td>–</td>
<td>92</td>
<td>Agrostis schraderana, Gnaphalium supinum, Polytrichum sexangulare, Salix herbacea, Soldanella pusilla</td>
</tr>
<tr>
<td>sal</td>
<td>Salix herbacea snowbed community Salicetum herbaceae</td>
<td>Ge</td>
<td>2460</td>
<td>–</td>
<td>–</td>
<td>85</td>
<td>Alchemilla pentaphylla, Cerastium cerastoides, Gnaphalium supinum, Salix herbacea, Taraxacum alpinum</td>
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<tr>
<td>salG</td>
<td>Salix herbacea snowbed community Salicetum herbaceae</td>
<td>Gr</td>
<td>2180</td>
<td>–</td>
<td>–</td>
<td>75</td>
<td>Arenaria biflora, Carex foetida, Gnaphalium supinum, Salix herbacea, Soldanella pusilla</td>
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<tr>
<td>ely</td>
<td>Elyna myosuroides turf Elynetum myosuroides</td>
<td>Ge</td>
<td>2275</td>
<td>W</td>
<td>0-5</td>
<td>87</td>
<td>Agrostis alpina, Arenaria ciliata, Elyna myosuroides, Oxytropis campestris, Potentilla crantzii</td>
</tr>
<tr>
<td>fir</td>
<td>Carex firma turf Caricetum firmae</td>
<td>Ge</td>
<td>2255</td>
<td>NW</td>
<td>24</td>
<td>90</td>
<td>Androsace chamaejasme, Carex firma, Chamorchis alpina, Dryas octopetala, Helianthemum alpestre</td>
</tr>
<tr>
<td>ses</td>
<td>Sesleria caerulea grassland Seslerio-Caricetum sempervirentis</td>
<td>Ge</td>
<td>2335</td>
<td>SE</td>
<td>27</td>
<td>64</td>
<td>Aster alpinus, Carduus defloratus, Carex sempervirens, Gentiana clusii, Sesleria caerulea</td>
</tr>
<tr>
<td>fer</td>
<td>Carex ferruginea grassland Caricetum ferrugineae</td>
<td>Ge</td>
<td>1895</td>
<td>NW</td>
<td>27</td>
<td>100</td>
<td>Anemone narcissiflora, Astragalus frigidus, Carex ferruginea, Festuca pulchella, Pulsatilla alpina</td>
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<tr>
<td>fes</td>
<td>Festuca violacea grassland Festuco-Trisetum thalii</td>
<td>Ge</td>
<td>2130</td>
<td>–</td>
<td>–</td>
<td>98</td>
<td>Alchemilla vulgaris, Crepis aurea, Festuca violacea, Poa alpina, Trifolium thalii</td>
</tr>
<tr>
<td>nar</td>
<td>Nardus stricta grassland Sieversio-Nardetum strictae</td>
<td>Ge</td>
<td>2125</td>
<td>SE</td>
<td>22</td>
<td>97</td>
<td>Arnica montana, Campanula barbata, Gentiana acuina, Geum montanum, Nardus stricta</td>
</tr>
<tr>
<td>curG</td>
<td>Carex curvula turf Caricetum curvulae</td>
<td>Gr</td>
<td>2240</td>
<td>S</td>
<td>0-22</td>
<td>82</td>
<td>Avenula versicolor, Carex curvula, Luzula lutea, Phyteuma hemisphaericum, Veronica bellidifolium</td>
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<tr>
<td>loiG</td>
<td>Loiseleuria procumbens heath Loiseleurio-Cetrarietum</td>
<td>Gr</td>
<td>2215</td>
<td>NE</td>
<td>17</td>
<td>80</td>
<td>Erythronium hermpaphroditum, Hieracium alpinum, Loiseleuria procumbens, Vaccinium gaultheroides, Vaccinium vitis-idaea</td>
</tr>
<tr>
<td>cic</td>
<td>Cicerbita alpina tall herb community Cicerbitetum alpinae</td>
<td>Ge</td>
<td>1765</td>
<td>SE</td>
<td>15</td>
<td>100</td>
<td>Achillea macrophylla, Adenostyles alliariae, Peucedanum oestruthium, Saxifraga rotundifolia, Viola biloba</td>
</tr>
</tbody>
</table>

*Abbr. = abbreviations of the community names used in the figures (syntax names according to Grabherr and Mucina, 1993); Area = study areas (Ge = Gemmi and Gr = Grimsel); Alt. = altitude in m a.s.l.; Exp. = exposure; Slope = slope angle in degrees; Cover = total vegetation cover in percent; Characteristic species = selection of species occurring in the communities under study.*
METHODS

Floristic Composition

In each plant community, the presence of vascular plant species was recorded for 10 randomly placed plots (1 m²) at the end of July 2002. The plots were spaced widely enough to minimize spatial autocorrelation within the visually homogenous surface of the community. The vegetation frequency data obtained in this manner were used for subsequent analyses.

Climatic Factors

Air temperature, relative air humidity, global radiation, and wind speed were measured in each plant community during the growing seasons of 2002 and 2003. Each climate station consisted of an anemometer (type f.555.1.18, Schiltknecht, Gossau, Switzerland, installed 100 cm above ground), an air-temperature and relative-air-humidity sensor (TRH 100, Pace Scientific Inc., Mooresville, N.C., USA, installed 15 cm above ground), a data logger (XR 440, Pace Scientific Inc., Mooresville, N.C., USA), and an amorphous solar cell (constructed at the Institute of Geography of the University of Bern, Switzerland, installed 40 cm above ground). Solar cells for measuring global radiation were produced and calibrated by Fischer (2002) using a pyranometer under natural irradiation conditions. The sensors were attached to a 1.3 m aluminum mast, with the part of the mast above the solar cells painted black to avoid reflection. Solar cells were mounted in a level position on the south side of the mast. Daily mean UV-B radiation was calculated from the measured daily mean global radiation data at the Gemmi and Grimsel Pass via an empirical model (Vonlanthen et al., 2004). Measurements of relative air humidity were converted to vapor pressure deficit (VPD; Warnecke, 1997).

Time and data were recorded in CEST (Central European Summer Time = UTC [Universal Time Coordinated] + 2 hours) in 10-minute intervals. These values then served as a basis on which to calculate the daily means. Missing daily mean values were interpolated using a linear regression. Microclimatic stations were intercalibrated in April 2002 (i.e., prior to the first field season), April 2003, and October 2003 (i.e., following the second field season). Days with a minimum temperature below 0°C (measured 15 cm above ground) during the growing season were defined as days with frost. Analyses are based on daily means of the period during which all climate stations were installed (July 12, 2002–September 19, 2002, and July 13, 2003–September 6, 2003).

Length of Growing-Season

Growing-season length was obtained for each community by determining the dates of snowmelt in spring and formation of a lasting snow cover in autumn, in 2002 and 2003. Plant communities were considered snow free as soon as snow had disappeared from 80% of the defined surface. Analyses are based on two-year mean values.
Pedological Factors

According to Körner (1994), periodic water shortage in the top 5 cm of soil may induce water stress in plant communities above the treeline. During periods of low precipitation, soil suction was therefore measured, using a Quick-Draw Tensiometer (Soil Moisture Equipment Corp., Model 2900F1, Santa Barbara, CA, USA) at a depth of 4 cm. Soil suction was measured once in July and once in August, both in 2002 and in 2003 (altogether four measurement campaigns). Each time, three randomly placed measurements were made within one day in every plant community. The Tensiometer was calibrated prior to each measurement. Analyses are based on mean values.

At the end of July 2003, five soil samples were randomly collected from the upper 5 cm of mineral horizons in each plant community. The samples were pooled to one composite sample per community. All soil samples for $N_{tot}$, NH$_4$, and NO$_3$ concentration measurements were placed in an icebox (–20º C) for up to three hours after sampling. Concentrations of soil nutrients, including $N_{tot}$, NH$_4$, NO$_3$, P, Mg, Ca, and K, as well as pH, were analyzed by Schweizer Samen AG (Thun, Switzerland) using standard methods described in FAL (1996). Concentrations of water-soluble K, Mg, and Ca were determined by atomic-adsorption spectroscopy, $N_{tot}$ by Kjeldahl distillation, and water-soluble NH$_4$, NO$_3$, and P by photometry. The content of $N_{org}$ was calculated as $N_{tot}$ – NH$_4$ – NO$_3$. Soil pH was measured by shaking 20 g of sieved soil with de-ionized water and measuring pH with a glass electrode in the solution extracted after 18 hours.

Geomorphological Factors

Frost heave was measured with an apparatus developed by the authors (Vonlanthen et al., 2004). In August 2002, in each plant community, a 1.4 m long steel rod was inserted 1 m into the ground. Two pipe clips were fixed onto the protruding part (40 cm) of the steel rod. The pipe clips held a transparent tube (28 cm) in a vertical position. A grey plastic tube (22 cm) passed vertically through the transparent tube, remaining free to move up and down with the heaving soil. A 3 cm long piece of foam rubber was placed inside the transparent tube on top of the grey tube. The foam rubber was able to move upwards but not downwards with the grey tube. Changes of position of the foam rubber piece were measured in August 2003. To protect the apparatus against freezing, it was covered by a 41 cm high plastic tube. This apparatus measures only the maximum extent of frost upheaval.

To measure lateral soil movement stones were labeled and aluminium stripes buried vertically to a depth of 40 cm in July 2002 in every plant community. The positions of the stones and the aluminium bands were measured in August 2002 and August 2003 using a Real-Time GPS (Leica GPS500, Heerbrugg, Switzerland, absolute precision 1.5 cm). Based on these data, changes in the position of the aluminium bands and the labelled stones were calculated. In summer 2003, the vertically buried aluminium bands were dug out to detect maximum soil movement at a depth of 0 to 40 cm.
The occurrence of avalanches in each community was estimated based on personal observations as well as on interviews with 10 persons familiar with the region. Avalanche frequency was quantified using a four-step scale from 0 (no avalanches) to 3 (regular occurrence of avalanches). Denudation of soil by water, snow, or wind was visually estimated and quantified using a five-step scale from 0 (more accumulation than denudation) to 4 (extremely high level of denudation).

Additional Factors

The proportion of waterlogged surface in each community was estimated (in %) during or after periods of heavy rainfall. In three permanently marked quadrats (0.25 m²) per community, wind damage (proportion of above-ground biomass damaged by wind, estimated to the nearest 5%), and herbivory (proportion of above-ground biomass removed by animals, estimated to the nearest 5%) were determined every two weeks during the growing season.

Data Analysis

The relationship between vegetation frequency data and environmental data was explored through ordination analysis, using detrended correspondence analysis (DCA) and nonmetric multidimensional scaling (NMDS; Kent and Coker, 1992; Ter Braak, 1995; Legendre and Legendre, 1998). We used both methods because there is currently no consensus on the most appropriate indirect ordination method (Kent and Coker, 1992; Ter Braak, 1995). DCA assumes a unimodal species response curve, whereas NMDS makes no such assumption, deriving configuration scores only from the rank order of the dissimilarities between samples or species (Faith et al., 1987). Where both methods produced similar results, we felt more confident that the patterns represented an inherent structure in the data. Because of the good agreement between DCA and NMDS, we only report the results obtained from the NMDS, which is the more appropriate choice for our dataset.

The analysis with NDMS was carried out with PC ORD (version 4.10 for Windows, McCune and Mefford, 1999). To reduce the noise of rare species, species occurring in fewer than three plots were deleted prior to analysis. The appropriate dimensionality for the ordination was determined by first running NMDS in autopilot mode with 50 runs for each of six dimensionalities; the lowest dimensionality was chosen that (1) showed substantial stress reduction compared to the next lowest dimensionality and (2) captured new information in all dimensions. In this dataset, ordinations were best described by two axes (instability < 0.00005). To ensure that the ordination avoids a local stress minimum, the analysis was then run 50 times using random starting configurations. The NDMS was run with 50 runs of the real data along with 100 runs with randomized data for a Monte Carlo test of significance.

Environmental variables were transformed to improve normality. The log (x) transformation was chosen for soil suction, Mg, K, P, herbivory, and frost upheaval; global radiation was square-root transformed.
RESULTS

Relationships between Floristic Composition and Environmental Factors (NMDS)

For examining patterns of community composition with respect to sites and environmental characters, a two-dimensional ordination obtained from NMDS was chosen (Fig. 2). A third dimension did not provide substantial stress reduction and did not add further information on environmental correlations. The ordination yielded a final stress value of 11.49 ($p < .01$), and the two axes accounted for 66% of the original variation in the dataset.

The arrows within the ordination diagram (Fig. 2) display the principal direction of variation and strength of correlation for major environmental variables. Only metric environmental variables with $r^2 > .35$, which influence every plant community investigated, are shown. Even though global radiation and Mg content also had $r^2 > .35$, they are not shown in the ordination diagram because these correlations are mainly driven by one site (Cicerbita tall-herb community). Axis 1 of the NMDS ordination is interpreted as a climate gradient (temperature/wind speed): the temperature increases and wind speed decreases along axis 1. Axis 2 is interpreted as a soil gradient (Ca/pH/soil suction): Ca, pH, and soil suction values increase along axis 2.

Fig. 2. NMDS: nonmetric multidimensional scaling of vegetation frequency data. Arrows indicate the direction and strength of correlation of variables with $r^2 > .35$. The sample sites are coded according to the phytosociological classes: ▲ = Mulgedio-Aconitetea; ◆ = Salicetea herbacea; ◆ = Loiseleurio-Vaccinietea; ▽ = Thlaspietia rotundifoli; △ = Seslerietea albicantis; □ = Carici rupestris-Kobresietea bellardii; ◆ = Caricetea curvulae. For abbreviations of the community names, see Table 1.
The plant communities of the Thlaspietea rotundifolii class (Thlaspi scree community and Leontodon scree community) are clustered in the upper left portion of the ordination space (Fig. 2), which is correlated with high pH values, high soil suction values, and high Ca contents. The Carex ferruginea grassland, the Carex firma turf, the Festuca grassland, and the Sesleria grassland, which belong to the class Seslerietea albicantis, have the same loadings on the soil-gradient axis but spread widely along the wind-speed and temperature gradient, with wind speed decreasing and temperature increasing from the Carex firma turf to the Carex ferruginea grassland. The Cicerbita tall-herb community (class Mulgedio-Aconitetea) is located on the right side of the diagram, corresponding to high temperature values and low mean wind speed. The Polytrichum snowbed and the two Salix snowbeds (class Salicetea herbaceae), the Loiseleuria heath (class Loiseleurio-Vaccinietea), and the Carex curvula turf (class Caricetea curvulae) occupy the lower left corner of the diagram, which corresponds to low pH values, low soil suction values, low Ca contents, and high mean wind speed. With the exception of the Salix snowbed at Gemmi Pass (situated on siliceous limestone; Döbeli, 1997), these plant communities occur on siliceous bedrock. Although the Nardus grassland belongs to the same class (Caricetea curvulae) as the Carex curvula turf, this plant community is situated in the middle of the ordination diagram. Finally, the Elyna turf (class Carici rupestris-Kobresietea bellardii) is located in the upper left corner of the diagram, corresponding to high wind speed, high Ca content, and high pH values.

Variation of Environmental Factors between and within Phytosociological Classes

Our study shows (Table 2; Fig. 3) that with the exception of the Nardus grassland and Carex curvula turf, plant communities belonging to the same phytosociological class are exposed to very similar environmental factor combinations when compared with communities belonging to other phytosociological classes. For example, all investigated snowbeds (class Salicetea herbaceae) were characterized by rare occurrence of avalanches (Fig. 3U), low pH (Fig. 3l), a low Ca content (Fig. 3L), short vegetation period (Fig. 3G), waterlogging (Fig. 3Q), and low soil suction values (Fig. 3H).

Moreover, this study reveals that scree slopes (class Thlaspietea rotundifolii) with their considerable soil movement and snowbeds (class Salicetea herbaceae) with their short vegetation period are extreme habitats for plants. Moreover, most of the grasslands investigated at Gemmi Pass (Carex ferruginea grassland, Carex firma turf, Festuca grassland, and Sesleria grassland—all from class Seslerietea albicantis) appear in the middle of the ordination (Fig. 2), thus indicating average conditions (Fig. 3) for the communities that we investigated. Furthermore, having favorable climate conditions and a good nutrient supply (Table 2; Fig. 3) the Cicerbita tall-herb community (class Mulgedio-Aconitetea) represents lush and ideal conditions for plant life near the treeline. Finally, even though the Elyna turf and Loiseleuria heath do not belong to the same phytosociological class, they occupy almost the same ecological niche, where plants have to deal with high wind speeds (Fig. 3E), a long snow-free period (Fig. 3G), and considerable frost heave (Fig. 3R). However, Loiseleuria heath is located on siliceous bedrock and Elyna turf on calcareous bedrock; hence, they differed completely in terms of soil nutrient contents (Figs. 3I–3P).
Fig. 3. Mean values of all environmental factors and their standard error (only for \( n > 1 \)) as measured in the 14 alpine plant communities listed in Table 1. (A) Global radiation (mean values from 2002 and 2003), (B) UV-B radiation (mean values from 2002 and 2003), (C) temperature (mean values from 2002 and 2003), (D) vapor pressure deficit (mean values from 2002 and 2003), (E) wind speed (mean values from 2002 and 2003), (F) days with frost (mean values from 2002 and 2003), (G) vegetation period (mean values from 2002 and 2003), (H) soil suction (mean values from 2002 and 2003), (I) \( \text{pH} \), (J) \( \text{P} \), (K) \( \text{Mg} \), (L) \( \text{Ca} \), (M) \( \text{N} \), (N) \( \text{NH}_4 \), (O) \( \text{NO}_3 \), (P) \( K \), (Q) \( \text{waterlogging} \), (R) frost heave (in the Sesleria grassland the apparatus was destroyed in winter 2002/2003), (S) soil movement recorded with the aid of aluminium strips, (T) soil movement recorded with the aid of marked stones, (U) avalanches, (V) denudation, (W) wind damage (mean values from 2002 and 2003), (X) herbivory (mean values from 2002 and 2003).
Even though plant communities belonging to the same phytosociological class are exposed to very similar environmental factor combinations, there is still considerable variation of the environmental factors remaining within phytosociological classes (e.g., lower wind speeds were measured in the Polytrichum snowbed than in the two Salix snowbeds).

**DISCUSSION**

*Relationships between Floristic Composition and Environmental Factors (NMDS)*

The measured metric environmental factors that were highly correlated with the floristic composition were soil suction, pH, Ca, temperature, and wind speed (Fig.
2). In the following, these factors will be discussed with respect to their linkage with plant community composition.

*Temperature.* Low temperatures affect biochemical reactions such as these involved in photosynthesis, thereby limiting plant productivity (Larcher, 1995; Brunold et al., 1996). Many experimental studies using open-top chambers to raise temperatures have shown that reproductive and growth processes in arctic and alpine species are limited by temperature (e.g., Henry and Molau, 1997). Apart from having direct effects on plant growth, higher temperatures most likely also lead to increased mineralization rates in soils (Haynes, 1986). Furthermore, temperature co-determines the length of the growing season, which is one of the frequently mentioned factors controlling the distribution of alpine plant species (e.g., Komárková, 1993; Stanton et al., 1994).

*Wind speed.* High wind speeds (e.g., measured in the Loiseleuria heath) can increase the abrasive mechanical effects of wind and lead to increased transpiration rates (e.g., Van Gardingen et al., 1991). Indirect effects of wind on vegetation may be even more important: (1) wind is the main factor in the horizontal distribution of snow (Franz, 1979); (2) it transports nutrient-rich soil particles (Franz, 1979); and (3) it accentuates the harsh microclimatic conditions of wind-exposed habitats (Körner, 1999).

*PH.* It is unlikely that pH per se affects plants, but there is evidence that mobilization and availability of nutrients increase with increasing pH (Sjörs, 1952).

### Table 2. Characteristics of Plant Communities Belonging to the Same Phytosociological Class

<table>
<thead>
<tr>
<th>Phytosociological classes</th>
<th>Main environmental similarities within phytosociological class</th>
<th>Main environmental dissimilarities within phytosociological class</th>
</tr>
</thead>
<tbody>
<tr>
<td>Scree slopes (class Thlaspietea rotundifolii)</td>
<td>Highest pH, highest soil suction values, regular occurrence of avalanches, highest denudation level, highest lateral soil movement</td>
<td>Climatic conditions, nutrient supply</td>
</tr>
<tr>
<td>Base-rich grasslands (class Seslietea albicantis)</td>
<td>Moderate ecological conditions, an exception is the high herbivory level</td>
<td>Climatic conditions, nutrient supply</td>
</tr>
<tr>
<td>Base-poor grasslands (class Caricetea curvulae)</td>
<td>Moderate herbivory level, low denudation level, low Ca content, moderate soil suction values</td>
<td>Climatic conditions, nutrient supply</td>
</tr>
<tr>
<td>Snowbeds (class Salicetea herbaceae)</td>
<td>Shortest vegetation period, low pH, low soil suction values, low Ca content, rare occurrence of avalanches, low denudation level, waterlogging</td>
<td>Climatic conditions, nutrient supply</td>
</tr>
<tr>
<td>Tall-herb community (class Mulgedio-Aconitetea)</td>
<td>Highest mean temperature, lowest mean global radiation, lowest mean wind speed, high contents of Mg and Ca</td>
<td>Nutrient supply</td>
</tr>
<tr>
<td>Loiseleuria heath (class Loiseleurio-Vaccinietea)</td>
<td>High wind speed means, longest vegetation period, considerable frost upheaval</td>
<td>Nutrient supply</td>
</tr>
<tr>
<td>Elyna turf (class Carici rupestris-Kobresietea bellardii)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Larcher, 1995). On the other hand, a high pH like that measured in the scree slopes lessens the availability of both micronutrient elements and the macro-element P for plants (Scheffer and Schachtschabel, 1998). Moreover, pH has an impact on the cation exchange capacity and is related to the base saturation. Recent investigations in the arctic tundra treat pH as a variable of interest in ordinations, often finding that it statistically explains a significant amount of variation among communities and species assemblages (van Raamsdonk, 1988; Timoney et al., 1993; Walker et al., 1994; Heikkinen, 1996; Heikkinen and Neuvonen, 1997).

Ca. The Ca content of soils mainly depends on soil pH and the geological substrate. Thus, it is no surprise that Ca content is also highly correlated with floristic composition. Many studies have shown that alpine plant distribution is strongly influenced by the abundance of calcium (e.g., Gigon, 1971; Körner, 1999; Michalet et al., 2002). This is corroborated in this study, in which plant communities on siliceous bedrock (Loiseleuria heath, Carex curvula turf, Polytrichum snowbed, and Salix snowbed on Grimsel Pass) and communities on calcareous bedrock form two well separated groups in the ordination (Fig. 2). Many species are found mainly on Ca-rich substrates (calciocole species) and others mainly on Ca-poor substrates (calciugue species).

Soil suction. On the scree slopes, where the driest soils occurred, water seeps away quickly but may be retained in deeper layers. The lack of water at the surface may be fatal during the juvenile stages of plants. Moreover, desiccation of the top soil layer can block mineral cycling (Körner, 1995). By contrast, in the snowbeds, with the wettest soils, waterlogging leads to anaerobic conditions during rainfall that can influence the floristic composition.

In summary, we found that temperature, pH, soil suction, wind speed, and Ca are likely to influence a community’s floristic composition directly or via their effects on other environmental variables, which, in turn, affect plant species occurrences directly. Temperature, soil suction, and pH (as an indicator of soil nutrient availability) are three of the indicator values identified by Ellenberg (e.g., Ellenberg et al., 1992). This study corroborates the importance of these factors in determining the ecological environment of plants. Other factors such as waterlogging, lateral soil movement, wind damage, and herbivory did not seem to play a primary role in controlling the floristic composition in most of the communities we studied.

Variation of Environmental Factors between and within Phytosociological Classes

Although, the Nardus grassland and Carex curvula turf plant communities belong to the same phytosociological class (Caricetea curvulae), these two communities differ considerably in site conditions and floristic composition (only 11% of all species are common to both plant communities). This difference is related to geologic substrate: our Carex curvula turf was located on siliceous bedrock, whereas the Nardus grassland was situated on calcareous bedrock. Therefore, the Nardus grassland harbors an unusually high proportion of calcicole species and shows affinities with the class Seslerietea albicantis. This might be a local deviation from what appears to be the general rule that plant communities that belong to the same phytosociological class are closely correlated with a specific combination of
environmental factors (Table 2; Fig. 3). Variation of environmental conditions within the classes are reflected in the floristic composition (e.g., the *Thlaspi* scree community and *Leontodon* scree community have only 13% of common species).

**CONCLUSIONS**

We found two environmental gradients to be most relevant to the linkage between the floristic composition of alpine plant communities and environmental conditions in the Swiss Alps: (1) the temperature/wind-speed gradient; and (2) the soil-suction/pH/Ca content gradient. The inverse relationship between wind speed and temperature along the first axis suggests that global change scenarios that only provide projections of temperature could also be used for alpine plant communities where wind is the dominant factor.

Our study reveals that with the exception of the *Nardus* grassland and *Carex curvula* turf, plant communities belonging to the same phytosociological class are exposed to very similar environmental factor combinations. Moreover, our study shows that the variation between phytosociological classes is much larger than within classes. Still, the variation of environmental factors within individual classes also leads to a further differentiation of the floristic composition. Overall, our study confirms the phytosociological classification, which assumes that differences in site conditions should translate into differences in plant communities in a predictable way.

Although this study generally supports existing phytosociological systems, it is highly recommended for future studies that existing databases should be expanded to include replicates of plant communities at different locations. This would allow a more detailed assessment of the extent to which each plant species responds to environmental factors independently and as a member of a community—that is, through interactions such as competition and facilitation and as affected by the existing species pool.

The plant communities investigated are all located within the central Swiss Alps and do not necessarily represent compositional patterns across the entire European Alps. It would be desirable to conduct similar studies in other alpine areas to improve the geographic scope of our scientific understanding of alpine plant communities.

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