Natural "gaps" in alpine meadows and plant population strategies

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6. Natural "gaps" in alpine meadows and plant population strategies

Vladimir G. ONIPCHENKO and Maria V. RABOTNOVA

6.1. INTRODUCTION

Species diversity of plant communities can be maintained by the ability of plants to occupy different regeneration niches (GRUBB 1977) according to the differing demands for seedling establishment and for development of young individuals. In the vegetation cover, disturbances create gaps of varying proportions in which different components of the plant community can be restored. This aspect of the new forest gap paradigm is widely confirmed by structural studies of different forest communities (c.f. review by PICKETT and WHITE 1985, KOROTKOV 1991). Natural disturbances are common for meadow and grassland ecosystems (COLLINS and BARBER 1986, RYSER 1990, PARISH and TURKINGTON 1990a,b). Still, the application of the regeneration niches concept in the different types of meadow communities calls for further research.

In the present paper the influence of zoogenic disturbances of differing degrees on the structure of alpine meadows is explored. The aim was to estimate the possibility of applying the "new forest gap paradigm" to alpine plant communities.

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6.2. MATERIALS AND METHODS

The object of this investigation was alpine meadows with *Hedysarum caucasicum* and *Geranium gymnocaulon* as main dominants (GHM, see Chapter 1.4 for detailed description). This type of meadow is subject to the intensive burrowing activity of small rodents, mainly voles *Pitymys majori* Thos. (FOMIN et al. 1989), and large mammals like wild boars (*Sus scrofa* L.) and bears (*Ursus arctos* L.). The two latter species consume the rhizome of *Hedysarum caucasicum* and other herbs. Therefore, GHMs seem very suitable for studying the influence of different scale disturbances on the composition of plant communities.

Two types of gaps were studied: 1) mesogaps (with the typical size of 1'000-10'000 cm^2) formed as a result of the burrowing activity of large mammals, 2) microgaps (with the typical size of 100-1'000 cm^2) formed as a result of vole's activity (Table 6.1). Mesogaps are characterized by changes in the upper soil horizon, a sharp increase in solar radiation and a considerable shift in microclimatic characteristics of the soil surface in comparison with undisturbed places. Vole burrowing also increases the availability of soil resources, slightly changing insolation of the soil surface because of shadowing by neighboring plants. In this aspect, the studied canopy gaps are analogous to different scale tree fall-out in forest plant communities (KOROTKOV 1991). Large gaps can take over 10 years to grow over, while vole burrowing places can easily recover in only a few (2-5) years. On the other hand, the latter often reappear after only a very short time.

Plots of 25x25 cm and 10x10 cm size were laid out on the disturbed places of mesogaps and microgaps respectively. The age of the studied mesogaps was about 3-5 years, and of microgaps about 1-2 years. Control plots were laid out near the gap plots on undisturbed places (not farther away than 1 m) in the same manner as the gap plots.

Table 6.1. Some features of zoogenic gaps in alpine meadows.

Burrowing mammals	mesogaps *Ursus arctos* L. *Sus scrofa* L.	microgaps *Pitymys majori* Thos.
Sizes of gaps, cm^2	1000 - 10000	100 - 1000
The periodicity of disturbances, years	> 10	1 - 8
The depth of soil disturbances, cm	5 - 20	1 - 8
Size of sample plots, cm	25 x 25	10 x 10
Number of replications (n)	270	250
Floristic diversity (number of species per plot, mean and standard error):		
gap plots	8.5 ± 1.8	5.0 ± 1.7
control plots	9.5 ± 1.3	7.3 ± 1.8

Table 6.2. Frequencies of alpine species under natural disturbances in GHM. Column "t" represents the significance level of differences according to the t-test: *** p >0.999, ** p >0.99, * p >0.95. GHM = *Geranium gymnocaulon - Hedysarum caucasicum* dominated meadows.

Species	Frequency (%)						number
	control	mesogaps	t	control	microgaps	t	of group
Agrostis vinealis	15.9	33.0	***	7.2	23.6	***	2
Anthemis iberica	17.0	37.4	***	10.0	11.2		1
Anthoxanthum odoratum	65.2	41.5	***	42.8	21.2	***	7
Campanula biebersteiniana	13.3	14.8		6.8	8.4		4
Campanula collina	14.8	9.6		29.2	26.4		4
Carex atrata	27.0	8.9	***	11.6	4.0	**	7
Carum meifolium	70.7	73.7		37.6	32.0		4
Catabrosella variegata	19.3	48.5	***	0.0	0.0		1
Corydalis conorhiza	47.8	34.4	**	0.0	0.0		5
Daphne glomerata	0.0	0.0		10.4	1.6	***	6
Deschampsia flexuosa	16.3	11.9		32.0	7.6	***	6
Draba hispida	0.0	0.0		5.2	14.4	***	3
Erigeron venustus	0.0	0.0		22.8	16.4		4
Euphrasia ossica	6.7	14.1	**	10.0	7.6		1
Festuca brunnescens	40.7	42.2		6.4	27.6	***	3
Festuca ovina	5.2	12.2	**	0.8	0.8		1
Gentiana septemfida	0.0	0.0		8.8	1.2	***	6
Geranium gymnocaulon	89.6	26.7	***	91.2	34.0	***	7
Gnaphalium supinum	2.2	43.7	***	0.0	0.8		1
Hedysarum caucasicum	47.8	34.4	**	70.4	35.6	***	7
Leontodon hispidus	35.2	27.8		42.4	31.2	*	6
Luzula multiflora	25.2	11.1	***	5.6	4.0		5
Matricaria caucasica	28.9	51.1	***	11.2	48.4	***	2
Minuartia aizoides	21.5	35.6	***	9.6	9.6		1
Minuartia recurva	11.9	28.1	***	8.4	4.4		1
Nardus stricta	42.6	15.6	***	28.8	11.2	***	7
Pedicularis condensata	0.0	0.0		18.8	10.8	*	6
Phleum alpinum	53.0	14.4	***	27.6	14.4	***	7
Potentilla aurea	29.6	13.0	***	5.2	4.4		5
Pulsatilla aurea	6.3	0.7	***	10.8	4.4	**	7
Ranunculus oreophilus	26.3	15.2	**	6.0	2.0	*	5
Rumex alpestris	43.0	10.4	***	21.2	13.6	*	7
Scorzonera cana	14.1	14.1		12.4	9.6		4
Sedum tenellum	3.3	38.1	***	1.6	5.6	*	1
Senecio taraxacifolius	10.0	1.1	**	0.0	0.0		5
Sibbaldia procumbens	24.8	48.5	***	5.6	11.6	*	2
Taraxacum stevenii	18.9	18.1		4.4	2.4		4
Veronica gentianoides	9.6	10.4		10.8	20.4	**	3

6.3. RESULTS AND DISCUSSION

Floristic diversity of control and disturbed plots did not significantly differ either in meso- or microgaps (Table 6.1). On the whole, 78 species of vascular plants were found on the plots under observation. The occurrence of the most abundant species is shown in the Table 6.2.

According to the RAMENSKY-GRIME concept, species with a positive response to disturbances belong to explerents (or ruderals) (RAMENSKY 1938, GRIME 1979, ONIPCHENKO et al. 1990).

The studied alpine species fell into the following groups, according to responses to different types of zoogenic disturbances :

1. Typical explerents. Species increasing their frequency in the mesogaps and not responding to the disturbances of a lesser scale: *Anthemis iberica, Catabrosella variegata, Euphrasia ossica, Festuca ovina, Gnaphalium supinum, Minuartia aizoides, Minuartia recurva, Sedum tenellum.* It seems that the development of these species is mainly determined by the increase of insolation.
2. Explerents which positively respond to different scale disturbances: *Agrostis vinealis, Matricaria caucasica, Sibbaldia procumbens. Agrostis vinealis* possesses the highest degree of vegetation mobility, using every possible canopy gap to form of new above-ground shoots. Other species from this group have a restricted vegetative mobility. They form a considerable soil seed bank and can rapidly resume from seeds in disturbed places (SEMENOVA and ONIPCHENKO 1990, 1991).
3. Species which increase in frequency only on microgaps and do not change (or only insignificantly) on mesogaps plots: *Draba hispida, Festuca brunnescens, Veronica gentianoides.* These species possess high tolerance to closed cover conditions and can indicate small scale disturbances.
4. Species which do not change in frequency on different scale disturbances: *Campanula biebersteiniana, Campanula collina, Carum meifolium, Erigeron venustus, Scorzonera cana, Taraxacum stevenii.* Most of the species have relatively large seeds and are tolerant to the wide range of ecological conditions: from open burrowing places to closed swards.
5. Species which decrease in frequency in the mesogaps and do not change (or only insignificantly) in microgaps: *Corydalis conorhiza, Luzula multiflora, Potentilla aurea, Ranunculus oreophilus, Senecio taraxacifolius.* These species adapted for growth in closed communities, but many of them can successfully resume in "small canopy breaks".

6. Species which decrease in frequency in "small canopy breaks" but do not change in mesogap plots: *Leontodon hispidus, Deschampsia flexuosa*. Besides these two species, *Daphne glomerata* and *Pedicularis chroorrhyncha*, not found in either mesogaps or control plots, were included in this group in advance.
7. Species which decrease in frequency both in meso and microgaps plots. This is a large group of species, which dominates or has a high frequency level in undisturbed places of the community: *Anthoxanthum odoratum, Carex atrata, Geranium gymnocaulon, Hedysarum caucasicum, Nardus stricta, Phleun alpinum, Pulsatilla aurea, Rumex alpestris*. Yet, most of them have comparatively large seeds and can resume under disturbances especially on microgaps. Therefore, for this group of species, natural zoogenic disturbances do not cause elimination, but on the contrary can promote successful establishment of seedlings.

Based on a comparison of the amount of species with different responses to meso- and microdisturbances, it is interesting to point out that under the transition from meso- to microgaps the portion of species which responds negatively to disturbances remains invariable. The portion of species which responds positively to disturbances decreases and the portion of species indifferent to disturbances increases (Fig. 6.1).

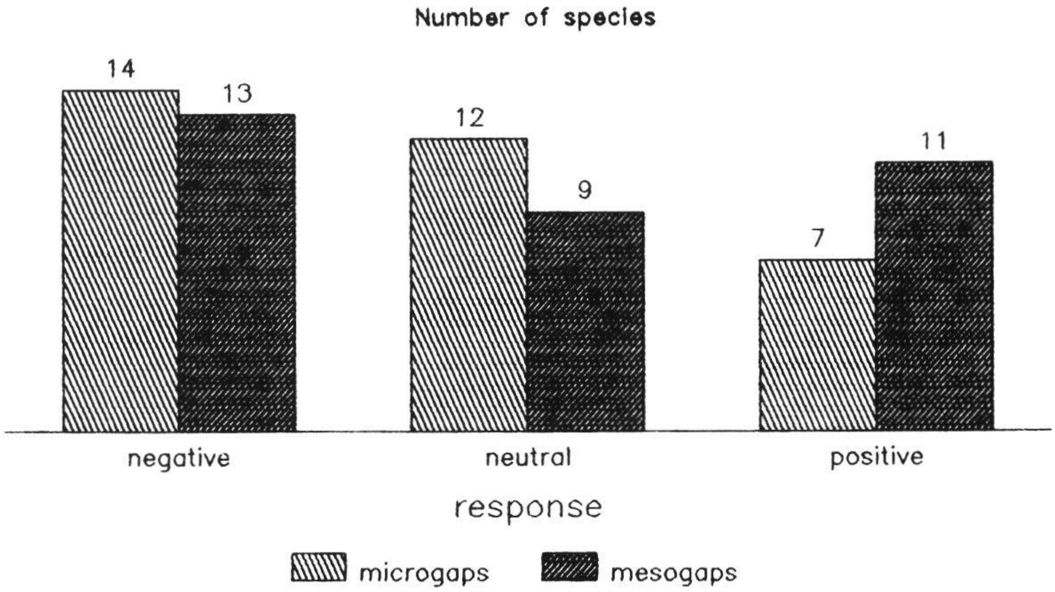

Fig. 6.1. Number of species with different responses to meso- and microdisturbances.

SUMMARY

Species occurrence on undisturbed plots and on zoogenic gaps was investigated in alpine meadow communities (GHM: = *Geranium gymnocaulon* - *Hedysarum caucasicum* dominated meadows) in the Northwestern Caucasus. Our results lead to the conclusion that the approach of "gap-paradigm" can be fruitfully applied to the investigation of the structure of alpine plant communities.
The floristic diversity of controlled and disturbed plots did not differ significantly in either meso- or microgaps. Depending on the species responses to different types of zoogenic disturbances, the studied alpine species fell into seven groups. Reactions of alpine species to different scale disturbances are discussed using the RAMENSKY-GRIME concept. The present results agree with the classification of population strategies, developed for alpine plants of the Northwestern Caucasus (ONIPCHENKO et al. 1990).