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MYCORRHIZA, VEGETATIVE MOBILITY AND RESPONSES TO DISTURBANCE OF ALPINE PLANTS IN THE NORTHWESTERN CAUCASUS

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Abstract: The hypothesis of a trade-off between vegetative mobility and mycorrhizal infection has been examined. The rate of root arbuscular-mycorrhizal (AM) infection and the extent of vegetative mobility (clonal with annual mobility more than 2 cm, clonal with annual mobility less than 2 cm, and non-clonal) was determined for 77 species in four alpine grassland communities in the Teberda Nature Reserve, the Northwest Caucasus, Russia. The percentage of AM species was similar (74–77%) in all four communities. The mean rate of AM root infection did not differ significantly between four communities. It was shown that vegetatively mobile species (annual mobility > 2 cm) had on average a lower rate of root AM infection than species with low or no vegetative mobility. Our results conform with the mycorrhizal infection-vegetative mobility trade-off hypothesis.

Gap-preferring species in a highly disturbed alpine meadow (burrowing activity of small and large mammals) had lower rate of root AM infection than species preferring undisturbed microsites. This pattern was also found within two larger families, viz. *Poaceae* and *Asteraceae*.

INTRODUCTION

Mycorrhiza is well represented in closed alpine communities (SELIVANOV 1981, READ & HASELWANDTER 1981, MAKSIMOVA 1986, SHAVKUNOVA 1987, BLASCHKE 1991, VARE et al. 1997), although effective mycorrhizal symbiosis is lacking at the highest elevation in the subnival belt (HASELWANDTER & READ 1980, SELIVANOV 1981). Arbuscular mycorrhiza (AM) as well as ericoid mycorrhiza are common types for high mountain areas (LESICA & ANTIBUS 1986, STOYKE & CURRAH 1991, GARDES & DAHLBERG 1996). Among the 120 studied alpine species (90 genera, 37 families) in the present study area (Teberda Nature Reserve), 83 species had AM, four species had ericoid mycorrhiza, three species had orchidoid mycorrhiza, two species had ectomycorrhiza and 28 species from 12 families were non-mycorrhizal (BAIKALOVA & ONIPCHENKO 1988).

In natural communities, both mycorrhizal (FITTER & NICHOLS 1988, READ & BIRCH 1988, SMITH et al. 1992) and clonal connections (STUEFER & HUTCHINGS 1994, STUEFER et al. 1996) may enhance the establishment of young plants by supplying them with resources, thus making them more tolerant of environmental harshness and increasing their competitive ability. However, since in both cases there is a considerable carbon cost either to feed mycorrhizal

hyphae (up to 20% of assimilates; FINLAY & SODERSTROM 1992) or to establish rhizomes or stolons (up to 40% of its parents dry weight; CALLAGHAN 1987), one may assume that plants will invest more in only one of these possibilities. In other words, we may observe a trade-off between vegetative mobility and mycorrhizal infection.

Mycorrhizal networks are sensitive to soil disturbance (JASPER et al. 1989, MCLELLAN et al. 1995). Yet, mycorrhiza seems to be less important for plants occupying disturbed areas where competition for nutrients and light is evidently reduced. For example, many species that can be classified as ruderals by GRIME et al. (1988) belong to *Brassicaceae* or *Caryophyllaceae*, and most of the species of these families are non-mycorrhizal (HARLEY & HARLEY 1987, SMITH & READ 1996). One would expect that such a pattern is also valid on a fine scale, i.e. species which are more dependent on mycorrhiza are those which mostly grow in dense established stands, while those species which clearly prefer gaps are less dependent on mycorrhiza or even non-mycorrhizal.

Severe abiotic conditions in the alpine zone make recruitment and nutrient absorption by plants more difficult, as compared to temperate grasslands (BLISS 1971). Alpine soils are poor in phosphorus, so mycorrhiza seems to be very important for alpine species (BLISS 1985). Alpine plant communities differ considerably in productivity, which influences mycorrhizal infection. Thus, alpine communities may be used to compare plant mycorrhizal status, clonal growth ability and inclination to grow in disturbed patches.

In this paper, information about the root colonization of alpine grassland species by AM fungi is provided. The rate (degree) of mycorrhizal infection is considered to be a useful parameter to describe the abundance of AM fungi in the roots (VAN DER HEIJDEN et al. 1998), although the degree of root infection is not directly related to the effectiveness of nutrient uptake, protection from pathogens, etc. by the fungal strains infecting the root (ALLSOPP & STOCK 1994). We focused on the correlation between the root infection rate, plant growth form and plant response to disturbance. In particular, we address three questions:

(1) What is the rate of root AM colonization in alpine grassland species and are there any differences between the four community types?

(2) Is mycorrhizal root colonization more extensive in plants without vegetative mobility?

(3) Is mycorrhizal root colonization less extensive in species preferentially occupying natural gaps in alpine meadows?

MATERIALS AND METHODS

Study area

The study area is located in the alpine zone of the Mount Malaya Khatipara, Teberda Nature Reserve, Karachaevo-Cherkessian Republic, the NW Caucasus, Russia; 43'16°N, 41'41°E; altitude: 2700–2800 m.

Four plant communities were investigated: alpine lichen heath (ALH); *Festuca varia*-grassland (FVG); *Geranium gymnocaulon-Hedysarum caucasicum* meadow (GHM); and alpine snowbed communities (SBC) (see ONIPCHENKO 1994a,b). Alpine lichen heaths (ALH) are communities of low productivity with fruticose lichens as the main dominants (mostly *Cetraria islandica*). They occupy windward crests and slopes. Snow cover in winter is thin or practically absent, and the stony soil freezes deeply. Grasslands dominated by *Festuca varia* (FVG) are firm-bunch-grass productive communities with great accumulation of a dead plant material in the aboveground layer. They occupy warm slopes and are relatively

rich in species. Forb meadows with predominating *Geranium gymnocaulon* and *Hedysarum caucasicum* (GHM) are the most productive alpine communities in the study area. They develop in sites with significant snow cover and a short growing season (2.5–3 months). High population density and the burrowing activity of a vole (*Pitymys majori* THOMAS) are typical for the community. Alpine snow-bed communities with low productivity occupy sites where snow accumulates (depressions and the bottoms of glacial cirques). Short-rosette and draft-trailing plants predominate in this community (*Sibbaldia procumbens, Taraxacum stevenii*, and *Gnaphalium supinum*); the growing period is usually less than 2 months.

The communities develop on alpine mountain meadow soils (Umbric Leptosols) which are the most widespread soil type in the area's alpine zone. The soils are shallow with a well developed turf horizon. They have a high stone content, acid or strong acid reaction, considerable humus accumulation in the upper horizons, and low rate of base saturation. The soils are poor in available nitrogen, phosphorus and calcium, but rich in potassium due to the parent rock material (ONIPCHENKO 1994a,b).

Sampling of AM

Thin roots (less than 2 mm in diameter) from at least five plants in each community were collected and fixed in 4% formaldehyde solution for mycorrhizal analysis. The roots were collected during the second half of August 1984. Fixed roots were macerated in 20% KOH for 2–3 months. This period of maceration was long enough to produce soft colourless roots. The more rigid dark roots of several species (*Anemone speciosa, Sibbaldia procumbens*) were additionally heated in the same solution for one hour. Then the roots were watered and stained with aniline blue (0.1 g aniline blue + 50 g lactic acid + 100 g water) for 1 hour. After removal from the stain solution the samples were put in pure lactic acid for half an hour. The root samples were then kept in glycerol. Thin roots (less than 0.5 mm in diameter) were studied microscopically where mycorrhizal infection was well represented. The total number of microscopic fields (× 120) was 130–150 for each sample. The amount of endophytic fungi was estimated on Selivanov's scale (SELIVANOV 1981) from absent (0) to very abundant (5 points):

Point	Description
1	Mycorrhizal fungi are present in few mesoderm cells
2	About 1/4 of mesoderm cells are occupied by fungi
3	About 1/2 of mesoderm cells are occupied by fungi
4	About 3/4 of mesoderm cells are occupied by fungi
5	Practically all of mesoderm cells are occupied by fungi.

The rate of mycorrhizal infection was calculated as:

$$\frac{S \,.\, 100\%}{N \,.\, K}$$

where S equals the sum of points for all microscopic fields, N is the number of microscopic fields, and K is the highest point of the scale (5). The full list of investigated species and their infection rates were published by BAIKALOVA & ONIPCHENKO (1988).

Vegetative mobility

Vegetative mobility was characterized by morphological investigations in the field (see POKARZHEVSKAYA 1995 for a description of the method). According to their morphological characteristics, the alpine community species studied were classified into 2 groups: (1) moderate or high vegetative mobility (annual rhizome/stolon increment more than 2 cm), and (2) no or low vegetative mobility (increment less than 2 cm per year). *Minuartia aizoides* and *Anthoxanthum odoratum* are typical representatives of mobile species, while *Carex* spp., *Festuca* spp. or *Geranium gymnocaulon* represent the group of species with low mobility (see Appendix for more detailed data).

Responses to disturbance

Responses to natural zoogenic disturbance (gap formation) were investigated in GHM by ONIPCHENKO & RABOTNOVA (1994). Two types of gaps were studied: (1) mesogaps (with a typical size of 1000–10,000 cm^2) formed as a result of the burrowing activity of large mammals (bears, wild boars); and (2) microgaps (with a typical size of 100–1000 cm^2) formed as a result of vole activity. We estimated the occurrence of alpine species in the gaps and the control (undisturbed plots) using small plots (100 cm^2 for microgaps and 625 cm^2 for mesogaps, $n = 250$ and 270, correspondingly). All species were divided into 2 groups: (1) species whose frequency was significantly higher in the meso- and/or microgaps in comparison with the control; (2) species whose frequency was the same or significantly lower in the meso- and/or microgaps. This information is used in the present work to check whether there was a difference in root AM colonization between the species of the two above mentioned groups. We collected root samples of the plants in different communities in a random manner to assess the tendency for plants with different disturbance ecology to have a different rate of mycorrhizal infection.

Data processing

We were interested in studying how vegetative mobility and community type influence the plant mycorrhizal status on the basis of all the communities vascular species which were frequent enough to enable root sampling. We used a mixed model (III) of two-way ANOVA for unbalanced data (ZAR 1999), with the mobility rate as a fixed factor and community type as a random factor (Statistica 5.0 – StatSoft, Inc. 1984–1995). Several species had no mycorrhizal infection (*Cyperaceae*, *Caryophyllaceae*, *Brassicaceae*), so all calculations were made with two data sets: with and without non-mycorrhizal species. When it was necessary to compare means, the *t*-test was used. Since clear gap structure was evident only in one community (GHM) and species with high vegetative mobility were very rare in this community, it was not possible to study the interactive effect of the two factors, viz. species vegetative mobility and response to disturbance, on the rate of mycorrhizal infection. A chi-square was used to check the relationship between species vegetative mobility and response to gap formation. One way ANOVA (reaction to the disturbance as a single factor) was used to compare the mycorrhizal infection rates between the species group (Microsoft Excel 97).

When comparing species traits, related species may share traits due to common ancestry, not due to adaptation, leading to a situation similar to pseudoreplication (SILVERTOWN & DODD 1996). Though our main task was not to study particular species, but rather a spectra of certain traits over the whole community, we nevertheless also tried to estimate the effect

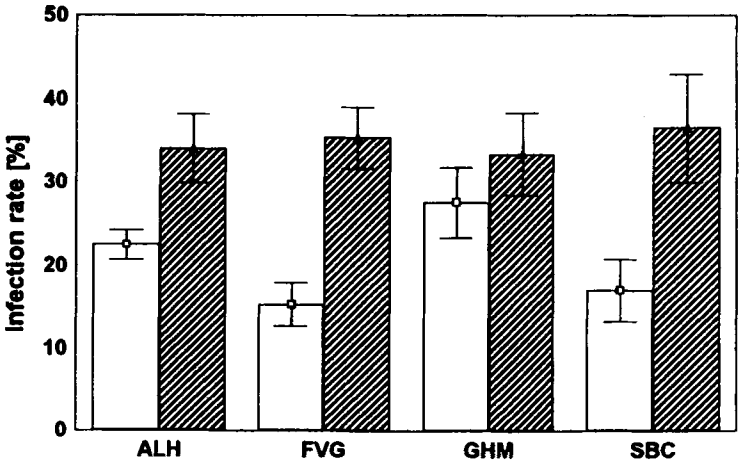

Fig. 1. Mycorrhizal infection rate and vegetative mobility of alpine species in different communities (means and standard errors; all species, including non-mycorrhizal ones). White columns – mobile species (more than 2 cm/year, see Appendix), dark columns – non-mobile/low-mobility species. ALH – alpine lichen heath, FVG – *Festuca varia* grassland, GHM – *Geranium gymnocaulon-Hedysarum caucasicum* meadow, SBC – alpine snow bed community.

of species vegetative mobility and response to disturbance on root AM infection within two larger families, *Poaceae* and *Asteraceae*.

RESULTS

Mycorrhizal infection and vegetative mobility

In the four community types studied (ALH, FVG, GHM, SBC), almost an equal percentage of species from the whole species list (74–77%) were arbuscular mycorrhizal (see the Appendix). The mean rate of mycorrhizal infection did not differ between communities as well. The ANOVA results showed the significant effect ($P < 0.01$) of vegetative mobility on the rate of root mycorrhizal infection for all species, as well as for mycorrhizal species only (Tab. 1). In all the studied communities the rate of infection was lower for mobile species (Fig. 1). The mean root infection rate did not differ between communities. Though there was no significant interaction between vegetative mobility and community type, it seems that the difference in infection rate between species groups with different mobility was least in the GHM community (Fig. 1).

Mycorrhizal infection and responses to disturbance

The mean rate of root mycorrhizal infection was lower for species preferring gaps (Tab. 2). According to the ANOVA the difference was significant for the whole list of investigated species. The same tendency (but non-significant, $P = 0.0786$) was observed for mycorrhizal species only.

We checked also whether there is a relationship between the gap preference and vegetative mobility of species. The chi-square test showed that this relationship was not significant (analysis not shown).

Table 1. Results of two-factor ANOVA (Model III) showing the effect of a vegetative mobility (1 – fixed factor) and community type (2 – random factor) on the rate of mycorrhizal infection.

Factor	d.f. effect	MS effect	MS error	d.f. error	MS *F*	*P*
All species included						
Vegetative mobility	1	2481.6	3	166.1	14.9	**0.031**
Community type	3	72.4	108	581.8	0.124	0.946
Interaction	3	166.1	108	581.8	0.286	0.836
Only mycorrhizal species included						
Vegetative mobility	1	4379.7	3	190.6	22.98	**0.017**
Community type	3	107.8	79	259.9	0.415	0.743
Interaction	3	190.6	79	259.9	0.733	0.535

Comparisons within families *Poaceae* and *Asteraceae*

In order to check whether the community-level pattern of plant traits holds when only species with similar phylogeny are included, the differences in the rate of root infection between mobile and non-mobile/low-mobility species were compared within two larger families, *Poaceae* and *Asteraceae*. In the case of *Poaceae* (4 mobile and 8 non-mobile/low-mobility species) we found that the rate of root mycorrhizal infection was significantly lower (*t*-test, $P = 0.020$) in mobile species (20%) than in non-mobile/low-mobility species (39%) (analysis not shown). The same tendency for non-mobile/low-mobility species to have a higher infection rate than mobile ones (39% and 52%, respectively) was also observed in *Asteraceae*. However, it was not possible to test the difference statistically because this family included only 2 mobile and 15 non-mobile/low-mobility species.

DISCUSSION

Our results show that 74–77% of plant species in the alpine grasslands of the Northwestern Caucasus were arbuscular mycorrhizal, while the rate of root colonization often exceeded 50%. A higher infection rate was observed in the case of immobile species. Since these species have only seed reproduction and there are no functional connections between the mother plant and seedlings, one may hypothesize that AM may fulfill a similar role to that of clonal connections (WILKINSON 1998). The AM network supports seedlings and young plants by providing organic components and nutrients, especially phosphorus, which are important in harsh (cold, nutrient poor) alpine environments. In natural communities, AM infection may develop rather quickly (FITTER & NICHOLS 1988) and the early integration of plants into the mycelial network would provide them with an absorptive surface at a relatively low energy cost (FRANCIS & READ 1994). It was shown that seedlings of alpine plants often had a higher rate of mycorrhizal infection than the adult plants (BAIKALOVA & ONIPCHENKO 1988). The improvement of nutrient conditions through the rapidly developing mycelial network may serve as an alternative to the translocation of carbon which otherwise would be needed to build a root system.

Also, AM extramatrical hyphae may serve as alternatives for vegetative organs in foraging soil resources over larger and often patchy areas. In conditions where root growth is restricted, the fungi can contribute up to 80% of the P absorbed (LI et al. 1991). At the same time, absorption of P can take place a long distance (up to 7 cm) away from the roots (RHODES &

Table 2. Mycorrhizal infection rate and the reaction to zoogenic disturbance of alpine species in *Geranium gymnocaulon-Hedysarum caucasicum* communities. Species groups: (1) species whose frequency was significantly higher in the meso- and/or microgaps in comparison with the control; and (2) species whose frequency was the same or significantly lower in the meso-and/or microgaps. *n* – number of studied species, Av. – average rate of mycorrhizal infection, %. Results of single factor ANOVA (reaction to zoogenic disturbance) showed below.

	Only mycorrhizal species included			All species included		
Groups	*n*	Mean	Variance	*n*	Mean	Variance
(1)	8	33.5	235	12	22.3	421
(2)	19	44.4	185	22	38.4	403

	Only mycorrhizal species included				All species included			
ANOVA	d.f.	MS	*F*	*P*-value	d.f.	MS	*F*	*P*-value
Between groups	1	671	3.36	0.0786	1	1995	4.88	**0.0345**
Within groups	25	200			32	409		
Total	26				33			

GERDEMANN 1975). In this way, otherwise sessile plants have the possibility to forage for nutrients beyond their own depletion zone, or to use the physical patchiness of the soil environment to forage resources in more fertile microsites. Another possible strategy for plants to forage in patchy environments is clonal growth (SVENSSON & CALLAGHAN 1988, STUEFER & HUTCHINGS 1994, STUEFER et al. 1996). The pattern of root AM infection, described in alpine grassland communities in the Northwest Caucasus, supports the view that these two possibilities are, at least to some extent, alternatives. Phylogenetically corrected analysis of species within two families (*Poaceae* and *Asteraceae*) supported this point of view as well.

It is interesting to note that the difference in infection rate for mobile and non-mobile/low-mobility species was the least for GHM communities. On the basis of our recent observations, this fact remains unexplained. It may be somehow related to the productivity of the plant community. These meadows are the most productive communities within the alpine area (ONIPCHENKO 1990). The microarthropodal consumption of AM fungi may lead to the decreasing of interplant connections (FINLAY 1985). The density of all microarthropod groups (*Oribatei*, *Trombidiformes*, *Gamasina*, and *Collembola*) was the highest in GHM in comparison with other alpine communities (NETUJILIN et al., unpubl.). Moreover, this type of meadow is subject to the intensive burrowing activity of small rodents, mainly a vole *Pitymys majori* THOMAS (FOMIN et al. 1989), and the Caucasian mole (*Talpa caucasica* SATUNIN) (ZENYAKIN & ONIPCHENKO 1997) as well as by large mammals like wild boars (*Sus scrofa* L.) and bears (*Ursus arctos* L.) (ONIPCHENKO & RABOTNOVA 1994). Frequent disturbances may have a negative effect on the mycorrhizal network in the soil and may decrease the importance of mycorrhiza for plants. All of the above-listed factors may decrease the role of AM connections between plants in GHM and lead to non-significant differences in mycorrhizal infection rates between mobile and non-mobile/low-mobility species (Fig. 1).

The results of our study show that a similar pattern may be observed also within the community – plants preferring undisturbed sites had higher rates of infection than plants preferring zoogenic gaps. Consequently, in alpine grasslands, the rate of mycorrhizal root infection is a good indicator of the relation of species to disturbances.

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APPENDIX

List of studied species, their mobility type and the rate of mycorrhizal infection (%) in the alpine communities. Vm – Vegetative mobility type: 1 – mobile species (more than 2 cm/year), 2a – clonal, but low-mobility species (less than 2 cm/year), 2b – non-clonal (non-mobile) species.

Species	Vm	Mean rate of the infection in the communities (%)			
		ALH	FVG	GHM	SBC
Ajuga orientalis L.	2a		56		
Alchemilla caucasica BUSER	2a	60			
Anemone speciosa ADAMS ex PRITZ.	2b	71			
Antennaria dioica (L.) P. GAERTN.	2a	61	57		
Anthemis cretica L.	2a	58	46	34	
Anthoxanthum odoratum L.	1		18	25	42
Arenaria lychnidea M. BIEB.	2a	0			
Aster alpinus L.	2a	49			
Campanula collina M. BIEB.	2a		40		
Campanula tridentata SCHREB.	2b	80	60	36	74
Carex atrata L.	2a		0	0	0
Carex oreophila C.A. MEY.	2a				0
Carex pyrenaica WAHLENB.	2a				0
Carex sempervirens VILL.	2a	0			
Carex umbrosa HOST	2a	0	0		
Carum caucasicum (M. BIEB.) BOISS.	2b	62	72		76
Carum meifolium (M. BIEB.) BOISS.	2b			68	76
Catabrosella variegata (BOISS.) TZVELEV	1				10
Cerastium purpurascens ADAMS	2a		0		
Corydalis conorhiza LEDEB.	2b				28
Deschampsia flexuosa (L.) TRIN.	2a			29	
Erigeron alpinus L.	2a	59			
Erigeron caucasicus STEV.	2a			59	
Eritrichium caucasicum (ALBOV) GROSSH.	2b	0			
Euphrasia ossica JUZ.	2b	0			
Festuca brunnescens (TZVELEV) GALUSHKO	2a		18		28
Festuca ovina L.	2a	21	43		
Festuca varia HAENKE	2a		51		
Fritillaria lutea MILL.	2b	15	43		
Gagea fistulosa (LAM. et DC.) KER-GAWL.	2a			23	
Galium verum L.	1		8		
Gentiana aquatica L.	2b	32			
Gentiana biebersteinii BUNGE	2b	54			
Gentiana pyrenaica L.	2a	15	9		
Gentiana septemfida PALL.	2b	35	33	22	
Gentiana verna L.	1	15			
Geranium gymnocaulon DC.	2a			57	
Gnaphalium supinum L.	2a		59		70
Hedysarum caucasicum M. BIEB.	2b			47	
Helictotrichon versicolor (VILL.) PILG.	2a	45			
Hyalopoa pontica (BALANSA) TZVELEV	1				8
Leontodon hispidus L.	1		35	45	
Luzula multiflora (RETZ.) LEJ.	2a			0	
Luzula spicata (L.) DC.	2a	0			
Matricaria caucasica (WILLD.) POIR.	2a		41	42	
Minuartia aizoides (BOISS.) BORNM.	1		0	0	0
Minuartia circassica (ALBOV) WORONOW	2a	0	0		

Species	Vm	Mean rate of the infection in the communities (%)			
		ALH	FVG	GHM	SBC
Minuartia recurva (ALL.) SCHINZ et THELL.	2a		0	0	
Myosotis alpestris F.W. SCHMIDT	2a		0		
Nardus stricta L.	2a		50	45	54
Oxytropis kubanensis LESKOV	2b	40			
Pedicularis comosa L.	2b	0			
Pedicularis nordmanniana BUNGE	2b				0
Phleum alpinum L.	1			40	25
Plantago atrata HOPPE	2b	65			
Polygonum bistorta L.	2b	0			
Potentilla crantzii (CRANTZ) BECK ex FRITSCH	2a			58	36
Potentilla gelida C.A. MEY.	2a	30			
Potentilla nivea L.	2a	58			
Primula algida ADAM	2b	30			
Primula ruprechtii KUSN.	2b	0			
Ranunculus oreophilus M. BIEB.	2a	50	53		
Rumex alpestris JACQ.	2a			0	
Scabiosa caucasica M. BIEB.	2a	46			
Scorzonera cana (C.A. MEY.) O. HOFFM.	2b	51	42	53	
Sedum tenellum M. BIEB.	2b			0	
Sempervivum caucasicum RUPR. ex BOISS.	1		0		
Senecio aurantiacus (HOPPE ex WILLD.) LESS.	2a		53		
Senecio kolenatianus C.A. MEY.	2a		30		
Sibbaldia procumbens L.	2a		59	58	55
Taraxacum confusum SCHISCHK.	2b		44		
Taraxacum stevenii (SPRENG.) DC.	2b	49			27
Trifolium polyphyllum C.A. MEY.	2a	52			
Trisetum flavescens (L.) P. BEAUV.	2a		27		
Vaccinium vitis-idaea L.	1	30			
Veronica gentianoides VAHL	2a	36	38	25	
Viola altaica KER-GAWL.	1		31		