

Population strategies in severe environments: alpine plants in the northwestern Caucasus

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Abstract. This study attempts to show a differentiation into strategy types among plant species of four alpine communities in the northwestern Caucasus, Russia. Four groups of population characteristics (traits) were examined: above-ground biomass, seed size, seed yield and occurrence of a persistent seed bank. In addition, values for relative growth rate and a morphology index were estimated. Agglomerative Cluster Analysis and Principal Component Analysis were applied to a data set with 42 species from these communities and six species characteristics. In the *Geranium gymnocaulon* meadow, the most productive community, large gaps occur created by wild boars and bears. Here, the response of 13 species to disturbance was also analysed.

Strategy types were approached both according to Grime: 'competitive', 'ruderal', 'stress-tolerating' and according to Ramensky, Rabotnov and Romanovsky: 'violent' ≈ dominant (V), 'explerent' ≈ explorative (E) and 'patient' ≈ enduring (P). Differentiation into strategy types was more obvious in productive alpine grasslands than in lichen heaths and snowbed communities. The grassland dominants *Festuca varia*, *Geranium gymnocaulon* and *Hedysarum caucasicum* showed a more or less 'violent' strategy. Species approaching an E-strategy, e.g. *Matricaria caucasica*, *Sibbaldia procumbens* and *Gnaphalium supinum*, were also found in the grasslands but prevailed in the snowbed communities. Species with a 'patient' strategy prevailed in the lichen heaths.

We conclude that plant strategy types are well-differentiated, this is also seen in plant communities occurring under severe high-mountain conditions. We also suggest that the approaches by Grime and Ramensky/Rabotnov/Romanovsky are not so similar as has been assumed earlier and that the R/R/R types are better differentiated and ecologically better interpretable.

We emphasize the gradient character of strategy 'types' and would characterize plant species by the degree of adaptation to conditions: (1) from small seed size and large persistent seed bank to large seed size and absence of a seed bank; (2) from high to low biomass and seed production, with relative growth rate as a less important partially correlated trait.

Keywords: Alpine meadow; Cluster Analysis; Lichen heath; Principal Components Analysis; Reproduction; Seed bank; Snowbed community.

Nomenclature: Largely according to Davis (1965-1988).

Introduction

A notion of life history strategy is found in the works of many ecologists, both Anglo-American (MacArthur & Wilson 1967; Pianka 1970, 1983; Grime 1977, 1979; Whittaker & Goodman 1979; Solbrig 1980) and Russian (Rabotnov 1975b, 1985, 1993; Mirkin 1983, 1994; Zaugolnova et al. 1988). However, until now there has been no unambiguous way of defining the different strategies (Stearns 1976, 1977, 1992; Jain 1979; Menges & Waller 1983; Romanovsky 1985, 1989a, b; Grace 1991; Oksanen & Ranta 1992; Rabotnov 1993).

Grime (1977, 1979) originally based his typology of plant strategies on a classification of habitats into three types with regard to stress and disturbance. He then described the characteristics of plants adapted to these environments. Important parameters were the maximum relative growth rate and an index of competitiveness (Grime 1979; Grime et al. 1988). However, he considered juvenile and adult phases of the life cycle separately. As a result, the strategies of different parts of the life cycle are hardly linked in his system.

Simultaneously with Grime, Rabotnov (1975a) attempted to introduce a typology of life history strategies, which was based on the work of Ramensky (1938). Ramensky, better known as the founder of gradient analysis, introduced a typology of three main types: 'violent', 'patient' and 'explerent', with which one can approach species coexistence and their role in plant communities. These are not proper English terms; they could be interpreted as 'dominant', 'endurant' and 'explorative'. We will discuss a more definitive terminology in a future study and will use the codes 'V', 'P' and 'E' in the present study.

In many respects Ramensky's types correspond to Grime's 'competitors', 'stress-tolerators' and 'ruderals' (Rabotnov 1975a, 1985, 1993). However, they show some significant differences in their definition and content. Rabotnov also used Ramensky's terms – originally coined as 'phytocoenotypes' – to indicate strategy types (Rabotnov 1975b). In addition, he proposed to distin-

guish life history strategies by referring mainly to population characteristics, in particular to population structure and reproductive pattern.

The population approach was further developed by the limnologist Romanovsky (1985, 1989a, b, 1992), working mainly with *Cladocera*, who based his concept of primary life history strategies on species responses to peculiarities of resource dynamics. According to this concept, there are two ways for a population to succeed in the competition for limiting resources:

- (1) reducing the equilibrium resource requirement, R^* (sensu Tilman 1982), i.e. the resource level at which population growth and loss rates are equal;
- (2) developing a high resource capture capacity and high population growth rate when the resource is available.

In the first case we deal with a P-strategy. Romanovsky pointed out that resistance of a population as a whole is determined by the tolerance of the most susceptible age group, i. e. the juveniles. A high population resistance to resource shortage is beneficial when the resource availability is steady (see also Abrosova et al. 1982; Tilman 1982). The ability to survive in resource-poor environments is associated with a low rate of resource consumption (Chapin 1980) and a low rate of population growth. As a consequence, species with a P-strategy show a lower competitive ability when resource availability fluctuates considerably. In other words, there is a trade-off between tolerance to resource scarcity and growth rate or offspring production.

In the second case, plants have higher rates of resource uptake when resources are available and survive unfavourable periods (e.g. periods of resource depletion) either in a dormant (latent) stage – the E-strategy – or, as adults, in a state of low activity – the V-strategy. Species of the latter category have an advantage in relatively undisturbed habitats. They do not need time for germination and growth, and can rapidly decrease resource availability for other species during periods of enrichment. These species have a strong impact on the resource regime within a community. Species with an E-strategy, in their turn, are adapted to a less predictable resource regime. This strategy is associated with a short life span, large seed production and avoidance of resource limitation via dormancy or migration.

The 'Grime' typology and the 'Ramensky/Rabotnov/Romanovsky' typology are similar, but not identical. The main difference is concerned with the definition of 'competitors' (V-strategy). According to Grime a competitor is a fast-growing perennial in a fertile environment. Such a viewpoint does not take into account the long-term survival of these species. Real long-term competitors must be able to tolerate low resource levels they themselves have contributed to the creation of; however, they usually are not very fast-growing. Thus, we at-

tribute dominants of the later stages of succession to real competitors, or V-species in Ramensky's typology, whereas the fast-growing species which can rapidly occupy free space (e.g. *Chamaenerion angustifolium* and *Urtica dioica*) are considered as E-species. The results presented in this paper should make this clear. It will be necessary to further compare these typologies as well as some others, which may culminate in a new typology. This study is under preparation.

We should also emphasize two additional points:

1. Plant strategy studies are usually based on a few morphological criteria (Grime 1979, 1984; del Moral 1983b), while some other studies only deal with reproductive criteria. From our viewpoint, particular features of different stages in the life cycle, as well as the performance and persistence of the species in the plant community, are more useful for the distinction of primary life history strategies than morphological indexes. Thus, investigations of reproductive patterns should be emphasized in this context (Rabotnov 1975b; Grubb 1977, 1988; Grime 1979; Angevine & Chabot 1979; Solbrig 1980; Eriksson 1989; Grime & Hillier 1992; Silvertown et al. 1993).

2. There are no pure V-, P- or E-species, because these primary 'strategies' result from three main directions of natural selection and manifest themselves in a complex combination of different adaptations. It only makes sense to consider the relative degree of competitiveness, endurance or exploration, i.e. relative to other species, populations, races, etc. (Rabotnov 1985). For instance, birch is more 'E' than spruce, but more 'V' than an annual growing under birch. Differentiation into strategy types occurs among plants of different habitats, including extreme ones (Yurtsev 1986).

Plant strategy analysis may be used to explore community structure and species coexistence under severe high-mountain conditions (Marchand & Roach 1980; del Moral 1983a, b, 1985; del Moral et al. 1985; Schimpf & Bann 1983; Urbanska 1984; Grabherr et al. 1987). This paper presents an attempt to show differentiation into strategy types among plant species of four alpine communities in the northwestern Caucasus. For this purpose we examined four characteristics, as presented in Table 1. These data were partially included in an earlier paper (Onipchenko et al. 1991). In addition we estimated the two main characteristics used by Grime, Relative Growth Rate and Morphology Index. In the case of the *Geranium gymnocaulon* meadow, the most productive community, large gaps occur created by wild boars and bears. Here we analysed a seventh characteristic, the response of 13 species to this disturbance, i.e. the relationship between gap colonization and occurrence under undisturbed conditions.

In discussions on a draft of this paper it became clear

Table 1. Three primary life-history strategies: definition and some population characteristics.

Competitive ability due to low equilibrated resource requirement; tolerance of juvenile stage 'P-strategy'	Advantage due to high resource capture capacity when resources are available. Survival of resource depletion in: adult tolerant stage 'V-strategy'	dormant stage 'E-strategy'
<ol style="list-style-type: none"> 1. Occurrence under unfavourable conditions (abiotic and biotic stress) 2. Negative response to biomass removal and slow reaction to resource availability, negative response to disturbance as a whole 3. High relative energy investment into offspring 4. Small persistent seed bank 	<ol style="list-style-type: none"> 1. Large biomass under more productive conditions 2. Negative response to biomass removal and positive reaction to resource availability; the result depends on the intensity of disturbance 3. High seed production with relatively large seeds 4. Lack of persistent seed bank 	<ol style="list-style-type: none"> 1. Occurrence under more productive conditions 2. Rapid reaction to resource availability and weak response to biomass removal, positive response to disturbance as a whole 3. High relative energy investment into reproduction 4. Large persistent seed bank or wide seed dispersal

that the logical outcome of our ideas would be an ordination rather than a classification of species and their traits. As a matter of fact, the idea of finding axes along which traits vary, was taken up by Grime's group (Anon. 1995; Thompson et al. 1996). Such an ordination would also take away some of the criticism by Loehle (1988) who, *i.a.*, attacked the triangular model as a geometrical construction. Approaches to the related issue of 'plant functional types' are similarly emphasizing the continuous variation in attributes along gradients (e.g. Bugmann 1996) and in ordination diagrams (e.g. Condit et al. 1996).

The main aim of this study is to show how species in different alpine communities differentiate and to find out which approach best fits to our results. We do not wish to support or reject any of these strategy systems, but we find it interesting to compare different approaches, as well as to inform people about another (the R/R/R) approach.

Material and Methods

Study area

The study area is situated in Teberda State Reserve, a part of the Karachaevo-Cherkessian Republic in the northwestern Caucasus, Russia. Study sites are located on Mount Malaya Khatipara (43° 27' N, 41° 41' E), in the alpine belt at 2700 - 2800 m a.s.l. Snow accumulation is the main controlling factor of the vegetation pattern of the area. Four alpine communities are included in the study: (1) Alpine lichen heath with dominance of fruticose lichens; (2) *Festuca varia* grassland; (3) *Geranium gymnocaulon*-*Hedysarum caucasicum* meadow; (4) Snowbed community (Fig. 1, Table 2). For a detailed description of the area, soil and vegetation types, see Onipchenko (1994).

Above-ground biomass

Above-ground biomass was estimated at the end of the growing season for three years; every year 20 quadrats, 25 cm × 25 cm, were clipped at ground level in each community. Each sample was sorted by species, oven-dried and then weighed by species; litter of the present year was also taken into account in order to approximate total values for above-ground production (Onipchenko 1985, 1990).

Seed production parameters

We examined the parameters: seed weight, seed yield, reproductive effort, and 'expenditure per offspring', i.e. relative biomass (energy) investment into offspring. 100 well-developed seeds (or one-seed fruits, e.g. of *Asteraceae*, *Anemone*, etc.) were sampled from each species and weighed. Seed number produced per m² was calculated from reproductive shoot density and mean seed productivity of a shoot. The latter was estimated in the following way: 100 reproductive shoots were cut, the number of fruit and seeds was counted for

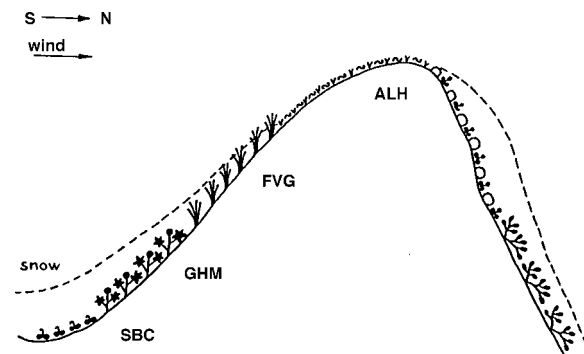


Fig. 1. Distribution of the communities over mesorelief forms. ALH = alpine lichen heaths; FVG = *Festuca varia* dominated grasslands; GHM = *Geranium gymnocaulon*-*Hedysarum caucasicum* meadows; SBC = snowbed communities.

Table 2. General characteristics of the four communities under study.

Community	Lichen heath	<i>Festuca</i> grassland	<i>Geranium</i> meadow	Snowbed comm.
Occupied relief forms	Crests, ridges, windward slopes	Slopes (often steep)	Leeward slopes, small depressions	Bottom of kars, deep depressions
Depth snow cover in winter (m)	0 - 0.3	0.5 - 1.5	1.5 - 3	≥ 4
Duration growing season (months)	4.5 - 5.5	3.5 - 4.5	2.5 - 3.5	2.0 - 2.5
Biomass (g/m ²):				
above-ground	110 ± 7	307 ± 17	319 ± 20	129 ± 5
below-ground	478 ± 42	636 ± 34	1392 ± 177	944 ± 128
Annual netto-production (g/m ²)	150	400	550	200
Mean no. of species/25 m ²	36	49	31	18
Zoogenic disturbances	Weak	Medium	Strong	Almost absent

each shoot, and a mean fruit and seed number per shoot was calculated. We counted almost ripe seeds; values, therefore, can characterize real seed productivity. Seed yield is the product of seed number and weight. Reproductive effort of the population may be defined as the proportion of total seed weight in the above-ground biomass (Markov & Pleshchinskaya 1987). Mean 'expenditure per offspring' was calculated from reproductive effort divided by seed number. In other words, it is the proportion of a seed in the above-ground biomass. Since real seed productivity and reproductive shoot number of alpine species vary significantly from year to year, we use mean values from three to four years of observations.

Occurrence of a seed bank

20 soil samples of 10 cm × 10 cm × 10 cm were collected from each community. The samples were exposed for seed germination in a greenhouse. Samples were taken in July-August, before seed-shedding but after spring seed germination. Thus, the results reflect the persistent seed bank (Thompson & Grime 1979). See further Semenova & Onipchenko (1990, 1991, 1994). This variable is calculated as number of seeds per m².

Response to soil surface disturbance

In certain parts of the *Festuca* grasslands and *Geranium* meadows, large-scale disturbance of the surface occurs through digging of wild boars (*Sus scrofa* L.) and bears (*Ursus arctos* L.); moreover, burrowing activities of voles (*Pitymys majori* Thomas) may occur in all communities, being most intensive in the *Geranium* meadows. The response to the strong disturbance in terms of gap colonization was measured by recording species occurrence in 30 plots of 25 cm × 25 cm in *Festuca* grasslands and 250 plots of the same size in

Geranium meadows which were established in places with visual evidence of recent disturbance by the large mammals mentioned. The number of plots in the *Festuca* grasslands was much smaller because here there were much fewer such disturbed areas. Control plots of the same size and numbers were examined in undisturbed areas, which could, however, be subject, to burrowing activities of voles. This aspect was not included in the present analysis; see, however, Oksanen & Oksanen (1989), Oksanen & Moen (1994). A more elaborate investigation was carried out in the *Geranium* meadows, which included a comparison between plots disturbed by large mammals and voles (Onipchenko & Rabotnova 1994).

Relative growth rate

Values for RGR were obtained from a recent study (Semenova in prep.) for 30 species, half of which are included in the present data set. For those species for which we have not yet obtained experimental data RGR was estimated on the basis of field observations and comparisons with data from Grime (1975), Grime et al. (1988) and van der Maarel (1988). By arranging the data according to a six-grade scale we obtained sufficient differentiation in RGR (mg mg⁻¹ week⁻¹):

Grade:	1	2	3	4	5	6
RGR	0.41	0.61	0.81	1.01	1.21	1.41
	- 0.60	- 0.80	- 1.00	- 1.20	- 1.40	- 1.60

Morphology index

Values for the morphology index were obtained according to the procedure described by Grime (1979, p. 74), i.e. calculated from the formula

$$M = (a + b + c) / 2 \quad (1)$$

where *a* is the estimated maximum height of the leaf canopy, *b* is the lateral spread and *c* is the estimated maximum accumulation of persistent litter. These three traits are given in interval scales, as follows:

- a:**
- | | | | | | | | | | | |
|------|------|-----|-----|-----|-----|-----|-----|------|------|-------|
| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | |
| (cm) | < 12 | 12 | 25 | 37 | 50 | 62 | 75 | 87 | 100 | > 112 |
| | | -24 | -36 | -49 | -61 | -74 | -87 | -100 | -112 | |
- b:**
- 0 small therophytes
 - 1 robust therophytes
 - 2 perennials with a compact unbranched rhizome or forming small (<10 cm diameter) tussocks
 - 3 perennials with a rhizomatous system or tussocks attaining a diameter of 10 - 25 cm
 - 4 perennials attaining a diameter of 26 - 100 cm
 - 5 perennials attaining a diameter of > 100 cm
- c:**
- 0 none
 - 1 thin discontinuous cover
 - 2 thin, continuous cover
 - 3 up to 1 cm depth
 - 4 1-5 cm depth
 - 5 > 5 cm depth

Data analysis

The data matrix contained 42 species for which the following features were included: above-ground biomass, seed weight, seed production per m² – henceforth called seed density – and size of the seed bank. For species found in two or three communities, we took the values which corresponded to the largest biomass value in any of the communities. A second matrix was prepared for 13 species of the *Geranium* meadow where, in addition to the four above-mentioned features, response to disturbance was indicated per species as the ratio of frequency of occurrence in disturbed plots to the frequency in control plots.

Two multivariate analyses were applied to the species in the resulting 42 × 4 and 13 × 5 matrices:

1. Agglomerative clustering with the Weighted Pair-Groups Method with Arithmetic Averages (WPGMA) using the Similarity Ratio (see van der Maarel et al. 1978; Gauch 1982). All data were transformed by dividing the values in every column by the maximum value of this column.
2. Principal Components Analysis as available in the program package CANOCO (ter Braak 1987). For this analysis we also prepared also 42 × 6 and 13 × 7 matrices with relative growth rate and morphology index in addition to the above-mentioned features. All data except RGR, M and the ratio were log-transformed.

Results

Above-ground biomass

Above-ground biomass values of alpine species in the four communities are given in App. 1. More detailed characteristics of the phytomass are presented in Onipchenko (1985, 1990). Relatively favourable conditions for plant production occur in the intermediate part of the snow accumulation gradient (Table 1), namely in the *Festuca* grassland and *Geranium* meadow, where the above-ground phytomass amounts to more than 300 g/m². *Festuca varia* and *Geranium gymnocaulon* strongly dominate in their respective communities. *Hedysarum caucasicum* (*Geranium* meadow) and *Nardus stricta* (both communities) also have a high biomass. The lichen heaths and snowbed communities develop under more severe conditions and have a lower production, their biomass amounts to less than 130 g/m² (Table 1).

Seed reproduction

All data are summarized in App. 1. *Hedysarum caucasicum*, *Geranium gymnocaulon*, *Anemone speciosa* and *Helictotrichon versicolor* have the largest seeds. The smallest seeds are found in *Primula algida*, *Gentiana pyrenaica*, *Luzula multiflora* and *Gnaphalium supinum*.

The dominants of the *Geranium* meadow, *Geranium gymnocaulon* and *Hedysarum caucasicum*, have the highest seed yield. Amongst the species of the lichen heath *Anemone speciosa* and *Carum caucasicum* have the highest seed yield and the highest 'expenditure per offspring'. The largest numbers of seeds (per m²) are produced by *Gnaphalium supinum*, *Sibbaldia procumbens* in the snowbed community; *Gentiana pyrenaica* in the *Festuca* grassland; *Geranium gymnocaulon*, *Hedysarum caucasicum*, *Matricaria caucasica* and *Anthoxanthum odoratum* in the *Geranium* meadow; *Gentiana pyrenaica*, *Carum caucasicum*, *Campanula tridentata* and *Primula algida* in the lichen heath.

Occurrence of a seed bank

The dominants of the *Geranium* meadows and *Festuca* grasslands hardly possess a persistent seed bank (App. 1). The main part of the soil seed bank consists of subordinate species, e.g. *Matricaria caucasica*, *Luzula multiflora*, *Anthoxanthum odoratum* and *Veronica gentianoides*.

Most species of the lichen heath and snowbed communities do not have a large stock of viable seeds, but they retain their germinating ability for a long time. However, the seed banks of *Gnaphalium supinum* and *Sibbaldia procumbens* in the snowbed communities were relatively large. On the whole, there is a closer correspondence between recent community composition and soil seed banks for communities developing under severe ecological conditions (lichen heath, snowbed community) than for more productive communities (*Festuca* grassland, *Geranium* meadow). It is interesting that *Gagea fistulosa* has a significant stock of dormant bulbs. This species greatly increases its quantity after artificial suppression of the vegetation (through shading experiments).

Relative growth rate

Species with the highest RGR (App. 1), e.g. *Matricaria caucasica*, *Luzula multiflora*, *Carex atrata*, *Phleum alpinum*, are subordinate species of the more productive communities. However, the dominants of these communities – *Geranium gymnocaulon*, *Hedysarum caucasicum*, *Festuca varia* – have a much lower RGR. The lowest RGR was found in seedlings of *Vaccinium vitis-idaea* and *Antennaria dioica*. On the whole, most species included in this study have relatively low RGR values.

Morphology index

Basically, the morphology index reflects the amount of plant biomass since it takes account of plant height, lateral spread and litter (although litter is usually considered as necromass). It is not surprising that these two variables are correlated (App. 1).

Table 3. Frequencies of alpine species under conditions of natural zoogenic disturbance in *Festuca* Grassland and *Geranium* Meadow, arranged in decreasing difference between ‘Disturbed’ and ‘Control’. Column *t* gives the significance level of differences according to the *t*-test: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, NS $p \geq 0.05$ (all data arcsin-transformed).

Species	Frequency (%)			Species	Frequency (%)		
	Disturbed	Control	<i>t</i>		Disturbed	Control	<i>t</i>
<i>Festuca</i> Grassland				<i>Geranium</i> Meadow			
<i>Festuca ovina</i>	87	27	***	<i>Gnaphalium supinum</i>	44	2	***
<i>Minuartia recurva</i>	63	17	***	<i>Sedum tenellum</i>	38	3	***
<i>Anthoxanthum odoratum</i>	73	37	**	<i>Catabrosella variegata</i>	49	19	***
<i>Veronica gentianoides</i>	43	17	*	<i>Sibbaldia procumbens</i>	49	25	***
<i>Anthemis cretica</i>	33	13	NS	<i>Matricaria caucasica</i>	51	29	***
<i>Luzula spicata</i>	20	3	*	<i>Anthemis cretica</i>	37	17	***
<i>Euphrasia ossica</i>	43	27	NS	<i>Agrostis vinealis</i>	33	16	***
<i>Anthemis marschalliana</i>	43	30	NS	<i>Minuartia recurva</i>	28	12	***
<i>Carum caucasicum</i>	23	10	NS	<i>Minuartia aizoides</i>	36	21	***
<i>Plantago atrata</i>	63	53	NS	<i>Euphrasia ossica</i>	14	7	**
<i>Campanula collina</i>	37	27	NS	<i>Carum meifolium</i>	74	71	NS
<i>Festuca brunnescens</i>	17	10	NS	<i>Campanula tridentata</i>	15	13	NS
<i>Minuartia circassica</i>	13	13	NS	<i>Festuca brunnescens</i>	42	41	NS
<i>Taraxacum confusum</i>	10	13	NS	<i>Scorzonera cana</i>	14	14	NS
<i>Potentilla crantzii</i>	17	20	NS	<i>Taraxacum stevenii</i>	18	19	NS
<i>Helictotrichon versicolor</i>	27	30	NS	<i>Deschampsia flexuosa</i>	12	16	NS
<i>Campanula tridentata</i>	7	17	NS	<i>Campanula collina</i>	10	15	NS
<i>Bromopsis variegata</i>	10	20	NS	<i>Leontodon hispidus</i>	28	35	NS
<i>Leontodon hispidus</i>	20	30	NS	<i>Ranunculus oreophilus</i>	15	26	**
<i>Ranunculus oreophilus</i>	20	30	NS	<i>Hedysarum caucasicum</i>	34	48	**
<i>Polygonum bistorta</i>	7	20	NS	<i>Luzula multiflora</i>	11	25	***
<i>Scorzonera cana</i>	10	23	NS	<i>Potentilla crantzii</i>	13	30	***
<i>Antennaria dioica</i>	3	17	NS	<i>Carex atrata</i>	9	27	***
<i>Scabiosa caucasica</i>	0	20	***	<i>Corydalis conorhiza</i>	6	24	**
<i>Anemone speciosa</i>	0	20	***	<i>Anthoxanthum odoratum</i>	41	65	***
<i>Calamagrostis arundinacea</i>	0	20	***	<i>Nardus stricta</i>	16	43	***
<i>Chaerophyllum roseum</i>	0	20	***	<i>Rumex alpestris</i>	10	43	***
<i>Hypericum linarioides</i>	3	30	**	<i>Phleum alpinum</i>	14	53	***
<i>Deschampsia flexuosa</i>	23	50	*	<i>Geranium gymnocaulon</i>	27	90	***
<i>Hedysarum caucasicum</i>	43	73	*				
<i>Nardus stricta</i>	0	33	***				
<i>Festuca varia</i>	17	60	***				
<i>Viola altaica</i>	17	60	***				
<i>Carex umbrosa</i>	3	60	***				
<i>Vaccinium vitis-idaea</i>	3	67	***				

Response to soil surface disturbance

Species of the *Festuca* grassland such as *Anthoxanthum odoratum*, *Minuartia recurva*, *Festuca ovina*, *Luzula spicata* and *Veronica gentianoides* increase their frequency on disturbed plots while *Festuca varia*, *Viola altaica*, *Nardus stricta* and many other species decrease (Table 3). Species such as *Catabrosella variegata*, *Sibbaldia procumbens* and *Gnaphalium supinum* increase their frequency under disturbance in the *Geranium* meadow while the main dominants, *Geranium gymnocaulon*, *Hedysarum caucasicum* and *Nardus stricta*, decrease. This confirms that alpine species differ in their rates of occupation of disturbed places in relatively favourable habitats such as *Festuca* grasslands and *Geranium* meadows, but that the dominants of these communities react negatively to such disturbance.

Cluster analysis

The dendrograms obtained by the cluster analysis are presented in Fig. 2. The 42 species from all four

communities (Fig. 2a) could be grouped into six clusters, at a similarity level of ca. 30%. At the first fusion level we obtained two big groups, where the second group (clusters 4, 5 and 6) consists of species from the lichen heath, and the first big group (clusters 1, 2 and 3) consists of species from all studied communities. The dominants of the *Festuca* grassland and *Geranium* meadow are separated in cluster 1. Cluster 3 includes species with moderate biomass, low seed weight, high seed production and a large seed bank: *Gnaphalium supinum*, *Luzula multiflora*, *Matricaria caucasica*, *Nardus stricta* and *Sibbaldia procumbens*.

The 13 species of the *Geranium* meadow (Fig. 2b) were divided into three groups at the second fusion level (similarity 28%). The dominants of the *Geranium* meadow with a large biomass, high seed weight, high seed production and lacking a seed bank (*Geranium gymnocaulon* and *Hedysarum caucasicum*) are separated in cluster 1. Species with low biomass, small seeds, high seed production, large seed bank and posi-

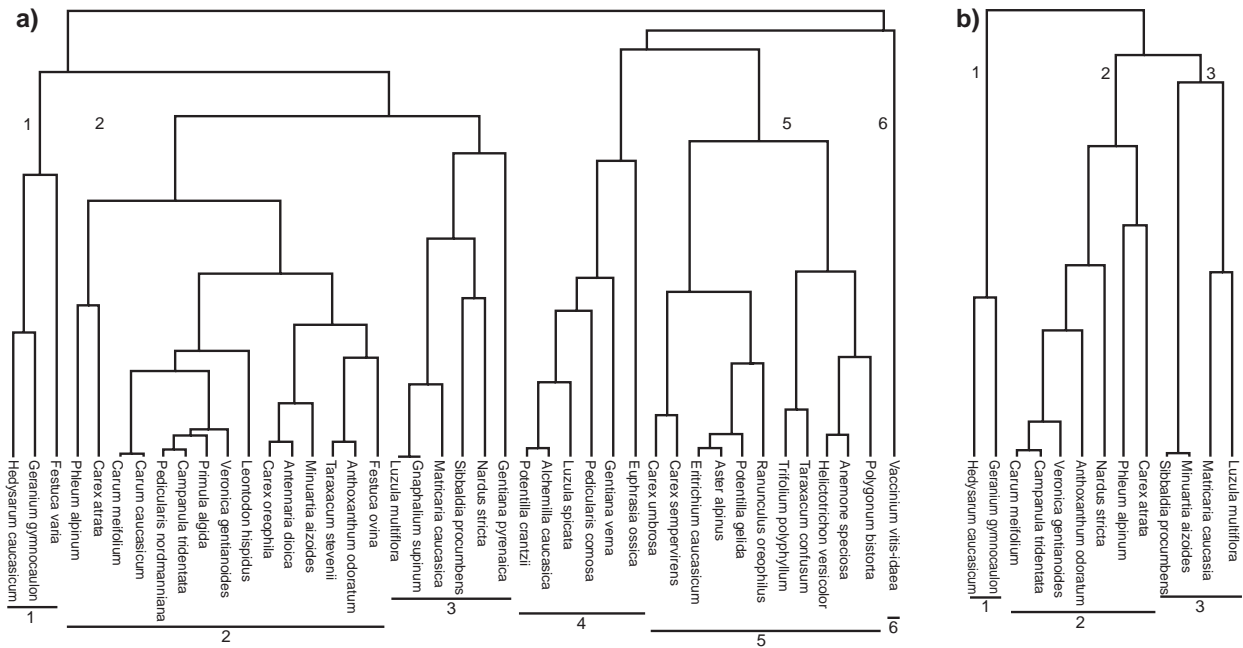


Fig. 2. Dendrograms of the hierarchical agglomerative clustering (TABORD) of 42 species of four alpine communities (a) and 13 species of the *Geranium* Meadow (b) in the northwestern Caucasus. Suggested cluster structure as indicated below the dendrograms.

tive response to disturbance are included in cluster 3. Cluster 2 consists of species with intermediate values of these characteristics.

Ordination

Fig. 3a shows the distribution of the species in the diagram of axes 1 and 2 of the PCA, while Fig. 3b indicates how the traits are correlated with the axes. There is a diagonal structure where seed bank and biomass are negatively correlated and largely linked to axis 1 and also to some degree to axis 2, where seed weight has even more correlation with axis 1 as biomass, but an opposite direction towards axis 2. Actually, biomass is more correlated with the third axis (0.80) which represents 10 % variance. Seed production is largely related to axis 2. The species with a large seed bank are found towards the right end of axis 1, the species with a high biomass in the lower left quadrant and the species with a high seed weight in the upper left quadrant. The variation in species position along axis 2 is mainly pronounced in the left part of axis 1, meaning that the species with a large seed bank and small seeds are not differentiated, but the species with a small or lacking seed bank and larger seeds are differentiated according to the variation in high seed production/high biomass vs low seed production/low biomass.

Figs. 4a and 4b show the results of the PCA with both the variables Relative Growth Rate and Morphology Index included. The four factors included in our

original study have similar positions as in Fig. 3b as far as Axis 1 is concerned. The two factors from Grime's scheme are slightly negatively correlated; the Morphology Index is very similar to Biomass, but RGR has its own position along axis 2 and is negatively correlated with both biomass and seed yield. Note that axis 2 is mirrored as compared with Fig. 3. In fact, there are now four axes of variation explaining 54 %, 19 %, 13 % and 10 % of the variance, respectively. The species are now differentiated in four directions rather than three. The seed bank species are still found at the right end of axis 1, but they are more separated on axis 2; the species with higher RGR are in the lower part, and the species with slower growth are in the upper part of the PCA diagram.

Figs. 5 and 6 show the results for the 13 species of the *Geranium* meadow. The species of this group are not clearly clustered, except for the dominants. In Fig. 5, seed weight and biomass are positively correlated and seed bank is negatively correlated with axis 1, while seed production and response to disturbance, being negatively correlated, represent the main variation along axis 2. Fig. 6 shows the PCA for 13 species of the *Geranium* meadows with RGR and M included. The seed bank species and the species with large seeds are still found at opposite ends of axis 1. It should be noted, however, that Morphology Index and Biomass are negatively correlated with RGR. Response to disturbance is largely correlated with axis 3 ($r = 0.98$) – representing 7 % of the variance.

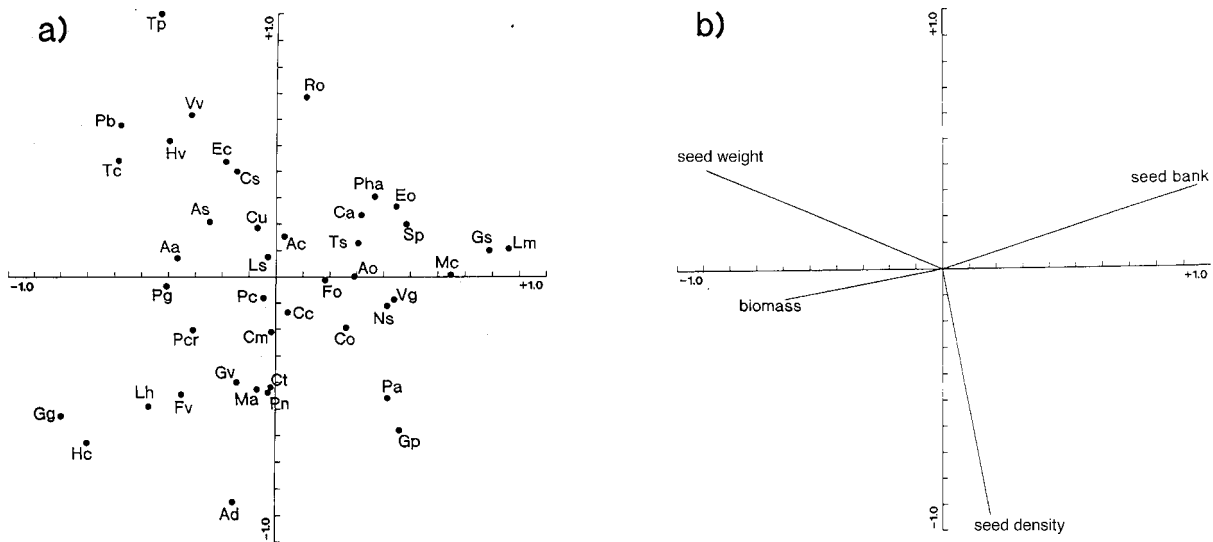


Fig. 3. Plots of the first two axes of a PCA ordination of 42 species (a) and their characteristics (b) in four alpine communities. Species codes: Aa = *Aster alpinus*; Ac = *Alchemilla caucasica*; Ad = *Antennaria dioica*; Ao = *Anthoxanthum odoratum*; As = *Anemone speciosa*; Ca = *Carex atrata*; Cc = *Carum caucasicum*; Cm = *Carum meifolium*; Co = *Carex oreophila*; Cs = *Carex sempervirens*; Ct = *Campanula tridentata*; Cu = *Carex umbrosa*; Ec = *Eritrichium caucasicum*; Eo = *Euphrasia ossica*; Fo = *Festuca ovina*; Fv = *Festuca varia*; Gg = *Geranium gymnocaulon*; Gp = *Gentiana pyrenaica*; Gs = *Gnaphalium supinum*; Gv = *Gentiana verna*; Hc = *Hedysarum caucasicum*; Hv = *Helictotrichon versicolor*; Lh = *Leontodon hispidus*; Lm = *Luzula multiflora*; Ls = *Luzula spicata*; Ma = *Minuartia aizoides*; Mc = *Matricaria caucasica*; Ns = *Nardus stricta*; Pa = *Primula algida*; Pb = *Polygonum bistorta*; Pc = *Pedicularis comosa*; Pcr = *Potentilla crantzii*; Pg = *Potentilla gelida*; Pha = *Phleum alpinum*; Pn = *Pedicularis nordmanniana*; Ro = *Ranunculus oreophilus*; Sp = *Sibbaldia procumbens*; Tc = *Taraxacum confusum*; Tp = *Trifolium polyphyllum*; Ts = *Taraxacum stevenii*; Vg = *Veronica gentianoides*; Vv = *Vaccinium vitis-idaea*.

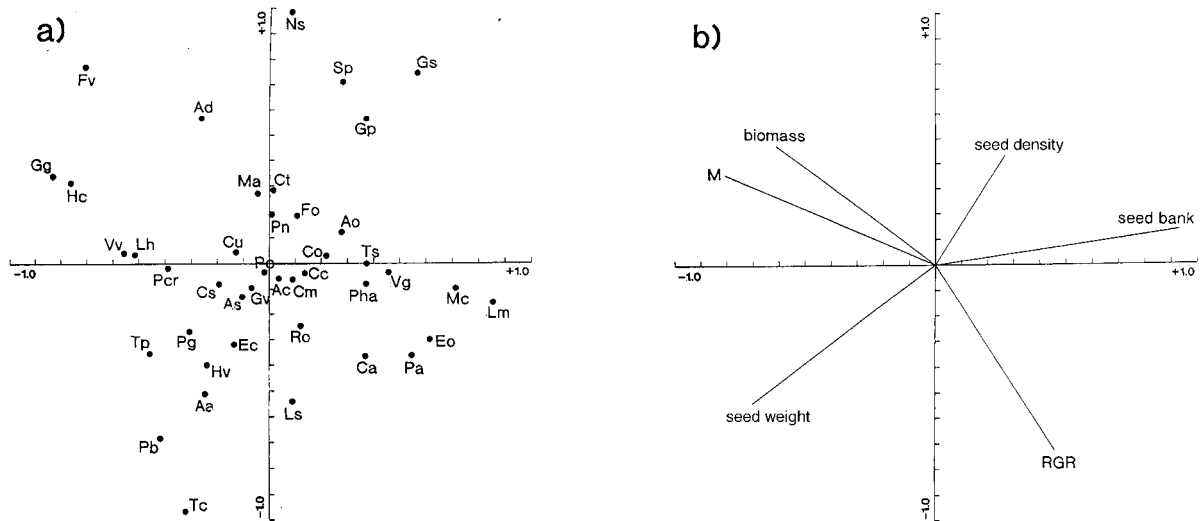


Fig. 4. Plots of the first two axes of a PCA ordination of 42 species (a) and their characteristics (b) in four alpine communities. Two characteristics are added as compared to Fig. 3: M = Morphology Index; RGR = Relative Growth Rate. Species codes as in Fig. 3.

Discussion

Our results confirm that species vary in their combination of traits, which means that they show degrees of V, E and/or P. Only a few species situated towards the periphery of the diagram may be indicated as 'pure

types'. The occurrence of transitional types has been recognized from the beginning, when Grime (1979) introduced C-S, C-R, S-R and C-S-R strategists, but in most publications on plant strategies the emphasis is on types. Our results show continuous variation between endpoints, so that we better speak of degrees of adaptation.

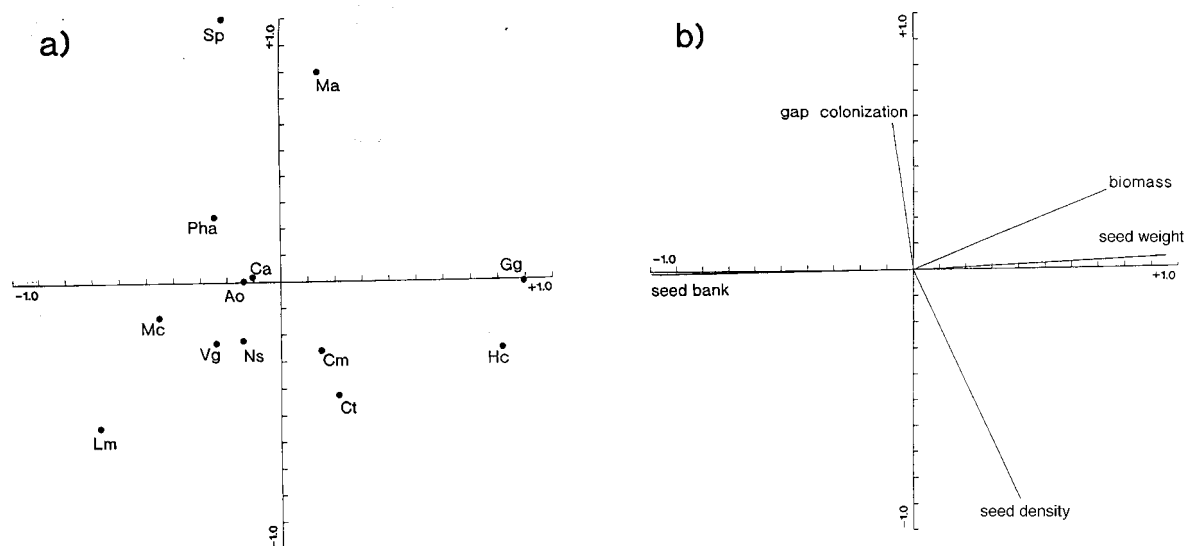


Fig. 5. Plots of the first two axes of a PCA ordination of 13 species (a) and four characteristics (b) of the species occurring in *Geranium* meadows. Key to species: Ao = *Anthoxanthum odoratum*; Ca = *Carex atrata*; Cm = *Carum meifolium*; Ct = *Campanula tridentata*; Gg = *Geranium gymnocaulon*; Hc = *Hedysarum caucasicum*; Lm = *Luzula multiflora*; Ma = *Minuartia aizoides*; Mc = *Matricaria caucasica*; Ns = *Nardus stricta*; Pha = *Phleum alpinum*; Sp = *Sibbaldia procumbens*; Vg = *Veronica gentianoides*.

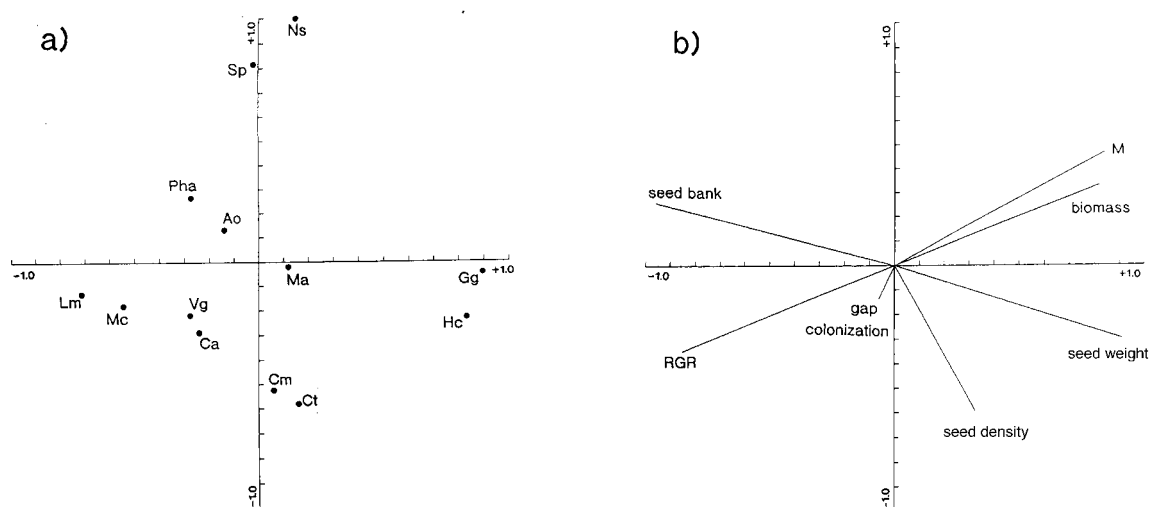


Fig. 6. Plots of the first two axes of a PCA ordination of 13 species (a) and six characteristics (b) of species occurring in *Geranium* meadows. Two characteristics are added as compared to Fig. 5: M = Morphology Index; RGR = Relative Growth Rate. Species codes as in Fig. 5.

The diagrams obtained by PCA should be interpreted in terms of traits and trait combinations. The following three endpoints arise from the diagram of Fig. 3a:

- Species with a large seed bank, small seeds and relatively low biomass;
- Species with a high biomass, large seeds and relatively high seed production;
- Species with large seeds, relatively low seed production and low biomass.

By definition, species with the V-strategy develop a large biomass under more productive conditions (Table 1). In our case this corresponds to the dominants of *Festuca* grasslands and *Geranium* meadows. The lichen heath and snowbed communities which occur in more severe habitats do not have real dominants. Species growing here can be considered as possessing a P-strategy, but in their turn they may differ by their population characteristics.

According to Romanovsky's concept, - species with a V-strategy have a high seed production;

- species with an E-strategy have a high reproductive effort;

- species with a P-strategy have a high 'expenditure per offspring'.

Our data on reproductive effort and expenditure per offspring are not accurate enough to enable us to distinguish between these strategies in alpine plants. Nevertheless, some trends are clear:

1. The main dominants of alpine meadows, with a large biomass, *Hedysarum caucasicum* and *Geranium gymnocalon*, have the largest seed yield, which corresponds to the V-strategy, while species with large numbers of small seeds (*Gnaphalium supinum*, *Sibbaldia procumbens*, *Anthoxanthum odoratum*, *Matricaria caucasica*, *Gentiana pyrenaica*, *Primula algida*) should be considered as species with an E-strategy.

2. The highest 'expenditure per offspring' values are found in some species of lichen heaths: *Polygonum bistorta*, *Ranunculus oreophilus*, *Aster alpinus*, *Helictotrichon versicolor*, *Euphrasia ossica*, *Eritrichium caucasicum*.

Our data on the soil seed bank confirm a tendency (Rabotnov 1975b, 1985) that species with a V-strategy – *Festuca varia*, *Geranium gymnocalon*, *Hedysarum caucasicum* in our case – usually do not accumulate viable seeds in the soil since they survive unfavourable periods in the adult stage. On the contrary, species with an E-strategy may have a large persistent seed bank (e.g. *Matricaria caucasica*, *Luzula multiflora*, *Gnaphalium supinum*, *Sibbaldia procumbens*).

The groups obtained by the clustering procedure are in agreement with such a scheme. For 42 species of all communities studied (Fig. 2a), we consider the species of the second major group (clusters 4, 5 and 6) as possessing the P-strategy, where cluster 4 consists of species with some features with an E-strategy; cluster 1 includes well-defined species with a V-strategy; species of cluster 3 are considered to possess the E-strategy; cluster 2 consists of species which also show many features with an E-strategy. For 13 species of the *Geranium* meadow (Fig. 2b), cluster 1 consists of well-defined species with the V-strategy; cluster 3 represents typical species with the E-strategy; cluster 2 is an intermediate group of species with many features with an E-strategy. Obviously, the ordination shows the pattern better than the classification.

Fig. 4a reveals a differentiation in four trends represented by the following groups:

- Species with a high biomass, high seed production, large seeds and low RGR towards the upper left corner, e.g. *Festuca varia*, *Geranium gymnocalon*, *Hedysarum caucasicum* (i.e. with rather a V-strategy):

- Species with a low biomass, low seed production and large seeds towards the lower end of axis 2, e.g. *Polygonum*

bistorta, *Taraxacum confusum*, *Trifolium polyphyllum*;

- Species with a large seed bank, small seeds and a high RGR towards the right end of axis 1, e.g. *Luzula multiflora*, *Matricaria caucasica*;

- Species with a large seed bank, high seed production and low RGR towards the upper right corner, e.g. *Gnaphalium supinum*, *Nardus stricta*, *Sibbaldia procumbens*.

The group which can easily be recognized in Fig. 3a, that with a large seed bank and small seeds, turned out to be divided according to the differences in RGR. Anyway, such an ordination seems to be more informative than Grime's triangle ordination, especially for plants of severe environments. In a triangle ordination of the 42 alpine species based on RGR and M according to Grime's (1979) scheme (Fig. 7), most species are situated in the S-corner; here the resolution of Grime's method is much lower. As remarked above, Grime's research group has also started to approach strategy types through ordination (Anon. 1995; Thompson et al. 1996). The question is which variables (meaning which traits) we should take into account. From our viewpoint, we get better information with more measurable characteristics, including reproductive traits.

Response to disturbance differs in different groups of plants. Any disturbance event has two consequences: (1) it limits the plant biomass by its direct destruction (Grime 1979) – a negative effect; (2) it creates a source of available resources – a positive effect. Plants with a P-strategy have a low biomass in grasslands and meadows, so their limitation by biomass removal is slight; but their response to resource availability is slow. Hence, on the whole, species with a P-strategy show a negative response to disturbance. Plants with a V-strategy lose more biomass because they are large. Their reaction to resource availability may be positive, but this depends on the intensity of the disturbance(s). When disturbance is low, adults of such species can capture free resources. Moreover, adult plants make new propagules which can occupy such gaps, and gaps are the necessary condition for recruitment of species with the V-strategy. Plants with an E-strategy hardly suffer from biomass removal, and greatly increase their abundance when resources become available, especially after severe disturbance. Thus, species with a positive response to intense disturbance, e.g. *Gnaphalium supinum*, *Sibbaldia procumbens* and *Veronica gentianoides*, have a largely E-strategy.

In this study we consider only intensive soil surface disturbance by bears and wild boars which must favour the E- (or 'ruderal') strategy. We did not take into account the influence of natural grazing, while this form of high-frequency and low-intensity disturbance may have a very heavy impact on vegetation (Huntly 1987; Oksanen & Oksanen 1989; Oksanen & Ranta 1992). However, the influence of ungulates is negligible in our

study area. Grasshoppers (*Acrididae*) and voles (*Pitymys majori*) have a higher impact, but their pressure was considered as an environmental factor so far (except the burrowing activity of voles, see Onipchenko & Rabotnova 1994). Nevertheless, the species which are known to tolerate grazing (e.g. *Festuca ovina*, *Gnaphalium supinum* and *Sibbaldia procumbens*) responded positively to large-scale soil surface disturbance.

The results of our investigation show that plants of lichen heaths are the species with the most pronounced features of a P-strategy, while among plants of more productive grasslands and meadows we can clearly distinguish species with the V-strategy – dominants of these communities – and species with an E-strategy, which have low biomass, but predominate in the seed bank and show a positive response to zoogenic disturbance. Species with clearly defined features with an E-strategy are abundant in snowbed communities; it is probably connected with the short growing season in these environments, where plants must possess an ability to develop rapidly. Del Moral (1983b) reached a similar conclusion. He showed, for subalpine meadows, that maximum differentiation into strategies occurred in intermediate habitats, namely in moderately stressed and disturbed sites with a productivity of ca. 300 g/m². Such conditions correspond to our *Festuca* grasslands and *Geranium* meadows, which are the most differentiated among the communities studied. Species of the lichen heaths and snowbed communities developing under significant abiotic stress are poorly differentiated. Our observations also confirm also his conclusion that “adaptive strategies may contrast sharply within a narrow range of environmental conditions”.

The approach proposed by Romanovsky (1989a, b) allows us to avoid some inherent contradictions of Grime's and other approaches. First, most habitat classifications by selection pressures define habitats along two independent axes: productivity (stress, adversity, harshness) and disturbance intensity. As shown above, in many environments productivity and disturbance are mutually related (see also Romanovsky 1989b; van der Maarel 1993). Some forms of disturbance may operate similar to stress in Grime's concept (Oksanen & Ranta 1992). Also, an environmental event such as flooding, can be stress and disturbance at the same time, causing plants either to escape such unfavourable conditions or to tolerate them (Menges & Waller 1983). According to Romanovsky (1989a, b), a one-dimensional gradient related to resource availability seems to be a more correct basis for the definition of primary life history strategies.

Romanovsky stressed that tolerance and competitive ability of the juvenile stage are important features. This idea is also found in recent literature (e.g. Rabinowitz et al. 1984; Grace 1985). It was shown that competitive

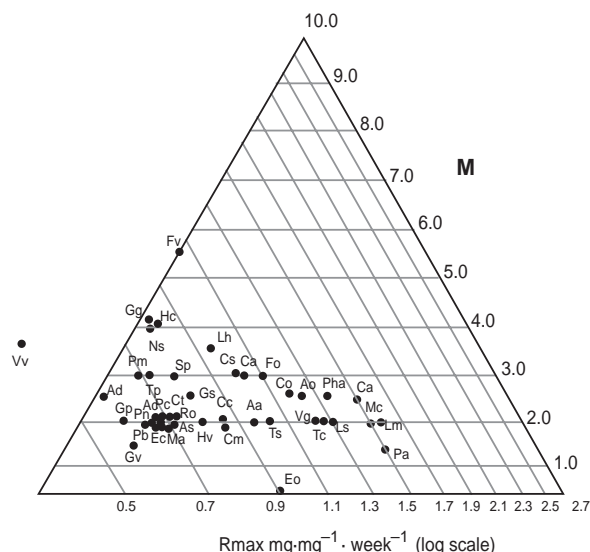


Fig. 7. A triangular ordination of 42 alpine species according to Grime (1979). M = Morphology index. Species codes as in Fig. 3.

abilities of juvenile and adult stages may change considerably. This is important for the V-strategy, since juveniles of such plants are shown to be weaker competitors, while juveniles of P-species must possess a vigorous competitive ability which permits their existence among established species with a V-strategy.

Shipley et al. (1989) also found ‘uncoupling’ of juvenile and adult traits. They suggest the distinction fugitive, r-selected vs. stress-tolerant, K-selected juvenile traits and fugitive, r-selected vs. competitive and K-selected adult ones. The juvenile and adult subsets may vary independently, resulting in four types of strategies:

1. Typical r-selected traits, both for juveniles and for adults;
2. Typical K-selected traits, both for juveniles and adults;
3. r-selected juveniles and K-selected adults;
4. K-selected juveniles and r-selected adults.

It seems to be not quite correct to apply the expressions ‘r-selected’ and ‘K-selected’ to juvenile and adult stages of the life cycle separately. Rather we should speak of differences in juvenile and adult mortality (see also Stearns 1977). Nevertheless, the first three strategies correspond to the E-, P- and V-strategy respectively. The fourth strategy (K-selected juveniles and r-selected adults) is a new one. It seems to be less common (it may be a special case of monocarpic perennials).

Our attempt to distinguish different strategies amongst alpine plants is not complete and definitive. For example, we did not consider possibilities of seedling establishment, competitive abilities and vegetative propagation. These issues are open for further investigations.

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App. 1. Characteristics of 42 alpine species occurring in different community types. ALH = alpine lichen heaths, FVG = *Festuca varia* grasslands, GHM = *Geranium gymnocaulon*-*Hedysarum caucasicum* meadows, SBC = snowbed communities. Comm. = community type; B = Above-ground biomass ($\text{g/m}^2 \pm \text{SE}$); Ws = Weight of 100 seeds (mg); Sp = Seed production ($/\text{m}^2, \pm \text{SE}$); Sy = Seed yield (mg/m^2); Re = Reproductive effort (%); Eo = Expenditure per offspring (%); Sb = Seed bank ($\text{seeds/m}^2, \pm \text{SE}$); RGR = Relative growth rate (rank), M = Morphology index (rank).

Species	Comm.	B	W	Sp	Sy	Re	Eo	Sb	RGR	M
<i>Alchemilla caucasica</i>	ALH	0.9	41	39 ± 5	16	1.8	0.045	12 ± 12	2	2
<i>Anemone speciosa</i>	ALH	12.1 ± 1.1	630	164 ± 11	1033	8.5	0.052	22 ± 11	2	2
<i>Anthoxanthum odoratum</i>	FVG	7.6 ± 1.4	45	168 ± 12	74	1	0.006	20 ± 9	4	2.5
	GHM	15.7 ± 2.2	45	234 ± 26	104	0.66	0.003	155 ± 61	4	2.5
<i>Antennaria dioica</i>	ALH	5.9 ± 0.9	6	192	12	0.2	0.001	0	1	2.5
<i>Aster alpinus</i>	ALH	0.2	70	19 ± 3	13	6.7	0.35	0	3	2
<i>Campanula tridentata</i>	ALH	12.1 ± 1.4	35	297 ± 27	104	0.86	0.003	11	2	2
	FVG	1.3 ± 0.8	35	37 ± 9	13	1	0.027	5 ± 5	2	2
	GHM	1.1 ± 0.5	35	50 ± 9	18	1.6	0.03	5 ± 5	2	2
<i>Carex atrata</i>	FVG	5.3 ± 2.0	54	5 ± 2	3	0.05	0.01	170 ± 42	6	2.5
	GHM	3.5 ± 0.8	54	116 ± 23	62	1.8	0.016	75 ± 20	6	2.5
<i>Carex oreophila</i>	SBC	2.1 ± 0.6	17	166	20	0.95	0.006	35 ± 21	4	2.5
<i>Carex sempervirens</i>	ALH	11.9 ± 1.1	106	21 ± 2	22	0.18	0.009	14 ± 5	3	3
<i>Carex umbrosa</i>	ALH	11.9 ± 1.1	94	58 ± 7	55	0.46	0.008	20 ± 7	3	3
	FVG	2.2 ± 0.7	94	33 ± 7	31	1.4	0.006	5 ± 5	3	3
<i>Carum caucasicum</i>	ALH	4.5	121	372 ± 22	450	10	0.03	36 ± 12	3	2
<i>Carum meifolium</i>	GHM	4.1 ± 0.7	137	443	607	15	0.03	24 ± 13	3	2
<i>Eritrichium caucasicum</i>	ALH	0.7	80	10 ± 2	8	1.1	0.11	4	2	2
<i>Euphrasia ossica</i>	ALH	0.1 ± 0.1	14	43 ± 7	6	6	0.14	100	3	0.5
<i>Festuca ovina</i>	ALH	23.7 ± 1.6	40	152 ± 32	61	0.26	0.002	15	4	3
<i>Festuca varia</i>	FVG	172 ± 21	116	344	399	0.23	0.001	5 ± 5	3	5.5
<i>Gentiana pyrenaica</i>	ALH	2.6 ± 0.4	6	646 ± 60	39	1.5	0.002	66 ± 23	2	2
	FVG	2.2 ± 0.5	6	458 ± 95	28	1.3	0.003	10 ± 10	2	2
	GHM	1.1 ± 0.5	6	137 ± 46	8	0.7	0.005	0	2	2
<i>Gentiana verna</i>	ALH	0.2	9	44 ± 10	4	2	0.045	0	2	1.5
<i>Geranium gymnocaulon</i>	GHM	137 ± 14	894	600 ± 117	5361	3.9	0.007	0	2	4
<i>Gnaphalium supinum</i>	SBC	11.0 ± 1.9	8	212 ± 7	17	0.15	0.001	1475 ± 333	2	2.5
<i>Hedysarum caucasicum</i>	GHM	33.5 ± 5.8	691	899 ± 230	6215	18.6	0.02	0	2	4
<i>Helictotrichon versicolor</i>	ALH	5.4	687	29 ± 2	199	3.7	0.13	7	2	2
<i>Leontodon hispidus</i>	FVG	5.6 ± 3.2	132	238 ± 48	313	5.6	0.02	0	3	3.5
<i>Luzula spicata</i>	ALH	1.5	28	30 ± 4	8	0.6	0.02	6	5	2
<i>Luzula multiflora</i>	GHM	0.7 ± 0.3	11	310 ± 90	35	5	0.02	1600 ± 406	6	2
<i>Matricaria caucasica</i>	GHM	10.8 ± 1.5	28	540 ± 157	151	1.4	0.003	1190 ± 196	6	2
<i>Minuartia aizoides</i>	GHM	3.5 ± 1.1	20	27 ± 8	5	0.1	0.005	5 ± 5	2	2
	SBC	13.4 ± 1.6	20	153 ± 10	31	0.23	0.002	5 ± 5	2	2
<i>Nardus stricta</i>	FVG	67.7 ± 9.3	35	378 ± 43	132	0.2	0.016	455 ± 190	2	4
	GHM	34.9 ± 4.3	35	496 ± 96	174	0.5	0.001	210 ± 58	2	4
<i>Pedicularis comosa</i>	ALH	0.8	42	75 ± 10	32	3.6	0.048	6 ± 3	2	2
<i>Pedicularis nordmanniana</i>	SBC	3.8 ± 0.8	41	333 ± 99	137	3.6	0.01	8 ± 6	2	2
<i>Phleum alpinum</i>	GHM	19.9 ± 2.7	47	101	47	0.24	0.002	328 ± 121	5	2.5
<i>Polygonum bistorta</i>	ALH	0.2	425	6 ± 1	26	12.8	2.13	0	2	2
<i>Potentilla gelida</i>	ALH	1.5	80	30 ± 4	24	1.1	0.037	0	2	2
<i>Potentilla crantzii</i>	SBC	0.2	45	47	21	10.6	0.225	0	2	3
<i>Primula algida</i>	ALH	0.2	5	276 ± 54	13	6.9	0.025	32	6	1.5
<i>Ranunculus oreophilus</i>	ALH	0.2	113	16 ± 2	18	9.04	0.565	48	2	2
<i>Sibbaldia procumbens</i>	GHM	5.6 ± 1.7	35	20 ± 6	7	0.1	0.006	110 ± 38	2	3
	SBC	49.4 ± 2.8	35	190 ± 10	67	0.14	0.001	765 ± 187	2	3
<i>Taraxacum confusum</i>	FVG	6.4 ± 1.8	220	6 ± 5	13	0.2	0.03	0	5	2
<i>Taraxacum stevenii</i>	SBC	17.8 ± 1.5	67	220 ± 28	147	0.83	0.004	245 ± 115	4	2
<i>Trifolium polyphyllum</i>	ALH	8.1 ± 2.2	307	1.3 ± 0.3	4	0.05	0.05	0	2	3
<i>Vaccinium vitis-idaea</i>	ALH	1.6	20	0	0	0	0	0	1	3.5
<i>Veronica gentianoides</i>	ALH	0.9	27	41 ± 5	11	1.2	0.03	45	4	2
	FVG	1.7 ± 0.6	27	64 ± 11	17	1	0.02	25 ± 12	4	2
	GHM	2.4 ± 0.5	27	310 ± 105	85	3.5	0.01	150 ± 71	4	2