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Facilitation in subnival vegetation patches

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Abstract. We examined spatial relationships among species in the subnival zone of the central Caucasus. The species composition of 300 vegetation patches was analysed. 144 of them contained only one species, whereas the other 156 contained 2.36 ± 1.31 species, with species numbers distributed as follows: 59 patches with two species, 41 with three, 39 with four and 17 with five species.

In the multi-species patches, the 22 most frequent species were examined and 46 statistically significant species associations, 36 positive and 10 negative, were found. Ten of these 22 species were typical subnival plants very rarely occurring at lower altitudes. The other 12 species are 'invaders' as they have broader altitudinal ranges of occurrence and are common in alpine and even in subalpine belts. Contrary to the typical subnival species the invaders were found exclusively in the patches with more than one species. Invader species were significantly more associated with subnival species while they were significantly less associated with other species than expected by chance. Our interpretation is that typical subnival species nurse plants from lower altitudes and facilitate their invasion to more adverse subnival environments.

Keywords: High elevation; Plant-plant interaction; Species association.

Nomenclature: Sakhokia & Khutsishvili (1975).

Introduction

Evidence for positive interactions among plants has been found in a wide range of stressful environments, such as deserts (Franco & Nobel 1989; Valiente-Banuet et al. 1991; Franco-Pizaña et al. 1995, 1996), arctic tundra (Carlsson & Callaghan 1991), salt marshes (Bertness & Leonard 1997; Hacker & Gaines 1997; Callaway 1994; Callaway & Sabraw 1994) and savannas (Belsky 1994; Callaway et al. 1991).

Positive plant-plant interactions have also been found in subalpine and alpine communities (Holtmaier & Broll 1992; Kikvidze 1996). At the alpine-subnival ecotone in the central Caucasus species interactions have been traced through the calculation of species associations. Positive associations appear to occur more often than negative associations and there is evidence for facilitation in small, developing vegetation patches found here (Kikvidze 1993).

Positive plant-plant interactions may be particularly important in severe environments (Callaway 1995; Callaway & Walker 1997; Holmgren et al. 1997). The subnival belt between 2900-3100 m and 3700-3800 m elevation of the Central Caucasus is an exceptionally adverse environment where small patches of vegetation exist in an 'alpine desert' within a matrix of bare ground (Nakhutsrishvili & Gamtsemlidze 1984). In this environment facilitation may be performed by some plants nursing others. If so, positive species associations between nurses and 'nursed' plants may be found in the patches of subnival vegetation. We compared spatial associations among typical species common to subnival and alpine zones in order to estimate the frequency, direction, strength and specificity of plant-plant interactions.

Material and Methods

The study area is located near the Mamisoni Pass (42° 39' N, 43° 41' E) with an elevation ranging from 3100 to 3750 m a.s.l. We randomly chose 300 vegetation patches (diameter 5 - 15 cm) and recorded their species composition. Patches with single species were considered ‘solitary plants’, species associations were tested in patches with more than one species using 2×2 contingency tables as described earlier by Kikvidze (1993).

Observed numbers of significant associations were compared to expected figures derived from the number of species. Significance of differences between observed and expected numbers were tested by the χ^2 criterion which was calculated by the following equation:

$$\chi^2 = \sum\left[\left(Observed - Expected\right)^2 / Expected\right] \qquad (1)$$

Results and Discussion

Of the 300 sampled patches 144 were composed of only one species, i.e. of solitary plants. The other 156 patches contained from two to five species (Table 1), with a mean value of 2.36 ± 1.31 (standard deviation). This extreme poverty of vegetation patches was also found by Kaźmierczak (1997; Kaźmierczak et al. 1995) in an entirely different wetland environment described with widely fluctuating water levels. In the multi-species patches, the 22 most frequent species (occurring in > 5% of the patches) were examined. Their altitudinal ranges and habitat characteristics, according to Dolukhanov (1968), Sakhokia & Khutsishvili (1975) and Nakhutsrishvili & Gamtsemlidze (1984), are shown in Table 2. Among these plants 46 statistically significant species associations, 36 positive and 10 negative, were found (Table 3).

Table 1. Species number in 300 vegetation patches in the alpine-subnival ecotone near the Mamisoni Pass, Central Caucasus.

Number of species	Number of patches
1	144
2	59
3	41
4	39
5	17

We examined our results by organizing species into two basic groups: (1) ‘subnival’ species which rarely occur at low altitudes and (2) ‘invaders’ which are also common in alpine (2600 - 3000 m a.s.l.) or even subalpine (1700 - 2600 m) belts. Two kinds of species may be distinguished. Ten of the 22 most frequent species are typically subnival species which very rarely occur at lower altitudes; they are marked by an asterisk in Table 3. The other 12 species are invaders. All of the 300 sampled patches contained at least one subnival species, whereas the invaders were found exclusively in patches with more than one species.

Remarkably, out of 65 possible interspecific combinations, invaders had developed 22 significant positive associations with subnival plants. Invader species were significantly more associated with subnival species and significantly less associated with other species

Table 2. The 22 most frequent species found in the vegetation patches.

Species	Occurrence	Altitudinal range	Habitat
Poa alpina	71	Alpine-subnival	Skeleton substrate
Alchemilla sericea	38	Subnival	Near stones
Anthemis sosnowskyana	38	Subnival	Skeleton substrate
Potentilla crantzii	29	Subalpine-subnival	Skeleton substrate
Minuartia inamoena	28	Alpine-subnival	Skeleton substrate
Carum caucasium	24	Subalpine-subnival	Skeleton substrate
Minuartia aizoides	23	Alpine-subnival	Skeleton substrate
Sibbaldia semiglabra	18	Alpine-subnival	Near snow
Saxifraga flagellaris	16	Subnival	Skeleton substrate
Saxifraga moschata	16	Subnival	Skeleton substrate
Alopecurus glacialis	15	Subnival-nival	Between stones
Potentilla gelida	15	Subnival	Skeleton substrate
Symphyoloma graveolens	15	Subnival	Skeleton substrate
Taraxacum porphyranthum	15	Alpine	Skeleton substrate
Tripleurospermum subnivale	15	Subnival	Between stones
Campanula biebersteiniana	14	Alpine-subnival	Between stones
Veronica minuta	14	Subnival	Skeleton substrate
Festuca supina	12	Alpine	Skeleton substrate
Minuartia trautvetteriana	11	Alpine-subnival	Skeleton substrate
Veronica gentianoides	9	Subalpine-subnival	Skeleton substrate
Cerastium cerastoides	8	Alpine-subnival	Skeleton substrate
Delphinium caucasium	8	Subnival	Skeleton substrate

Table 3. Statistically significant species associations in subnival vegetation patches.

*Alchemilla sericea**																					
Alopecurus glacialis	–																				
*Anthemis sosnowskyana**	·	·																			
Campanula biebersteiniana	+	·	·																		
Carum caucasium	·	·	·	+++																	
Cerastium cerastoides	·	·	·	·	+																
*Delphinium caucasium**	·	·	·	·	·	·															
Festuca supina	·	·	++	·	·	·	·														
*Minuartia aizoides**	++	·	++	·	·	·	·	·													
Minuartia inamoena	·	·	·	·	–	·	·	·	·												
Minuartia trautvetteriana	·	·	·	++	+	·	·	·	·	·											
Poa alpina	·	– –	++	·	·	·	–	·	+	+	·										
Potentilla crantzii	++	·	+	·	·	·	·	·	+	·	·	·									
*Potentilla gelida**	·	·	–	+	+++	·	·	·	·	·	+++	·	·								
*Saxifraga flagellaris**	·	·	–	·	+++	·	·	·	·	·	+++	·	·	+++							
*Saxifraga moschata**	++	·	–	·	·	++	+	·	·	·	·	–	·	·	·						
Sibbaldia semiglabra	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·					
*Symphyoloma graveolens**	·	·	·	·	·	·	·	·	·	+	·	+	·	·	·	·	·				
Taraxacum porphyranthum	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·			
*Tripleurospermum subnivale**	·	·	–	·	·	+++	·	·	·	·	·	·	·	·	·	·	·	·	·		
Veronica gentianoides	·	·	·	·	·	·	·	·	+	+	·	+	·	·	·	·	·	·	·	·	
*Veronica minuta**	·	·	·	+	+++	+++	·	·	·	·	+++	·	·	+++	+++	·	·	·	·	·	·

* = Typical subnival species. Significance: +, – = $p < 0.05$; ++, – – = $p < 0.01$; +++, – – – = $p < 0.001$.

than expected by chance ($\chi^2 = 9.5$; df = 1,3; $p < 0.01$). The proportion of positive associations among subnival species were as expected from the species number (8 versus 8.3). Subnival species appear to nurse plants from lower altitudes and facilitate their occupation of much more adverse environments.

It should also be noted that a large number of one-species patches consisting of subnival species may not have a 'partner' amongst the invading species. Only 23 of the 144 one-species patches included were formed by the 10 subnival plants listed in Table 2 (those marked with an asterisk in Table 3). All other patches with one species (121) were formed by solitary subnival plants found very rarely in multispecies patches. They are listed in Table 4 and discussed by Nakhutsrishvili & Gamtsemlidze (1984).

Our results suggest that positive interactions are crucial to the structure and diversity of subnival communities, and that these interactions are not random among species, but highly species-specific.

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Table 4. Subnival species occurring as solitary plants in one-species patches (121) which were very rarely found in multispecies patches.

Aetheopappus caucasicus	*Coridalis alpestris*	*Lamium tomentosum*	*Scrophularia minima*
Alopecurus dasianthus	*Draba supranivalis*	*Lloidia serotina*	*Sedum tenellum*
Androsace albana	*D. bryoides*	*Luzula spicata*	*Senecio karjaginii*
Antennaria caucasica	*D. siliquosa*	*Nepeta supina*	*S. sosnowskyi*
Arenaria lychnidea	*Erigeron uniflorus*	*Phrine huetii*	*S. taraxacifolius*
Campanula saxifraga	*Eunomia rotundifolia*	*Podospermum meyerii*	*Silene lychnidea*
Cerastium polymorphum	*Gnaphalium supinum*	*Primula bayernii*	*Thlaspi pumilum*
Cerastium kazbek	*Jurinella moschus*	*Pseudovesicaria digitata*	*Trisetum spicatum*
Chaerophyllum humile	*J. subacaulis*	*Saxifraga exerata*	*Viola minuta*
Colpodium versicolor	*Jurinia filicifolia*	*S. sibirica*	*Ziziphora puschkinii*

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