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Principal component analysis of ecological indicator values of swiss alpine flora

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Abstract

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Indicator values for eight ecological parameters of 303 Swiss alpine and subalpine species were used to evaluate the preferences of the species and of main vegetation units, and to study the relation between the parameters. The species were divided into 15 different groups representing formal vegetation units which were indicated as snow fields, rocks and screes, meadows, swamps, arid vegetations, scrubs and forests. Most of these categories splitted according to calcareous or aciduous preferences. After principal component analysis the eight parameters were divided into three groups encompassing humus content, soil structure, humidity and continentality (group 1), light, temperature and nutrients (groups 2), and acidity (group 3). The humidity and acidity of the soil appeared to be the most important ecological parameters. The ecological preferences of species and vegetation units are discussed. Special attention was paid to species with identical indicator values and to the range in ecological preference of the species composition of six particular plots.

Key words: ecology, vegetation analysis, indicator values, Swiss alpine flora.

Introduction

Organisms can only survive when adapted to the conditions of their own habitat. Especially plants are strongly influenced by climatic and edaphic factors. A close relationship exists between soil and vegetation especially in alpine regions. The acidity, humidity, temperature and structure of the soil on a particular site determine largely the floristic composition of typical vegetations.

Ecological indicator values of the Swiss flora were gathered by Landolt (1977). Each species included was characterized by the response to ten ecological parameters, i.e. humidity, acidity, nutrients, humus, soil structure (dispersion and aeration), light, temperature, continentality, salt tolerance and life form. The last two parameters mentioned dealing with the alpine flora were omitted by Landolt (1984). The growth and vigour of plant species depends on the ability to compete and on the relation between ecological parameters, and can hardly be indicated by a few figures used like weighted averages (ter

Braak and Barendrecht 1986), without indication of variation and differentiation. However, numerical representations make easy evaluation and comparison of ecological preferences of species possible. An indication of ecological circumstances of a particular location can be obtained by using as many species as possible (Landolt 1977).

The classification of vegetation units is based on the occurrence of indicator and differential species and, on the highest levels of the system, on physiognomy. The associations and other categories described in this manner can be characterized by a special preference for only one or two ecological parameters and tolerance for large fluctuations of others. The classes of alpine scree, snow field and rock vegetations are subdivided in groups of associations preferring calcareous and aciduous soils, respectively. Associations growing under wet and moist conditions, and those which are found in arid situations are placed into several not related classes (Ellenberg 1978).

The indicator values compiled by Landolt (1977) were used to analyse ecological preferences of species and of particular locations.

Material and methods

At first a selection of mainly alpine and some subalpine species with the vegetation units in which they occur was taken from Rothmaler (1976). Species occurring in several different vegetation types like snowfields, rocks and meadows were gathered in two main groups of general calcicole or general calcifuge soils, respectively. From this first selection a list of 303 species of the Swiss alpine and subalpine flora was compiled with indicator values taken from Landolt (1977) and modified according to Landolt (1984). Special attention was paid to the indicator and differential species mentioned by Ellenberg (1978) and Runge (1986). The eight ecological parameters are:

- humidity of the soil
- acidity of the soil
- contents of nutrients in the soil
- content of humus in the soil
- soil structure (particle size and aeration)
- average light emittance
- average temperature during vegetation period
- continentality (fluctuations of air temperature and humidity)

The 303 species were divided in 15 different groups which are comparable to formally described vegetation units as indicated by Rothmaler (1976). These groups are:

- | | |
|--|--|
| 1 general calcicole species | |
| 2 general calcifuge species | |
| 3 snowfieldvegetation,
calcareous | Arabidetalia caeruleae |
| 4 snowfieldvegetation, aciduous | Salicetalia herbaceae |
| 5 rock and scree vegetation,
calcareous | Potentilletalia caulescentis,
Thlaspietalia rotundifolii |
| 6 rock and scree vegetation,
aciduous | Androsacetalia vandelli, Androsacetalia alpinae |
| 7 alpine meadows, calcareous | Seslerietalia variae |
| 8 alpine meadows, aciduous | Caricetalia curvulae, Nardetalia |
| 9 nutrient-rich meadows | Arrhenatheretalia |
| 10 wet meadows and swamps | Tofieldietalia, Caricetalia fuscae,
Montio-Cardaminetalia |
| 11 arid vegetations | Sedo-Scleranthetalia, Seslerietalia p.p.,
Festuca-Brometea p.p., a.o. |
| 12 serpentine rock vegetations | Drabetalia hoppeanae |

- | | |
|--|----------------------------------|
| 13 subalpine forests (low light conditions) | Erico-Pinetea, Vaccinio-Piceetea |
| 14 general meadow species without preference for groups 7 or 8 | |
| 15 alpine and subalpine scrub vegetation | Adenostyletalia, Artemisietalia |

The a-priori group division was used to prove the consistency of the present classification of vegetation units after an analysis of ecological indicator values.

The program package IRIS for multivariate analysis was used (van Raamsdonk 1986). Three steps were involved in the analysis. First, the Pearson correlation coefficients between the parameters were studied. Weighting factors were established for each parameter based on the correlation matrix and used to calculate the covariances. Secondly, principal component analysis was carried out according to the usual way based on the covariance matrix. The third step was the calculation of a weighted covariance matrix based on six parameters excluding humidity and acidity. Principal components were calculated in order to investigate the possibility of defining the two excluded parameters by means of the other six parameters used.

The species composition of six different localities were analysed by selecting the species in the principal component plots based on the covariance matrix of eight parameters. The localities were:

	elev.	exp.	type
Kühboden, Fiesch (Wallis)	2200	SE	silicate meadow
Märjelensee, Fiesch (Wallis)	2450	—	silicate scree
Lago di Cadagno, Val Piora (Tessin)	1930	—	swamp, dolomite
Albulapass (Graubünden)	2200	N	silicate rock, undeep soil
Albulapass (Graubünden)	2680	S	calcareous scree
Strelapass, Davos (Graubünden)	2300	SE	dolomite meadow

Results

A number of species showed the same indicator values. These species are listed in tab. 1. Nine out of 48 species preferring meadows on calcareous soils (group 7) belong to the Papilionaceae against one out of 53 in meadows on silicate soils. Similar observations can be made concerning nutrient-rich meadows (group 9: 12 monocotyledons out of 21 species) and wet meadows and pastures (group 10: 11 Cyperaceae out of 26 species). In four genera two or three species showed identical indicator values. These are listed in tab. 1. Three groups of ecological parameters could be recognised based on Pearson correlation coefficients. Values higher than ± 0.4 were given in tab. 2. Humidity, amount of humus, soil structure and continentality appeared to be closely related. The highest correlation was found between humus and soil structure, and between humidity and continentality. The amount of nutrients, light and temperature formed a second group. Correlation coefficients between acidity and the other parameters were below ± 0.3 , thus forming a parameter of its own.

The weighting factors of soil structure, light, temperature and continentality were set to 0.5 prior to calculating the covariance matrix, leaving the other weighting factors to 1.0. This setting was made because of the calculated correlation coefficients and of relative importance of ecological circumstances in the environment.

The first principal component was mainly determined by acidity (-0.738), humus (0.687) and humidity (0.516) and accounted for 39.89% of total variation. Acidity and

Tab. 1. List of taxa with identical indicator values. The scores on the first and second principal components of the points indicated in figure 2 are added.

Name	Group (IRIS code)	Indicator values	Component scores on	
			1st pc	2nd pc
<i>Hutchinsia alpina</i>	3	4 4 2 3 2 5 1 2	-0.021	0.051
<i>Soldanella minima</i>				
<i>Arenaria biflora</i>	4	4 2 2 4 4 4 1 2	0.096	0.002
<i>Primula integrifolia</i>				
<i>Cerastium latifolium</i>	5	3 4 2 2 2 5 1 3	-0.072	0.005
<i>Papaver rhaeticum</i>				
<i>Sedum atratum</i>				
<i>Saxifrage biflora</i>				
<i>Saxifraga moschata</i>				
<i>Galium helveticum</i>	5	3 5 2 2 2 5 1 3	-0.100	0.046
<i>Chrysanthemum halleri</i>				
<i>Achillea atrata</i>				
<i>Poa laxa</i>	6	4 2 2 2 2 4 1 3	0.007	-0.044
<i>Ranunculus glacialis</i>				
<i>Cerastium uniflorum</i>	6	3 2 2 2 2 5 1 3	-0.016	-0.079
<i>Eritrichium nanum</i>				
<i>Achillea nana</i>				
<i>Anemone narcissiflora</i>	7	3 4 3 3 4 4 2 3	-0.004	0.066
<i>Trifolium badium</i>				
<i>Trifolium thalii</i>				
<i>Hedysarum hedysaroides</i>				
<i>Astragalus frigidus</i>				
<i>Polygala alpestris</i>	7	2 4 2 3 3 4 2 3	-0.046	0.007
<i>Scabiosa lucida</i>				
<i>Bupleurum stellatum</i>	8	2 2 2 3 3 4 1 4	0.004	-0.090
<i>Armeria alpina</i>				
<i>Pedicularis kernerii</i>				
<i>Carex curvula</i>	8	2 2 2 3 3 5 1 4	0.000	-0.097
<i>Gentiana alpina</i>				
<i>Phyteuma globularifolium</i>				
<i>Senecio carniolicus</i>	8	2 2 2 4 3 5 1 4	0.027	-0.087
<i>Senecio incanus</i>				
<i>Pulsatilla alba</i>	8	2 2 2 4 4 4 2 3	0.052	-0.058
<i>Antennaria dioica</i>				
<i>Nardus stricta</i>	8	3 2 2 3 4 4 2 3	0.045	-0.040
<i>Geum montanum</i>				
<i>Potentilla aurea</i>				
<i>Gentiana kochiana</i>				
<i>Androsace carnea</i>	8	3 2 2 4 4 4 1 3	0.071	-0.034
<i>Androsace obtusifolia</i>				
<i>Androsace brigantiaca</i>				
<i>Euphrasia minima</i>				

Tab. 1. (continued)

Name	Group (IRIS code)	Indicator values								Component scores on	
		1st pc	2nd pc								
<i>Coeloglossum viride</i>	8	3	2	2	4	4	4	2	3	0.072	-0.030
<i>Astrantia minor</i>											
<i>Plantago alpina</i>											
<i>Campanula barbata</i>											
<i>Arnica montana</i>											
<i>Hypochaeris uniflora</i>											
<i>Leontodon helveticus</i>											
<i>Hieracium aurantiacum</i>											
<i>Crocus albiflorus</i>	9	3	3	4	4	4	4	2	3		
<i>Crepis aurea</i>											
<i>Phleum alpinum</i>	9	3	3	4	3	4	4	2	3		
<i>Poa alpina</i>											
<i>Veratrum album</i>	9	4	3	3	4	5	4	2	3		
<i>Trollius europaeus</i>											
<i>Trichophorum alpinum</i>	10	5	2	2	5	5	5	2	3		
<i>Eriophorum angustifolium</i>											
<i>Trichophorum cespitosum</i>	10	4	2	2	5	5	4	2	3		
<i>Carex nigra</i>											
<i>Sedum annuum</i>	11	2	2	1	3	3	5	2	3		
<i>Sempervivum montanum</i>											
<i>Nigritella nigra</i>	14	3	3	2	4	4	4	2	3		
<i>Thesium alpinum</i>											
<i>Bulbocodium vernum</i>	14	2	3	2	3	3	4	3	4		
<i>Lilium bulbiferum</i>											

Tab. 2. Pearson correlation coefficients (R) between seven ecological parameters. All values higher than ± 0.4 are shown, values below that limit only between parameters of the same group.

Humus content	1.0							
Soil structure	0.674	1.0						
Humidity	0.331	0.410	1.0					
Continentality	-0.219	-0.227	-0.625	1.0				
Light					1.0			
Temperature					-0.456	1.0		
Nutrients					-0.443	0.259	1.0	
	humus	soil	humid.	cont.	light	temp.	nut.	
			group 1			group 2		

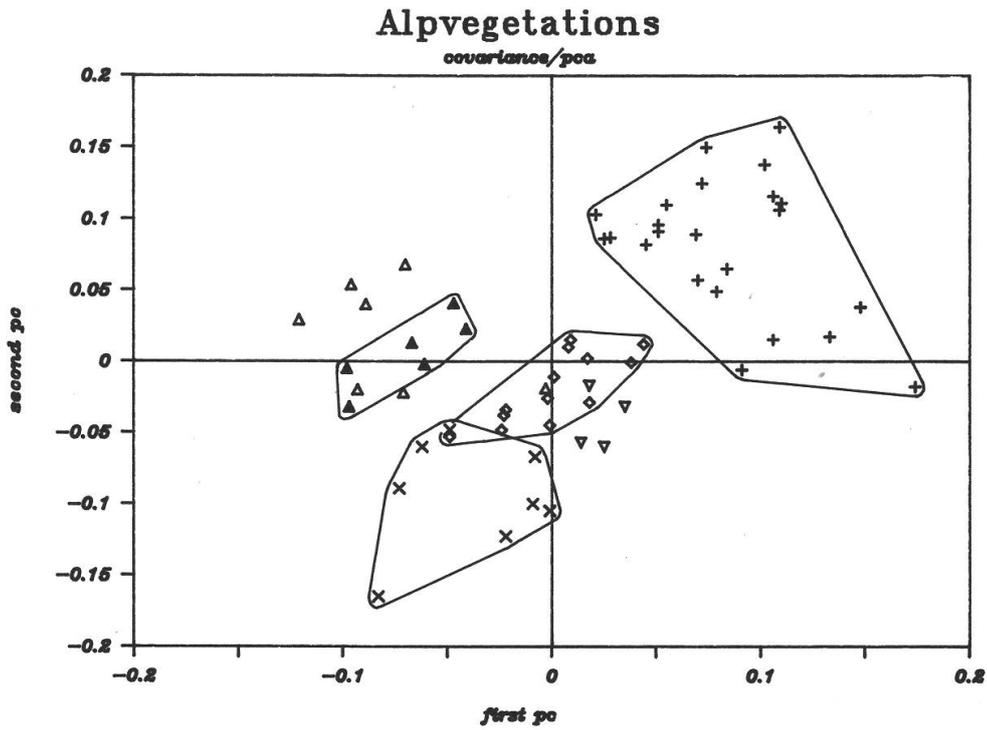


Fig. 1. Principal component diagram based on a weighted covariance matrix of ecological indicator values. Species preferring general calcicole soils (upper open triangles), general calcifuge soils (lower open triangles), general meadows (rhombs), serpentine (upper solid triangles), wet places (plus-signs) and arid places (×) are indicated.

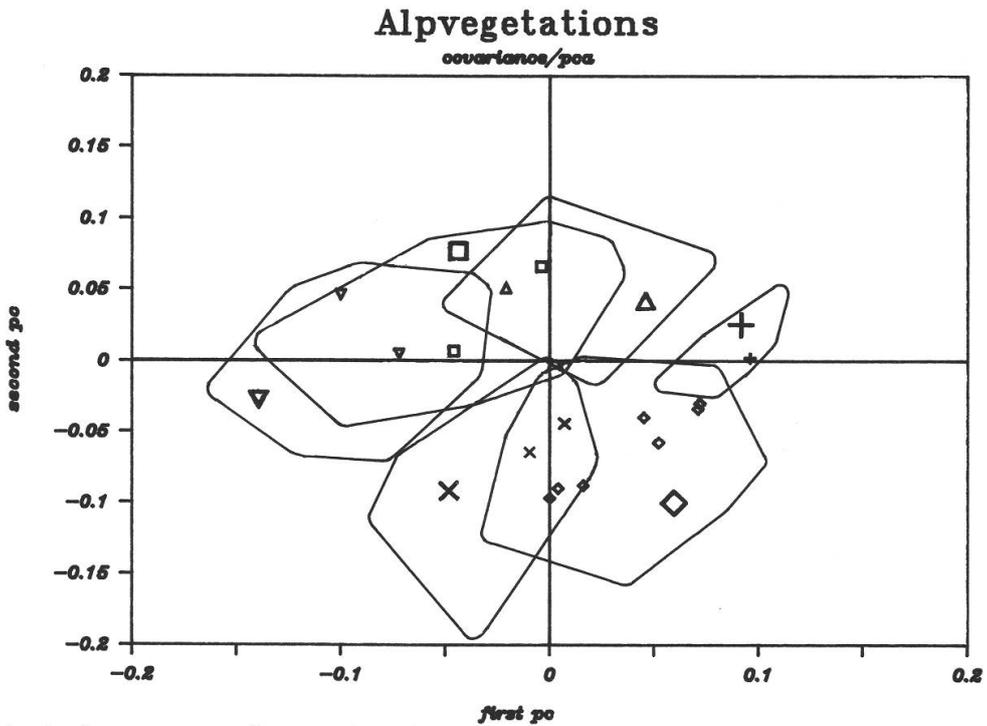


Fig. 2. Principal component diagram based on a weighted covariance matrix of ecological indicator values. Species preferring snowfields (calcareous: upper triangles, acidous: plus-signs), meadows (calcareous: squares, acidous: rhombs), screes and rocks (calcareous: lower triangles, acidous: x-es). Only one general sign each and the species with identical indicator values listed in table 1 are plotted. Individual plots of other species are deleted.

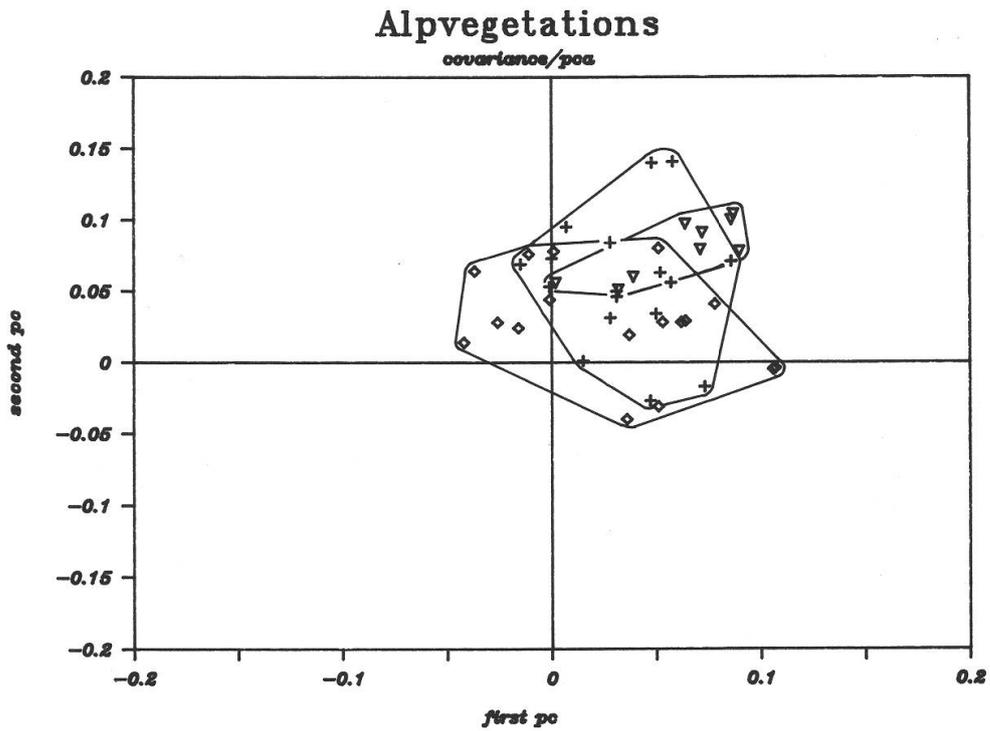


Fig. 3. Principal component diagram based on a weighted covariance matrix of ecological indicator values. Species preferring nutrient-rich meadows (plus-signs), forests (rhombs) and scrubs (lower triangles) are plotted.

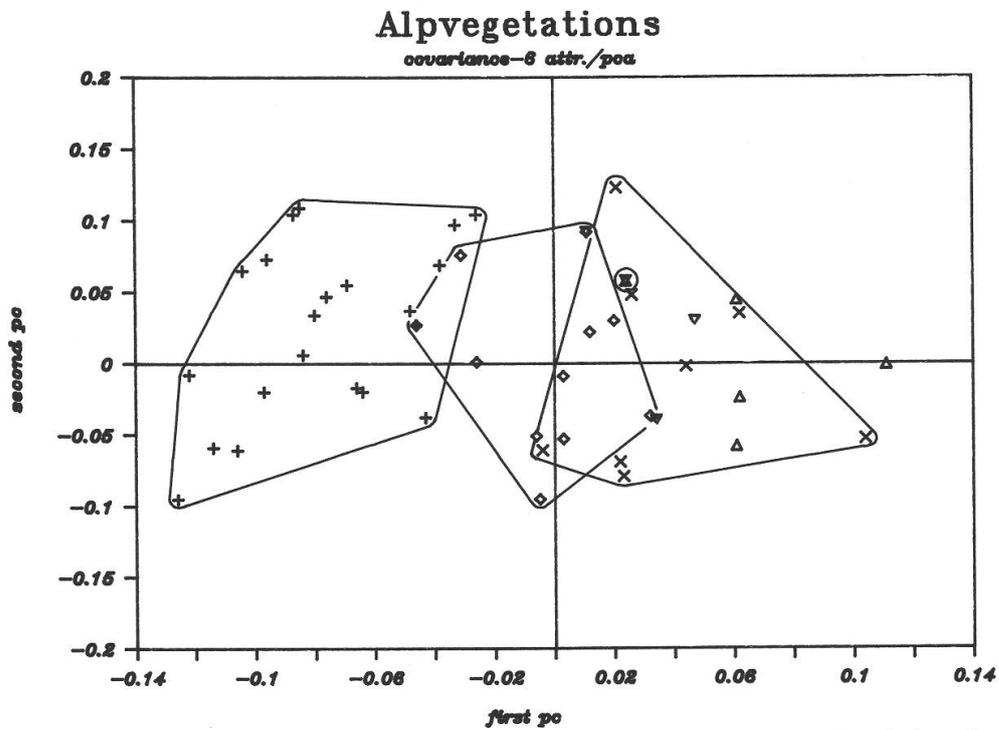


Fig. 4. Principal component diagram based on a weighted covariance matrix of six selected ecological indicator values. Species originating from wet places (crosses), general meadows (rhombs), general calcicole species (upper triangles), general calcifuge species (lower triangles) and arid places (times-sign) are plotted.

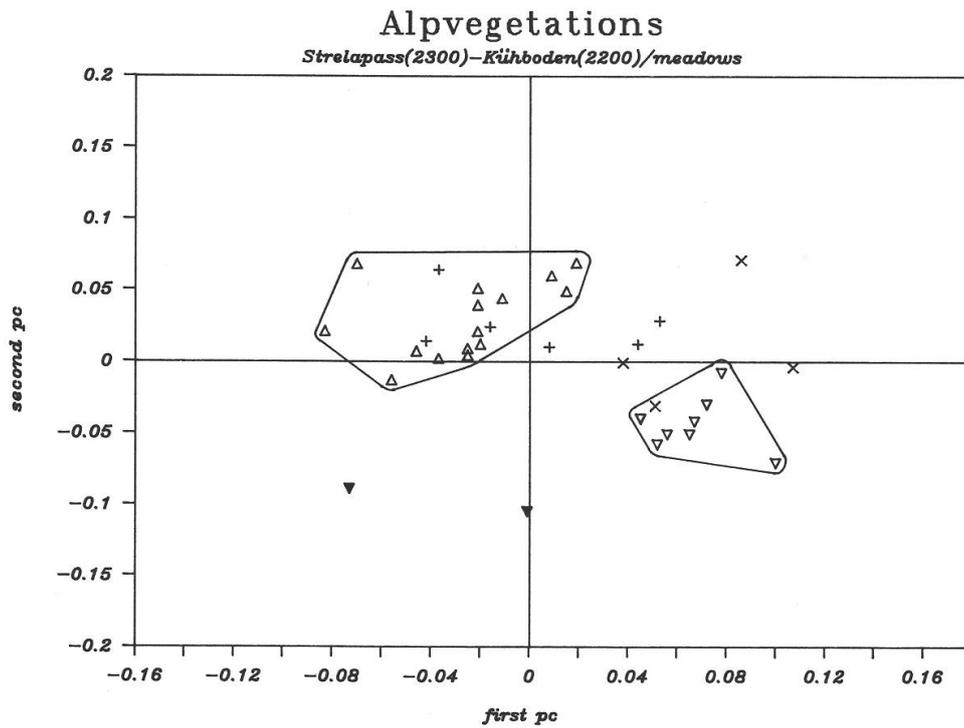


Fig. 5. Principal component diagram based on a weighted covariance matrix of ecological indicator values. Species originating from meadows on Strelapass (Graubünden; upper triangles, scrub inhabitants: plus-signs) and Kühboden (Wallis; lower triangles, scrub inhabitants: x-es, *Sempervivum* species: solid lower triangles) are plotted.

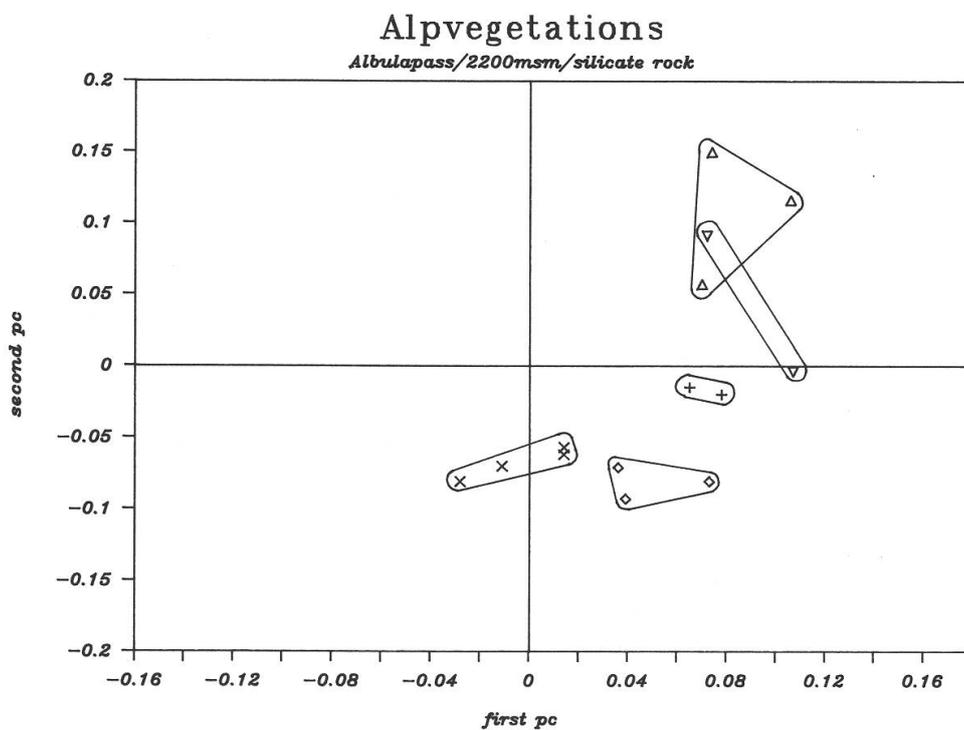


Fig. 6. Principal component diagram based on a weighted covariance matrix of ecological indicator values. Species originating from silicate rock on Albulapass (Graubünden) are plotted. The preferences are: rocks (x-es), meadows (rhombs), snowfields (plus-signs), low light conditions (lower triangles) and wet places (upper triangles).

humidity showed also high factor loads on the second principal component (0.720 and 0.484 respectively with 26.03% of total variation). Soil structure showed a moderately high factor load (0.410) on the first component unless the weighting factor of 0.5.

The component scores of each species were plotted against the first and second principal component. Some general groups were shown in fig. 1. One diagonal is determined by humidity with moist preferring species in the upper right part and species of arid places in the lower left part. Silicate preference is located in the lower right part against limestone preference in the upper left part of the plot. Species predominantly found on serpentine act like inhabitants of calcareous soils. Scree and rock vegetations, snow field vegetations and meadows are shown in fig. 2. Snow fields appeared to be moist on the average, while rocky places have a low humid soil compared to meadows. Fig. 3 shows the regions covered by representatives of nutrient-rich meadows, forests and scrubs. These prefer more or less moist habitats such as deep soils with good water capacity.

An attempt was made to compose humidity and acidity axes based on the other ecological parameters by setting the weighting factors of the two parameters to zero. The first principal component (50.15% of total variation) was mainly based on soil structure (-1.029) and humus content (-0.711) which determined a cline from wet to dry in fig. 4. Acidity was not expressed. Representatives of meadows on limestone and silicate shared the same region. Limestone and silicate preferring species were even located on the same place (circle in fig. 4). Inhabitants of meadows without special preference took an intermediate position in fig. 4.

The position of the inhabitants of two meadows is presented in fig. 5. The variability in ecological amplitude found in the dolomite meadow (Strelapass) is greater than represented by the inhabitants of the silicate meadow (Kühboden). All four species showing ecological parameters identical to *Nardus stricta* as listed in tab. 1 were found in the silicate meadow together with for instance *Arnica montana* and *Campanula barbata*. *Sempervivum montanum* and *S. tectorum* were accompanying species on dry patches. Several species were found on both locations which are also representatives of forest vegetations. Species with very different ecological preferences were found on a location of about 30 square metres on a steep rock with some soil patches at the Albulapass (fig. 6). Representatives of rock vegetations, silicate meadows, snow fields, forests and marshes were abundant, representing a whole range from dry to wet conditions. Species adapted to low light conditions survive because of the northern exposition and shady places. Two different species-poor locations on scree together with a marsh were analysed, demonstrating contrasts between dry and wet conditions, and between calcareous and silicate rock. The inhabitants of the marsh show a large ecological amplitude.

Discussion

The occurrence of related species in exactly the same habitat needs a close examination in relation to the possibility of sympatric evolution in plants (Grant 1981). The species pairs *Saxifraga moschata* and *S. biflora*, and *Trifolium thalii* and *T. badium* possess identical ecological preferences (tab. 1). However, the two species in both pairs belong to different species groups within the genus which indicates a parallel evolution (Hess et al. 1970). *Senecio carniolicus* and the related *S. incanus* are two geographically distinct species which are very closely related (Merxmüller 1952; Landolt 1984). These species can be regarded as being involved in a process of geographic evolution. The

allopatric species *Androsace carnea*, *A. obtusifolia* and *A. brigantia* belong to the same species group. The first two species are diploid inhabitants of silicate meadows and differ in some minor morphological characters. The morphologically intermediate *A. brigantia* occurs in a limited region in the southwestern Alps, is an aneuploid on the tetraploid level and shows a greater ecological amplitude compared to the other two species (Hess et al. 1970). *A. brigantia* can be considered to be an allotetraploid derivative of *A. carnea* and *A. obtusifolia*.

Several ecological circumstances vary greatly in relation with elevation (Ellenberg 1978): on higher levels in mountainous areas more light, especially ultraviolet, lower temperatures, greater temperature fluctuation (continentality) and a lower rate of production of soil (erosion) can be found compared to lower altitudes. When considered within the frame of the alpine flora these ecological parameters show less variation compared to factors like humidity, acidity and nutrient content of the soil (Ellenberg 1978). This relative importance is in agreement with the chosen weighting factors and the proposed groups of parameters.

The situation that acid soils are usually low in nutrient amount is not expressed in a high correlation. The nutrient content of the soil is associated with the occurrence of flowing ground water which offers an additional supply of nutrients. The floating water situation is not included in the numerical value of soil humidity, but in an additional letter (Landolt 1977). In an analysis of South African heath vegetations Low (1987) found no strong relation between high calcium content (acidity) and other high nutrient levels. Species with a low nutrient tolerance preferred acid soils with a low level of calcium. High nutrient preference was not related to calcareous soils (Low 1987). The range of acid preference in the inhabitants of wet places is far greater compared to drought-preferring species, which grow exclusively on silicate soils (fig. 1). This situation is due to the fact that large silicate mountain ranges are located predominantly in the dry inner Alps (Hess et al. 1967). Richard (1985) analysed 46 plots by using factor analysis based on the species composition. The first and second factor appeared to be determined by mainly the acidity and the mobility of the soil. A fairly large range of altitude was involved (Richard 1985).

A reverse relationship is indicated by Landolt (1977) between humidity and continentality which is illustrated by a strong negative correlation coefficient (tab. 2). Similarly a relation was found between the seed set and some climatic parameters in the *Ornithogalum umbellatum/angustifolium* group. Species originating from the coastal parts of western Europe (low continentality) showed a higher seed set in wetter seasons than in dryer years, while continental species showed the reverse situation (van Raamsdonk 1985).

A high humus content is strongly associated with low permeability, low ventilation and varying water content. The highest correlation coefficient was found in this group of parameters. For instance peat is mainly inhabited by indicators for oxygen deficiency (Landolt 1977).

Several microspecies were distinguished in the *Ranunculus montanus* group and in the *Cardamine pratensis* group which differ within each group with respect to humidity and acidity preference of the soil (Landolt 1971). These examples illustrate the important impact of both these ecological parameters on the vegetation structure. The correctness of classification of vegetation units according to acidity and humidity of the soil (Ellenberg 1978; Runge 1986) could not be proved for both parameters, since it was impossible to generate an acidity axis in the principal component plots based on the remaining parameters contrary to humidity which appeared to be related to several other parame-

ters (fig. 4 and 5). Indicator values for moisture obtained from Ellenberg (1979) were used to calculate average moisture values per plot based on the species composition (ter Braak and Gremmen 1987). Response curves were calculated for each species based on the average moisture values of the plots where each species was found. A reasonable consistency was found between the indicator values of Ellenberg (1979) and the recalculated averages from the response curves per species (Ter Braak and Gremmen 1987).

Landolt (1977) used the indicator values of species listed from several plots to discuss the ecological circumstances on these particular plots. The usefulness of multivariate methods to summarize the circumstances on selected locations is illustrated by the examples discussed.

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