

Plant species associations in alpine-subnival vegetation patches in the Central Caucasus

Kikvidze, Zaal

*Institute of Botany of the Georgian Academy of Sciences, Kojori Road 1, 380007 Tbilisi, Georgia;
Tel. +7 8832 997448; E-mail 20 BOTANY@COMPMATH.AOD.GEORGIA.SU*

Abstract. Patches of herbaceous vegetation found at the boundary of the alpine and subnival belts in the Central Caucasus (3000 m) were analysed for species composition, interspecific associations, as well as for relations between age, size and diversity of the patches. 34 plant species were recorded. Positive and negative associations were found among the most frequent species. A model is presented that describes the cumulation of species in patches during succession. In the final and stable successional stage, the maximum number of species within a patch was nine.

Species composition varies in patches of different age, typical alpine species being more frequent in older ones. The results are interpreted as evidence for niche differentiation and selection of species composition through the 'sieve' of interspecific relations, taking place during succession in the studied patches.

Keywords: High-mountain vegetation; Interspecific relation; Niche differentiation; Succession.

Abbreviations: FO = Frequency of occurrence; FC = Frequency of contacts; NS = number of species; MD = Mean diameter.

Nomenclature: Sakhokia & Khutsishvili (1975).

Introduction

Increased severity of environmental conditions at higher altitudes causes a fragmentation of the continuous vegetation cover of alpine meadows. Similar to the timberline, there is a 'meadowline', occurring at a fixed altitude, which serves as a demarcation line between the alpine and subnival belts. In the Central Caucasus the meadowline occurs at 3000-3100 m (Nakhutsrishvili & Gamtsemlidze 1984). The patches of this fragmented vegetation typically contain both alpine and subnival species, as well as those showing a wider altitudinal range. On the whole, the species composition is poor, in comparison with that of alpine meadow communities.

The aim of this study was to elucidate whether

interspecific associations have developed in the vegetation patches and whether such associations play a role in the formation of species composition.

Study area and Methods

Investigations were carried out at 3000 m a.s.l. near the Mamisoni Pass (43° 98' E, 43° 99' N) in August and September 1989. The climate of the area is humid, with short cool summers and long severe winters. The growing season starts at the end of June and lasts for only 10 weeks. The average temperature for January is ca. -12 °C and for July and August ca. 10 °C; average precipitation during the growing season is about 250 mm.

The studied vegetation patches are situated on a terrace on the edge of the main range at 3000 m. This terrace includes ca. 600 m² of skeleton soil surface covered with vegetation patches of mostly ellipsoid shape, which are more or less regularly scattered over the terrace. I have investigated 110 vegetation patches and performed separate relevés in each. The following data were recorded in addition to the species composition:

- MD, Mean diameter, calculated as the geometric mean of the largest and shortest diameters of a patch;

- NS, Number of species in a patch.

The relevés were combined into a table; the following values were calculated for each species:

- FO, Frequency of occurrence;

- FC, Frequency of contacts; a contact is defined as the joint occurrence of two species in the same patch, meaning that all the species in a patch were considered neighbours (Table 1).

From these data, 2×2 contingency tables were constructed and the data were analysed following Turkington, Cavers & Aarssen (1977). χ^2 values for interspecific associations were calculated in the usual way using Yate's correction (Yarranton 1966). If the contingency table has a large value for cell *d* (i.e. both species absent) species associations tend to be positive, unless *a* (frequency of cases with both species present) is zero.

To avoid this complication, associations of infrequent species, i.e. with $FC < 35$ were not calculated. The results of this analysis were confirmed using the association coefficient of Cole (1949) as modified by Hurlbert (1969). Both methods gave similar results. For most purposes the χ^2 method has been used.

Results

Interspecific associations

34 plant species were found in the vegetation patches (Table 1). Values for FO and FC, and altitudinal range according to Sakhokia & Khutsishvili (1975) and Dolukhanov (1968) are also indicated. The average values of FO and FC are 14 ± 17 and 58 ± 64 , respectively. Theoretically, there is a positive relation between FO and FC: the higher FO, the higher FC is. The regression equation is actually:

$$FC = 8.18 + 5.58 FO, r^2 = 0.92 \quad (1)$$

However, several species deviate strongly from this relation, showing FC significantly higher or lower than the theoretical values calculated from the above regression equation. Some species are most frequent in patches with higher NS-values: *Campanula biebersteiniana*, *Festuca ovina*, *Myosotis alpestris*, *Potentilla crantzii*; others are more frequent in patches with lower NS-values: *Aetheopappus caucasicus*, *Campanula saxifraga*, *Poa alpina*. This may imply that different combinations of species occur more frequently in patches with high NS-values, which in its turn would mean that species are replaced by other species during succession (see below).

FO-values of species may be taken as a function of their abundance. The frequency distribution appeared to be satisfactorily approximated by a log-normal relation (Fig. 1), which may indicate that interspecific associations determine the species distribution to some extent.

Species with FC-values < 35 could not be analysed because of their low frequency. Therefore, the species were divided into two groups:

(a) frequent or with $FC > 35$: 15 species (Table 1);

(b) infrequent species with $FC < 35$: 19 species.

The altitudinal range and, accordingly, the ecological characteristics of species differ considerably within and between these groups. The frequent species are predominantly represented by plants of a wider ecological range (8 of 15 species). Typical alpine plants are also involved, with five species, while typical subnival species are few, with only two. The group of infrequent species is ecologically more homogeneous; this group

Table 1. Statistics on plant species found in alpine-subnival vegetation patches: FO: Frequency of occurrence; FC: Frequency of contacts; FC*: theoretical values calculated from the regression equation, see text.

Species	FO	FC	FC*	Altitudinal range
Frequent species				
<i>Minuartia aizoides</i>	75	243	277	Alpine-subnival
<i>Potentilla crantzii</i>	47	202	175	Alpine
<i>Poa alpina</i>	41	125	155	Subalpine-subnival
<i>Campanula biebersteiniana</i>	58	190	144	Alpine-subnival
<i>Anthemis rudolfiana</i>	37	169	141	Higher alpine
<i>Festuca ovina</i>	31	148	119	Alpine
<i>Veronica gentianoides</i>	27	100	105	Subalpine-subnival
<i>Aetheopappus caucasicus</i>	26	74	101	Alpine-subnival
<i>Campanula saxifraga</i>	24	51	94	Alpine subnival
<i>Alchemilla sericea</i>	19	95	76	Subnival
<i>Anemone speciosa</i>	12	56	51	Alpine
<i>Androsace albana</i>	10	53	44	Subnival
<i>Draba hispida</i>	7	36	33	Alpine-subnival
<i>Arenaria lychnidea</i>	6	36	30	Alpine (talus)
Infrequent species				
<i>Luzula spicata</i>	6	33	30	Alpine
<i>Symphyloma graveolens</i>	6	28	30	Subnival
<i>Matricaria caucasica</i>	5	27	26	Alpine-subnival
<i>Saxifraga exarata</i>	5	17	26	Alp.-subniv. (talus)
<i>Carex tristis</i>	4	23	23	Alpine
<i>Anthemis iberica</i>	3	18	19	Alpine
<i>Kobresia schoenoides</i>	3	18	19	Alpine
<i>Polygonum viviparum</i>	3	23	19	Alpine
<i>Taraxacum confusum</i>	3	16	19	Alpine
<i>T. steveni</i>	3	13	19	Alpine
<i>Vaccinium vitis-idaea</i>	3	25	19	Alpine
<i>Campanula ciliata</i>	2	14	15	Alpine
<i>Pedicularis crassirostris</i>	2	13	15	Alpine
<i>Pulsatilla violacea</i>	2	13	15	Alpine
<i>Saxifraga kolenatiana</i>	2	7	15	Alpine (talus)
<i>Gnaphalium supinum</i>	1	1	12	Alpine (talus)
<i>Helictotrichon asiaticus</i>	1	3	12	Alpine
<i>Potentilla gelida</i>	1	3	12	Subnival
<i>Thlaspi pumilum</i>	1	6	12	Subnival

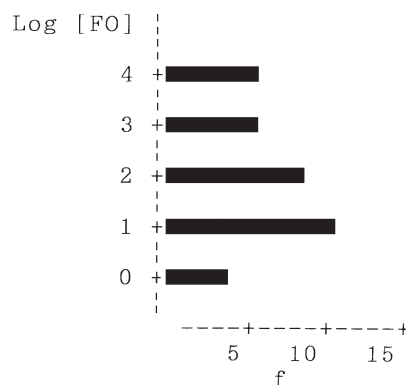


Fig. 1. Frequency distribution of plant species occurrence, FO, in vegetation patches.

consists predominantly of typical alpine meadow species (14 out of 19). Three species can be considered subnival and only two species have a wider altitudinal range.

The results of the association analysis are shown in Table 2. Five species: *Androsace albana*, *Anemone speciosa*, *Draba hispida*, *Poa alpina* and *Veronica gentianoides*, show a statistically significant (positive or negative) association with one another.

Two central species are *Campanula biebersteiniana* and *Potentilla crantzii*, showing interspecific associations with eight and six other species, respectively. The other species occupy middle positions in this range. However, no relation was found between FO and the number of associations ($r^2 = 0.14$).

Succession

In connection to succession there should be a relation between NS, as a parameter for species diversity, and MD, as a parameter for age. The statistical distributions of both values are similar, with coefficients of asymmetry equalling 0.8 ± 0.2 and 0.7 ± 0.2 , respectively, for NS and MD (Fig. 2). Mean NS is 4 ± 2.3 species per vegetation patch and MD averages 16 ± 6.7 cm. Hence a relation between the two variables may be suggested.

The relation can be analysed and modelled on the basis of the following observations and considerations: NS is higher in larger vegetation patches, i.e. with higher MD. However, increase in NS is limited by the carrying capacity *A*, or the maximum number of ‘vacancies’ for species in a community. We assume that the probability of the increase in NS with an addition of a new species is determined mainly by the difference $A - NS$, or the number of ‘vacancies’ at the given stage. Then the increment of NS during the growth in size of

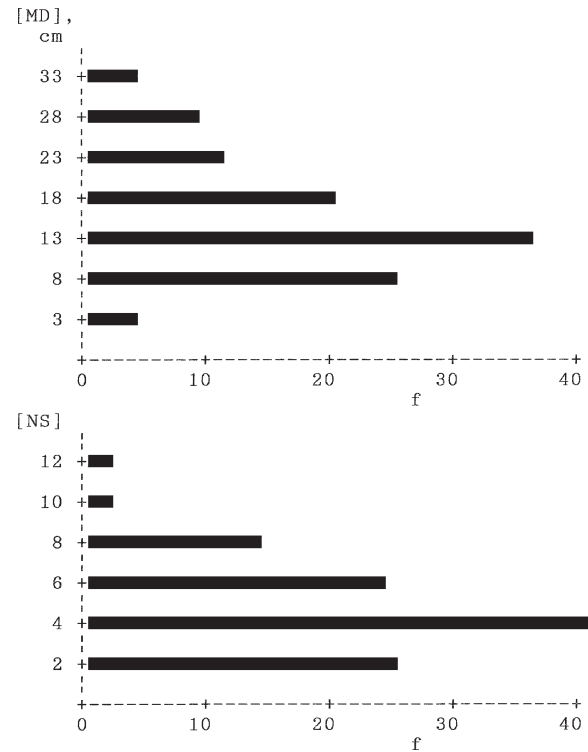


Fig. 2. Frequency distribution of number of species, NS, and mean diameter, MD, in alpine-subnival vegetation patches.

vegetation patches is expected to be proportional to the probability:

$$d[NS]/d[MD] = (A - [NS]) * k \tag{1}$$

where *k* is the proportionality coefficient of the probability of the growth of NS per cm of MD.

Integration and simple algebraic conversions give:

Table 2. Significant interspecific associations detected by χ^2 - analysis; + positive; – negative.

	Mai	Pcr	Pal	Cbi	Aru	Fov	Vge	Aca	Csa	Ase	Mal	Asp	Aal	Dhi	Aly			
<i>Minuartia aizoides</i>	x	-	+	—	—			
<i>Potentilla crantzii</i>	-	x	.	+++	.	.	.	—	—	+	.	.	++	.	.			
<i>Poa alpina</i>	.	.	x	—			
<i>Campanula biebersteiniana</i>	.	+++	.	x	+	+++	.	—	—	++	++	++	.	.	.			
<i>Anthemis rudolfiana</i>	.	.	.	+	x	++	.	.	-			
<i>Festuca ovina</i>	.	.	.	+++	++	x	.	.	-	.	+			
<i>Veronica gentianoides</i>	+	x	+	-	$p < 0.05$
<i>Aetheopappus caucasicus</i>	.	—	—	—	.	.	.	x	++	—	$p < 0.01$
<i>Campanula saxifraga</i>	.	—	.	—	-	-	.	.	x	-	+++	—	$p < 0.001$
<i>Alchemilla sericea</i>	.	+	.	++	-	x	+++	+
<i>Myosotis alpestris</i>	.	.	.	++	.	+	.	.	.	+++	x	+
<i>Anemone speciosa</i>	.	.	.	++	x
<i>Androsace albana</i>	.	++	x
<i>Draba hispida</i>	—	x
<i>Arenaria lychnidea</i>	—	+	+	x

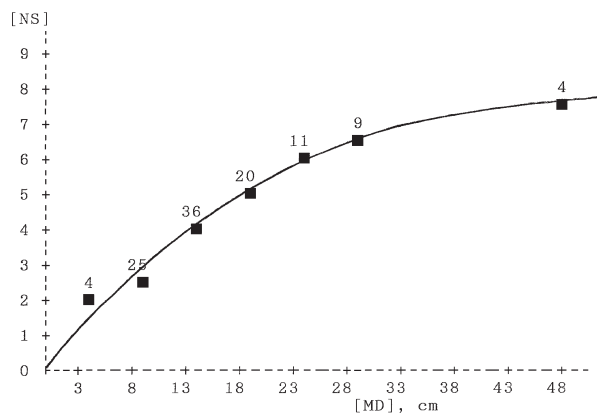


Fig. 3. Modelling the relation between number of species, MS, and mean diameter, MD, in vegetation patches.

■ = Mean values of class intervals. Numbers above symbols show statistical weight of each mean value.

$$[NS] = A \{1 - \exp(-k * [MD])\} \quad (2)$$

The equation represents an exponential hyperbolic function without extremes or turning points at $NS > 0$ and $MD > 0$, asymptotically tending to the limit $(NS) = A$. The model can be fitted by choosing the highest coefficient of correlation between the observed data and the values calculated theoretically from the regression equation $NS = A - A * x$, where $x = \exp(-k * MD)$, for different values of k . This gives (Fig. 3):

$$[NS] = 9 \{1 - \exp(-0.45 * [MD])\} \quad (3)$$

($r^2 = 0.98$). Hence, a close approximation is obtained. However, it should be noted that the relation is statistical, i.e. it can be found when a significant number of records are ranked in class intervals and the relation between the means are estimated.

The main idea of the model is that vegetation patches are gaining new species while growing in size, consequently, both NS and MD can serve as a measure of vegetation patch age. The relation between size and age is used, e.g. for dating of moraines by means of size measurements of *Silene acaulis* cushions (Benedict 1989). I preferred to use the value of NS, since it is directly related to the diversity of species composition. Accordingly, the vegetation patches may be condition-

Table 3. Distribution of plant species in the vegetation patches with different number of species.

Col. 1: Pioneer stage (NS = 2); Col. 2: Seral stage (NS = 3 - 4); Col. 3: Climax stage (NS = 5 - 8).

Species	% patches containing the species		
	1	2	3
<i>Minuartia aizoides</i>	64	67	70
<i>Potentilla crantzii</i>	4	31	74
<i>Poa alpina</i>	28	49	35
<i>Campanula biebersteiniana</i>	0	26	65
<i>Anthemis rudolfiana</i>	0	26	65
<i>Festuca ovina</i>	0	19	54
<i>Veronica gentianoides</i>	4	26	61
<i>Aetheopappus caucasicus</i>	28	31	14
<i>Campanula saxifraga</i>	36	26	7
<i>Alchemilla sericea</i>	0	9	35
<i>Myosotis alpestris</i>	0	2	28
<i>Anemone speciosa</i>	0	9	20
<i>Androsace albana</i>	4	0	20
<i>Draba hispida</i>	0	2	12
<i>Arenaria lychnidea</i>	0	2	11
Number of infrequent species	11	13	32

ally divided into three age groups:

- younger ones containing 2 species (25 patches);
- medium ones with 3 - 4 species (42 patches);
- older ones with 5 - 8 and more species (43 patches).

FO-values for frequent species in these three groups are presented in Table 3. FO-values for infrequent species are not included; instead, their total numbers per patch type are given. As one can see, species show clear differences in their distribution throughout the age groups indicating succession in the vegetation patches.

Discussion

The species may be divided into two groups: (a) frequent species showing statistically significant inter-specific associations, and (b) infrequent species without such relations. The low FO-values and predominance of alpine meadow plants in the latter group may be accounted for by the occasional occurrence of these species over their ecological range. On the other hand, the larger ecological heterogeneity of frequent species may be explained by the boundary position of the studied vegetation patches between alpine and subnival belts. The rarity of typical subnival plants may be due to the relatively low altitude of the study site and the neighbouring influence of the West Caucasus which is characterized by a poor subnival flora - the Mamisoni Pass is the west point of the Central Caucasus. In turn, the high frequency of eurytopic species may indicate extreme

ecological conditions.

There is clear evidence for a succession taking place in the vegetation patches, where species composition is selected through the sieve of interspecific relations:

1. The frequent species show statistically significant associations.
2. The maximum number of species in a vegetation patch, the 'carrying capacity' (A) as estimated by means of the regression model, equals 9, which is significantly lower than the total number of recorded species, even considerably less than the number of frequent species, suggesting a strong selection and substitution of species through successional stages.
3. FO-values for different species vary strongly in vegetation patches of different age (Table 3).

Consequently, the species can be arranged into four types according to their relation to succession:

- highly frequent at every stage, 'dominant type', represented by *Minuartia aizoides*;
- species found predominantly at the pioneer stage, 'pioneer type', represented by *Campanula saxifraga* and, to some extent, also by *Aetheopappus caucasicus*;
- species found mostly at an intermediate stage, 'seral type', represented by *Poa alpina* and partly *Aetheopappus caucasicus* and *Veronica gentianoides*;
- species found mainly in the final stage, 'climax type', represented by all other frequent species and especially by alpine meadow plants constituting the majority of infrequent species (Table 3).

No interspecific associations were observed in the vegetation patches of the pioneer stage. At the seral stage the dominant species, i.e. *Minuartia aizoides*, shows positive association with *Veronica gentianoides*, while a negative association is found between *Aetheopappus caucasicus* and *Poa alpina*. Most of the associations are found in the final stage: *Minuartia aizoides* shows negative associations with *Arenaria lychnidea*, *Draba hispida* and *Potentilla crantzii*. Positive associations occur quite frequently among almost all climax species; most of the positive associations are shown by the frequent species *Potentilla crantzii*, *Campanula biebersteiniana*, *Alchemilla sericea* and *Myosotis alpestris*.

Negative associations may be of two kinds: the first type is due to competition between ecologically equivalent species. This may result in the exclusion of one species by another without changing the ecological niche structure in the community. The second type reflects the substitution of species during succession and is connected with niche differentiation. Obviously, the first type particularly includes negative associations between species of the same successional stage, such as *Poa alpina* vs. *Aetheopappus caucasicus*, or *Minuartia aizoides* vs. *Potentilla crantzii*, vs. *Draba hispida* and

vs. *Arenaria lychnidea*. Apparently, competition in these pairs is due to a similar strategy and life form: the last-mentioned four species build loose cushions.

The second type of negative association may be attributed to the competition between plants of subsequent successional stages. Examples:

Campanula saxifraga vs. *Potentilla crantzii*
Campanula biebersteiniana
Anthemis rudolfiana
Festuca ovina
Alchemilla sericea
Aetheopappus caucasicus vs. *Potentilla crantzii*
Campanula biebersteiniana

Positive associations in most cases may be explained by the growing together of species with different life forms and/or strategies. For instance, maintenance of favourable conditions can be provided for the germination and growth of plants in the cushions built up by other plants. This is the case with *Veronica gentianoides* in cushions of *Minuartia aizoides*, *Androsace albana*, *Alchemilla sericea* and *Campanula biebersteiniana* in cushions of *Potentilla crantzii*, *Alchemilla sericea* and *Myosotis alpestris* in cushions of *Arenaria lychnidea*. Similar positive relations have been reported for severe environments, for instance in arid communities in central Mexico between cacti and 'nurse' shrubs (Valiente-Banuet et al. 1991).

Certain specific plant interactions in these alpine vegetation patches may imply a selective 'sieve' for nearby potential invaders. This may explain why many abundant species of alpine meadows at the same altitude such as *Sibbaldia parviflora*, *Geranium gymnocaulon* and *Phleum alpinum* can not penetrate into the vegetation patches, whereas species such as *Potentilla crantzii*, *Anthemis rudolfiana*, *Festuca ovina* and *Anemone speciosa* occur there frequently.

Considering the ecological properties of the species which are replaced during succession, one may conclude that the survival conditions within vegetation patches change considerably for many plant species with growing age of the patch, with a trend of facilitating the invasion of more specialised alpine species. This may explain the significantly increased frequency of typical alpine species in the climax stage. It is remarkable that *Campanula saxifraga*, which occurs in pioneer patches is a petrophyte, whereas *Campanula biebersteiniana*, which substitutes the former species in climax patches, is a typical species of alpine carpets and meadows.

Hence, the ecological conditions, predominantly the soil structure, change during the growth and formation of patch communities. Similar developments were found by Ohsawa & Yamane (1988) in patch communities on

maritime rock outcrops.

Conclusion

The results of this analysis demonstrate that vegetation patches at the boundary of the alpine and subnival belts possess the principal properties of 'real' plant communities, including interspecific relations and succession with niche differentiation. The quantitative simplicity and simultaneous presence of communities of different age make them a convenient model for ecosystem research.

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