

Plant strategies along mountain vegetation gradients: a test of two theories

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Abstract. We test the predictions of two theories on plant strategies along vegetation gradients of a North Scandinavian mountain area, from herb-rich birch forests at 250 m. a.s.l. to the summit at 1530 m. a.s.l. According to Grime's theory, stressful physical conditions select for an adaptational syndrome called *S*-strategy. The theory predicts that the prevalence of *S*-strategic features increases monotonically from forests to high-alpine boulder fields. Alternatively, the traits that Grime regards as *S*-strategic can be interpreted as adaptations to high natural-grazing pressure which culminates in moderately stressful habitats: productive enough to sustain grazers but yet so barren that moderate grazer densities suffice to deplete the vegetation. The observed vegetation patterns support this alternative view. We thus suggest that Grime's triangle should be revised as to make the role of grazing as the central causal factor behind the third strategy explicit.

Keywords: Alpine; Arctic; Competition; Disturbance; Grazing; Iddonjårga Mountains; Northern Scandinavia.

Introduction

According to the plant strategy scheme of Grime (1977, 1979, 1988; see also Grime, Hodgson & Hunt 1988; Thompson 1987), adaptations to competition, stress and disturbance represent a 'zero sum game' where gains in one direction imply losses in others. This view has two important corollaries. First, habitats with high levels of both stress and disturbance are predicted to be devoid of plant life. Second, the viable plant strategies can be arranged into a triangle where the corners (*C*, *S* and *R* strategies) represent adaptations to 'pure' selective pressures (intense competition without stress or disturbance, intense stress without competition or disturbance and intense disturbance without stress or competition). Secondary strategies (*C-S*, *C-R* and *S-R*) represent compromises between two selective pressures and lie along the sides of the triangle, while the generalist strategy (*C-S-R*) is in the center.

The underlying assumptions of Grime's triangular scheme have been criticized e.g. by Tilman (1987, 1988) and Taylor, Aarssen & Loehle (1990). Tilman stated that competitiveness cannot be defined without reference to limiting resources and that environmental stresses only change the optimal tactics of competition such as allocation patterns (Tilman 1988, 1990) and the tuning of the photosynthetic apparatus to different temperatures and light intensities (Kershaw 1975; Lechowicz 1978; Bazzaz 1979). Moreover, Tilman's approach builds on MacArthur's (1972, Figs. 2-13) vision on the kinetics of interspecific competition, where competitive interaction is won by the species which tolerates the lowest levels of limiting resources. Thus, in their view, stress-tolerance and competitiveness are two aspects of the same property. Taylor, Aarssen & Loehle (1990, see also Kautsky 1988), claim that there is a major logical lapse in Grime's theory. While stress (adversity, impoverishment) indeed lowers *K* (the maximum sustainable plant biomass), this has nothing to do with the intensity of competition which depends on the % difference between plant biomass and *K*. The emphasis and formulation of Tilman and Taylor et al. are somewhat different but the central logics are the same.

There is also a slight ambiguity in the way how Grime's (1977, 1979) introduces the idea of *S*-strategy. The main theme is the direct impact of stress on optimal life history strategy, resource allocation, physiology and morphology. However, Grime also points out that even low frequencies of grazing can inflict great losses to the slowly growing plants of stressful habitats, which explains the low palatability of *S*-strategists. Thus, Grime's reasoning contains a central element of the theory of exploitation ecosystems which was developed by Fretwell (1977) and Oksanen (1980, 1983; Oksanen et al. 1981; Oksanen & Oksanen 1981). The central idea of this theory is that the population dynamics of grazers change along gradients of primary productivity. In productive habitats, grazers are regulated by carnivores and

natural grazing pressure is light. In moderately barren habitats, grazers are strictly resource-limited and, consequently, natural grazing pressure is intense. In extremely barren habitats, grazers cannot persist and natural grazing pressure is practically non-existent.

Although Grime was among the first to connect stress to natural grazing pressure, he did not pursue this lead. We have not found a single statement where Grime regards grazing as a necessary condition for the evolution or ecological persistence of *S*-strategic plants. Moreover, Grime (1979, Fig. 11) considered secondary succession as a path from the prevalence of ruderals to the dominance of *S*-strategists. The implication that climax plants of mesic forests are *S*-strategists is in total conflict with the idea of grazing as a cause for the *S*-strategy. This issue has been a problem for Grime as well: British climax trees are not regarded as *S*- but as *C*- and *C-S*-strategists, or their intermediates (Grime, Hodgson & Hunt 1988.) Thus, Grime does not seem to be satisfied with his scheme as far as stressful but lightly grazed habitats are concerned. However, he does not tackle this discrepancy and seems to imply that stress per se is both a necessary and a sufficient condition for the predominance of *S*-strategic plants.

The relative importance of stress and grazing as causal mechanisms behind the *S*-strategy is not just an academic issue. A habitat can be extremely stressful and totally ungrazed, because its plant cover is too scanty for grazers to persist (Oksanen et al. 1981) or because it is on a grazer-free island (Collins, Baker & Tillbrook 1975). Conversely, man-managed habitats (Ellenberg 1978) and isolated islands with herbivores but without carnivores (Merton, Brown & Hnatiuk 1976) can be both highly productive and intensely grazed. Moreover, the situation may change due to introductions of grazers (Leader-Williams, Scott & Pratt 1981) or changes in land use (Pettersson 1958). Without understanding the causal background of our strategy concepts, we cannot use them for predicting vegetation responses to natural or man-made environmental changes.

An alternative to Grime's triangle

Another possible source for a triangular ordination scheme is the heterogeneity of disturbance as a set of selective pressures (see Stearns 1976). The classical *r*-strategy of MacArthur & Wilson (1963) and the equivalent *R*-strategy of Grime (1977, 1979) represent adaptations to disturbances of such high intensity, that no organisms can survive in situ (e.g. explosive outbreaks of volcanoes, massive landslides, intense forest fires). Then the speed of recovery depends on the rate of arrival of propagules and on the reproductive poten-

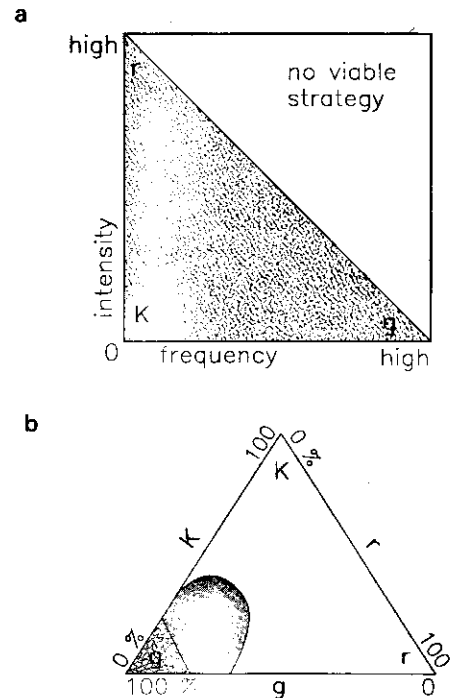


Fig. 1. Schematic presentation of the alternative for Grime's plant strategy triangle. a. Combinations of different frequencies and intensities of disturbance. Low frequency and low intensity implies *K*-selection, low frequency and high intensity implies *r*-selection, high frequency and low intensity implies *g*-selection, high frequency and high intensity is lethal. b. A trade-off triangle for responses to these three selective pressures. Heavy shading refers to pure *g*-strategy (ericoid and *Dryas* variants). Light shading refers to the graminoid variant of *g*-strategy, selected for by intermittently heavy grazing, which also contains some elements of *K*-strategy (capacity for shoot competition by means of internodal growth) and *r*-strategy (potential for strong generative reproduction, if floral shoots are not grazed).

tial of the invaders. When local survival is possible, survivors are likely to outnumber invading propagules and the speed of recovery depends on the product of the number of survivors times their rate of reproduction or vegetative expansion. Consequently, disturbance of low or moderate intensity can select for traits like copious allocation of resources to below-ground organs and high potential for vegetative spreading which radically differ from the classical *r*-strategy. Grazing is a prime example of high-frequency, low-intensity disturbance, where one incident seldom kills individual genets. Instead of favouring the classical *r*-strategy, grazing thus favours maximization of the ratio e/a , where e stands for the rate of expansion of the plant and a represents the likelihood of losing a unit of biomass to a grazer within a unit of time (i.e. a reflects the palatability of the plant, see Holt 1977).

Indeed, disturbance can be both very intense and

frequent. Examples of this (e.g. strip mining, gravel removal, dumping of mining waste, rapid bank erosion in hydro-electric reservoirs) are abundant in our environment. Such habitats can harbour seedlings or patches of translocated vegetation, but the occurrence of plants is accidental and entirely dependent on the existence of viable plant populations in the surroundings (Grelsson 1986; Borgegård 1990). Thus, in a rectangle where the sides represent the intensity and frequency of disturbance (Fig. 1a), higher plants can only cope with habitats to the left of the diagonal. The intensity of environmental stresses determines where the line of demarcation runs; otherwise, stress is not part of the strategy scheme.

We can thus envisage three classes of selective pressures which select for totally different combinations of traits and thus impose an adaptational zero sum game on organisms. One class consists of high-intensity, low-frequency disturbances like the explosion of Mt. St. Helens (e.g. Halpern et al. 1990). They initiate transient dynamics which favour classical *r*-strategists (ruderals) with a short life cycle and copious production of light propagules. The other class consists of high-frequency, low-intensity disturbances like the highly selective nibbling by sedentary, small-sized grazers. This kind of disturbance favours plants which roughly correspond to Grime's (1979) description of *S*-strategists (see Huntly 1987; Oksanen 1990; Oksanen & Oksanen 1989), with low stature, tough and narrow leaves, low palatability or low shoot/root ratio, chiefly vegetative reproduction (because inflorescences and floral buds are sensitive to grazing, see Tihomirov 1959; McNaughton 1979; Ericson & Oksanen 1987) and lack of concentrated and palatable perennation organs. We will call this adaptational syndrome the *g*-strategy.

The third pole represents the *K*-strategy, i.e. adaptations to undisturbed competition; see MacArthur (1972), Tilman (1982, 1987, 1988, 1990), but also Cajander (1909), Ellenberg (1954, 1978) and Walter (1964, 1968). Competitiveness means an ability to slowly but surely establish a permanent control over limiting resources by keeping their levels below the tolerance limits of other species (exploitation competition where competitiveness is closely related to stress-tolerance) or by denying competitors an access to limiting resources (interference competition where competitive hierarchies may be generated; see Keddy 1990).

In the triangular plant strategy scheme thus derived (Fig. 1b), also secondary strategies can be distinguished. However, this seems premature before the basic idea is subjected to a critical test. In the present paper, we will thus use a coarse version of the scheme, where all plants are assigned to some primary strategy. The three variants of *g*-strategy identified by Oksanen (1990) are only discussed to the extent which is necessary for identify-

ing *g*-strategists as a group. In brief, the ericoid variant encompasses plants with low palatability but also low growth rate, due to the costs of defence. The *Dryas* variant comprises plants with lower levels of defence (higher palatability and higher growth rate; the relative advantages of these variants depend on the availability of mineral nutrients, see Bryant, Chapin & Klein 1983; Oksanen 1990). The graminoid variant represents adaptations to intermittent grazing and covers the area between the extreme *g*-strategy corner and the middle parts of the triangle (Fig. 1b).

We will call this alternative scheme the *MacArthur-Fretwell* triangle to emphasize that (1) it builds on MacArthur's view of competition and directly uses his theory of *r*- and *K*-selection and (2) natural grazing pressure is included in a way which was introduced by Fretwell (1977). The MacArthur-Fretwell scheme is compatible with the existence of generalized adversity or impoverishment selection (see Taylor, Aarssen & Loehle 1990), which could be represented as a third dimension in the scheme. However, it is prudent to fully explore the potentials and limitations of two-dimensional schemes before introducing a third dimension.

Predictions and outlines for a test

Both theories imply that the vegetation of moderately stressful habitats (steppes, semi-deserts, arctic and alpine tundras) is dominated by plants which are somehow outside the axis between competitiveness and ruderalness or *r*- and *K*-strategies. However, predictions concerning extreme habitats diverge. Grime's theory implies that the prevalence of *S*-strategic features increases monotonically with increasing intensity of environmental stresses. Conversely, the MacArthur-Fretwell scheme implies that the scanty vegetation of extreme habitats (arid and polar deserts, high-alpine boulder fields) is dominated by plants which lie along the *r*-*K* axis.

If Grime's *S*-strategists and MacArthur-Fretwell *g*-strategists were exactly the same species, the above prediction would give an opportunity to perform a straightforward test in any gradient from productive to sterile habitats. However, plants which are *K*-strategists of cold or dry habitats in the MacArthur-Fretwell scheme are treated as *S*-strategists by Grime (1979). This applies to desert shrubs (e.g. *Encelia californica*), robust, cushion-building mosses (e.g. *Racomitrium lanuginosum*) and many fruticose and foliose lichens. Also evergreen, prostrate dicotyledons are regarded as *S*-strategists, whereas in the MacArthur-Fretwell scheme, robust, evergreen cushion and rosette plants are regarded as *K*-strategists, specialized to monopolize favourable microsites in a generally hostile habitat.

The risk for an ambiguous outcome can be minimized by choosing a vegetational gradient where plants of the most extreme habitats occur as relatively dense patches, so that eventual competitive interactions will, at least partially, take place between shoots for light (or for the warming effect of direct solar radiation). The boreal and subarctic mountains of Scandinavia satisfy this condition. Vascular plants are patch-wise abundant even in high-alpine boulder fields (Nordhagen 1927, 1943; Gjaerevoll 1956). This does not prove that competition is important. The patch-wise occurrence of Scandinavian high-alpine plants is used as evidence for the mutualistic nature of interactions between high-alpine plants, see Callaghan & Emmanuëlsson (1985). However, if competition is important, it will favour plants which are competitive even by the standards of Grime.

Material and Methods

Study area, field procedure and vegetation typification

The material consists of sample plots representing different topographical and altitudinal aspects of the Iddonjårga Mountains at Lyngshalvöya in northernmost Norway, 69° 30' N and 20° E, from 250 m, the upper limit of heavy human impact, in the North-boreal zone (Ahti, Hämet-Ahti & Jalas 1968) to the summit of Njállavári, 1530 m above the firm line. The climate is oceanic (mean temperatures at sea level: July +13 °C, February -6 °C, Anon. 1957), but with moderate precipitation (570 mm/yr, 200 mm during June-September, Anon. 1949). Geologically, the Iddonjårga massif consists of an intrusion of igneous material into the Scandes, providing homogeneous bedrock conditions at all altitudes (Lindström 1987). Between 200 and 500 m, the land is used as a summer range for sheep. The higher country is a summer range for reindeer. Due to transportation problems, reindeer numbers are well below levels typical for the coasts of northernmost Norway and comparable to the wild reindeer densities of Hardangervidda (N. Sara, pers. comm.; Gaare & Skogland 1975).

Sampling proceeded as follows. Hillocks on relatively gentle slopes were chosen at altitudinal intervals of 25 m, each as close to the previous one as possible. From the crest of each hillock to the nearest depression, a rope of 15 m was fixed and plots of 0.8 m by 0.8 m were sampled at intervals of 2 m along the rope, up to the altitudinal limit of continuous vegetation at 1025 m. Higher up, vegetation fragments were sampled upon encounter (the first four encountered patches with terricolous vegetation for each altitudinal interval of 25 m). The chosen plot size gave fairly homogeneous samples on the alpine tundra. In the forest, the plots were too

small to be regarded as adequate phytosociological relevés, whereas in the boulder field zone the plots were too large to represent homogeneous sites. In each plot, plant species cover was estimated using an 11-class modified Scandinavian scale (Oksanen 1976), with the class boundaries roughly at 70, 35, 18, 9, 4, 2, 1, 0.5, 0.25 and 0.12%; estimations of low cover values were aided by means of cardboard squares representing class limits. Cover values were transformed to $\frac{1}{2}$ log values. The sampled vegetation was arranged into community types by means of the divisive clustering procedure TWINSpan (Gauch 1982), applied both to the entire material and to sections covering 250 m of altitude (the latter to check whether the indicator values of species changed with altitude). 25 clusters were interpreted as local plant community types and used for calculations. Ecological relations were studied by means of Detrended Correspondence Analysis (program DECORANA, version Hill 1979, with default values, see Gauch 1982).

Calculation of strategy scores

The assignment of vascular plants into Grime's scheme was based on the criteria and examples provided by Grime (1979) and Grime, Hodgson & Hunt. (1988). In cases of inconsistency, priority was given to the summary table of Grime (1979, Table 6). Morphological characteristics were checked in the field, reproductive characteristics were evaluated mainly on the basis of Söyrinki (1939). Data on palatability were taken from Aleksandrova et al. (1964) and Skjenneberg & Slagsvold (1968).

The assignment of cryptogams to Grime's categories was problematic. Lichens were regarded as *S*-strategists (Grime 1979, Fig. 18e and p. 36). According to Grime (1979, Fig. 18f and pp. 65-66), the majority of bryophytes represent the *R-S*-strategy. However, Grime (1979, p. 23) includes bryophytes in his list of arctic-alpine stress-tolerators, and the overwhelmingly most abundant species in our material, *Dicranum fuscescens*, is positively identified as a *S*-strategist (Grime 1979, p. 36 and p. 65). On the basis of Grime's (1979, Table 6) summary, robust mosses could be treated as *C-S*-strategists. However, no bryophytes were placed to this part of the triangle by Grime (1979, Fig. 18f) and one robust bryophyte, *Racomitrium lanuginosum*, was identified as a pure *S*-strategist (Grime 1979, p. 65). By that standard, we regard all bryophytes in our material as *S*-strategists. The assignment of plants to the MacArthur-Fretwell scheme followed the reasoning summarized in section 2 (see also Oksanen 1990). The treatment of different plant categories in both schemes is summarized in Table 1. As a rule, Grime's *S*, *C-S-R* and *C-R*-strategists are *g*-strategists in the MacArthur-Fretwell

Table 1. Assignment of plants to different strategies according to Grime and MacArthur-Fretwell (MAF) schemes. Symbols in Grime's scheme as defined in Grime (1979). Symbols in the MAF-scheme: *K* = *K*-strategists, adapted to undisturbed habitats; *r* = *r*-strategist, adapted to frequent physical disturbance; *ge* = the ericoid variant of the grazing-tolerant strategy; *gd* = the *Dryas* variant of the grazing-tolerant strategy; *gg* = the graminoid variant of the grazing-tolerant strategy.

Plant group	Grime	MAF
Erect, mesomorphic woody plants	<i>C</i>	<i>K</i>
Erect, broad-leaved, mesomorphic herbs	<i>C</i>	<i>K</i>
Erect-semiprostrate, mesomorphic woody plants	<i>C-S</i>	<i>K</i>
Semiprostrate, broad-leaved, mesomorphic herbs	<i>C-S</i>	<i>K</i>
Robust rosette and cushion plants	<i>S</i>	<i>K</i>
Prostrate, mesomorphic dwarf shrubs and herbs	<i>S</i>	<i>gd</i>
(Semi-)prostrate, narrow-leaved, evergreen dwarf shrubs	<i>S</i>	<i>ge</i>
Wood rushes with copious inflorescences	<i>S-R</i>	<i>r</i>
Annuals	<i>R</i>	<i>r</i>
Mesomorphic graminoids	<i>C-R</i>	<i>gg</i>
Small-leaved, erect, mesomorphic herbs	<i>C-R</i>	<i>gg</i>
Broad-leaved herbs with copious seed production	<i>C-R</i>	<i>K</i>
Tough-leaved, xeromorphic graminoids	<i>C-S-R</i>	<i>gg</i>
Crustose lichens	<i>S</i>	<i>ge</i>
Fruticose lichens exclusive <i>C. stellaris</i>	<i>S</i>	<i>ge</i>
<i>Cladonia stellaris</i>	<i>S</i>	<i>K</i>
Cup lichens (<i>Cladonia</i> subg. <i>Cladonia</i>)	<i>S</i>	<i>r</i>
Foliose lichens	<i>S</i>	<i>K</i>
Small and medium-sized mosses (typical)	<i>S</i>	<i>ge</i>
Typical hepatics	<i>S</i>	<i>gd</i>
Bryophytes with good colonizing capacity	<i>S</i>	<i>r</i>
Layer-forming mosses	<i>S</i>	<i>K</i>
Cushion or bank-forming mosses	<i>S</i>	<i>K</i>

scheme, Grime's *C*- and *C-S*-strategists are *K*-strategists, and Grime's *R*- and *S-R*-strategists are *r*-strategists. The main exceptions are as follows. 1. Robust cushion and rosette plants are regarded as *K*-strategists, so are equivalent cryptogam groups (mosses and lichens capable of making thick, compact cushions or mats, foliose lichens). 2. Cup lichens and club mosses are regarded as *r*-strategists (see Ahti 1959). 3. Broad-leaved herbs with copious generative reproduction would have been best regarded as representatives of the secondary *K-r*-strategy, but as secondary strategies are not used, they are treated as *K*-strategists. (For the assignment of individual species, see App. 1.)

For each community type we calculated the prevalence scores (percentage of the strategy out of the total plant cover) of the different strategies according to the two schemes. The Grime strategy prevalences were computed separately for primary and secondary strategies. Also, the prevalence score (%) of each primary strategy was computed as a weighted sum of the prevalence scores of the primary and secondary strategies, where the primary strategy was weighted by a factor 1, the secondary strategies flanking the primary one by 0.5

and the *C-S-R*-strategy by 0.33. As an example, prevalence of strategy *C* (%) = $C + 0.5 (C-S) + 0.5 (C-R) + 0.33 (C-S-R)$. The scores were then placed in the centre of the space occupied by the community type in the ordination, and strategy patterns were drawn as contour maps. Scores for individual community type will be summarized below. Our treatment of cryptogams is open to criticism. First, considering all of them as *S*-strategists created the situation where increasing predominance of cryptogams automatically leads to increasing *S*-strategy score. Second, prevalence scores based on cover values grossly overestimate the contribution of the smallest cryptogams to the plant biomass. Thus, we checked our results by performing corresponding computations based on vascular vegetation only.

Results and Discussion

Community variation

The ordination of the sample plots (Fig. 2) echoes the traditional view of the importance of altitude and snow conditions for Fennoscandian oro-arctic (alpine) vegetation (Nordhagen 1927, 1943; Kalliola 1939; Dahl 1956; Gjaerevoll 1956). The first axis correlates with altitude ($r = +0.94$). However, plots in extreme topographic positions get invariably higher scores on this axis than other plots from the same altitude, while three boulder-field plots with much vegetation got scores typical for middle altitudes. Thus, axis 1 seems related to intensity of stress due to alpine conditions. Axis 2 is related to thickness and duration of snow cover, with bare-blown ridges on the left and late snowbeds on the right. At low altitudes, where ridges offer somewhat stressful conditions and depressions are more luxuriant sites, topographic differentiation occurs along the first axis. The TWINSPAN community types separate relatively well along the two first axes at low and middle altitudes, less so in the boulder-field zone. The distribution of the main species over the types is summarized in App. 1.

Abundance relationships between different strategies - Grime's scheme

Prevalence scores of strategy types in the 25 community types are shown in Fig. 3. Ruderal features are not especially prevalent anywhere along the vegetational gradients (Fig. 4; see below). Where substantial *R*-strategy scores are obtained, they are mainly generated by a moderate abundance of *C-S-R*, *S-R* and *C-R*-strategists. The highest *R*-strategy scores are obtained in

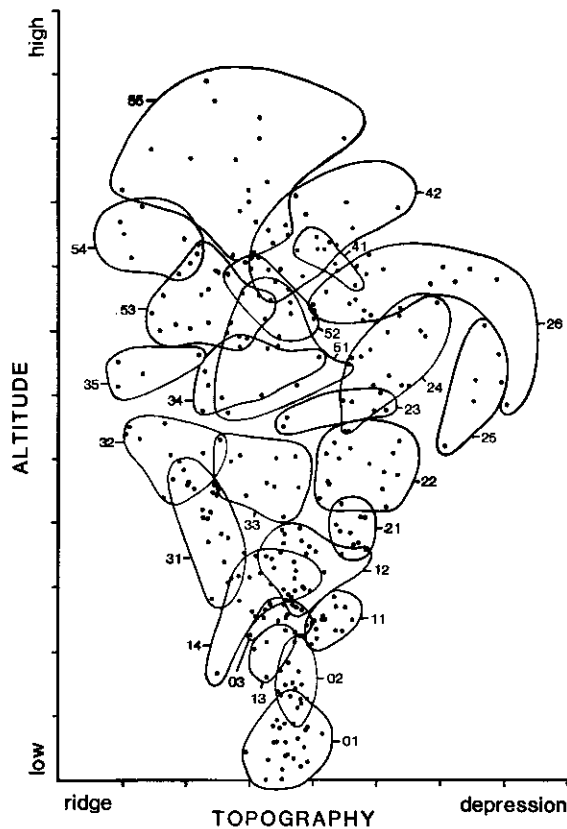


Fig. 2. Distribution of the sample plots and community types in the ordination space with axis 1 (vertical) reflecting altitude and axis 2 topography (depth of the snow cover). Community type numbers as in Table 2. The first number identifies broader vegetation categories: 0 = forest floor, 1 = low alpine heath, 2 = low-to-middle alpine snowbed, 3 = low-to-middle alpine windbarren, 4 = high alpine snowbed, 5 = windbarren.

the vegetation fragments of the boulder-field zone. This high-altitude peak in the *R*-strategy score is still more pronounced in computations based on vascular plants only (Fig. 3b). The two lower peaks in the *R*-strategy landscape correspond to typical snowbeds and forests. The latter one is probably due to sheep grazing, whereas the snowbed peak is difficult to interpret.

The compatibility between these results and Grime's theoretical views can be argued. Ruderal features are most prevalent in habitats with plausible sources of disturbance - sheep grazing, frost-boiling and formation of patterned ground. The abundance of ruderal features culminates in high-alpine boulder fields, where frost-generated physical disturbance is especially intense. The correspondence between *R*-strategy and plausible sources of disturbance conforms to Grime's proposi-

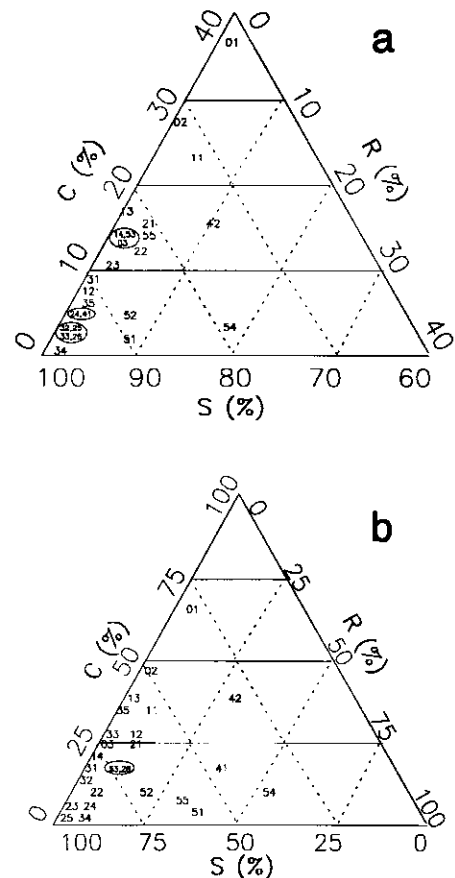


Fig. 3. Position of the plant communities in Grime's triangle on the basis of all species (a) and vascular plants only (b). Overlapping positions are circled.

tions. However, the existence of plants adapted to both severe stress and intense disturbance is difficult to reconcile with Grime's (1977, 1979, 1988) basic assumptions on the non-existence of a strategy which deals with both severe stress and intense disturbance.

Grime's competitive (*C*-strategic) features do not dominate in any plant community (Fig. 5; see below), whereas his stress-tolerant (*S*-strategic) features are more or less prevalent in all community types (Fig. 6; see below). This is partially due to the relative abundance of cryptogams in all plant communities. However, in computations solely based on vascular plants, only seven of the 25 community types obtain *C*-strategy scores higher than 35 and only two reach over 50 (Fig. 3b). At this level, the results conform well to Grime's theory. The samples span from northern bo-

real woodlands to high alpine boulder fields, i.e. from moderately stressful habitats to extremely stressful ones by Grime's standards.

From woodlands to middle-alpine heaths and snowbeds, the *C*-strategy score decreases from 30 to 0, while the *S*-strategy score increases from 60 to above 90. In computations based on vascular plants only, the trend was even more dramatic: the *C*-strategy score dwindles from 64 to 1, while the *S*-strategy score rises from 32 to 95 (Fig. 3b). However, the pattern is reversed in high-alpine communities (Fig. 6), where the *S*-strategy score is consistently below 87, i.e. at levels which otherwise are only encountered in the two most productive forest communities (01 and 02), and in the least stressful alpine communities (see Dahl 1956): timberline shrublands (community 13) and early snowbeds (communities 11, 21 and 22). Moreover, the *S*-strategy score has a deep minimum, corresponding to high-alpine snowbed fragments (community 42). The position of the heavily cryptogam-dominated community 55 highest up on the first axis tends to support Grime's theory, at least to some extent.

However, the dominating cryptogam of this community, *Polytrichum norvegicum*, a robust, erect moss with broad and mesomorphic leaves, could have been regarded as a *C-S*-strategist on the basis of Grime's (1979, Table 6) criteria. Moreover, the *S*-strategy score has a deep minimum, corresponding to high-alpine snowbed fragments (community 42). The *C*-strategy score behaves in the opposite way and has a clear maximum in community 42 (Fig. 4). In computations based on vascular plants only, these anomalies are still more pronounced: community 42 obtains a *C*-strategy score of 39, whereas its *S*-strategy score is only 33. Moreover, all high-alpine vegetation fragments (communities 51-55, 41 and 42) and the most extreme wind barrens (communities 32, 19 and 35) and snowbeds (community 26) of middle altitudes obtain relatively low *S*-strategy scores. This further strengthens the impression that the discrepancy between the data and Grime's theory is to some extent masked by our collective treatment of cryptogams and is definitely not an artifact due to it.

Abundance relationships between different strategies - the MacArthur-Fretwell scheme

Prevalence scores of strategy types in the 25 community types are shown in Fig. 7. The *r*-strategists of the MacArthur-Fretwell scheme show a rather straight-forward increase in abundance from woodlands to summits (Fig. 8). As compared to the *R*-strategy score of Grime's scheme (Fig. 4), the pattern is more monotonic and the snowbed and low-altitude peaks are missing. Also a clear topographic pattern can be observed: *r*-strategists

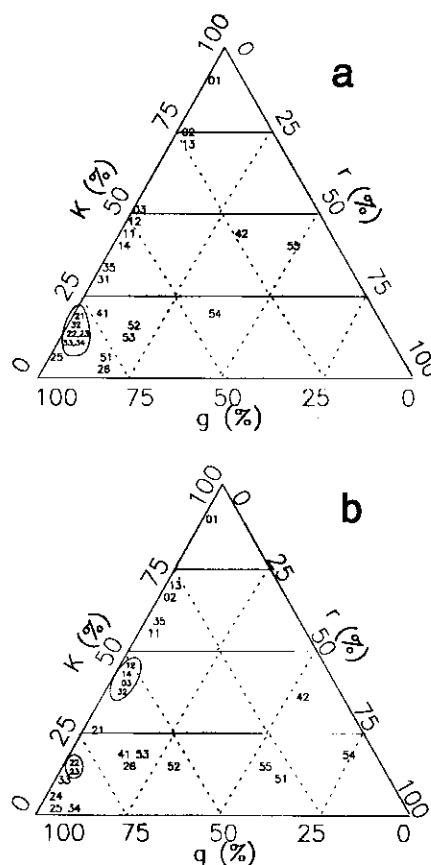


Fig. 7. Position of the plant communities in the MacArthur-Fretwell triangle on the basis of all species (a) and vascular plants only (b). Overlapping positions are encircled.

tend to be least abundant on wind-exposed ridges and most abundant on slopes and plateaux, where the cryopturbation of the soil is most intense (judged on the basis of the occurrence of stone rings, frost-boil surfaces and solifluction lobes, see also Dahl 1956). Thus, *r*-strategists are most abundant in habitats with most intense physical disturbance, as they ought to be. The abundances of *K*-strategists shows a trimodal pattern in the ordination space (Fig. 9). The highest abundances are achieved in the most benign low-altitude habitats (community 01 in Fig. 3). High-alpine snowbed fragments (community 42) represent another region where *K*-strategists abound and a third abundance peak is represented by rocky ridges at the boulder-field limit (community 35). The first-mentioned peak represents the most productive vegetation of the area, whereas the two other ones coincide with extremely barren but physically relatively stable conditions.

The prevalence of *g*-strategists, in turn, culminates at middle altitudes (Fig. 10). The value of 90 is exceeded in moderate snowbeds and middle-alpine heaths. On

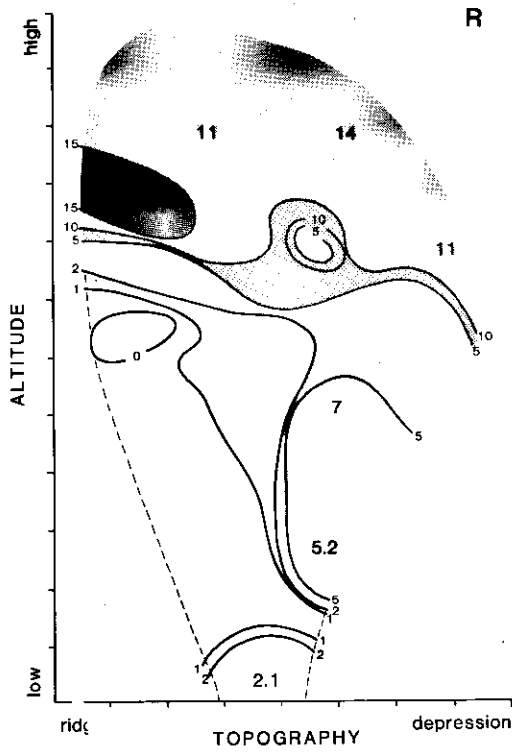


Fig. 4. Distribution of *R*-strategy prevalence scores (%) in the ordination space of Fig. 3. See text for explanation.

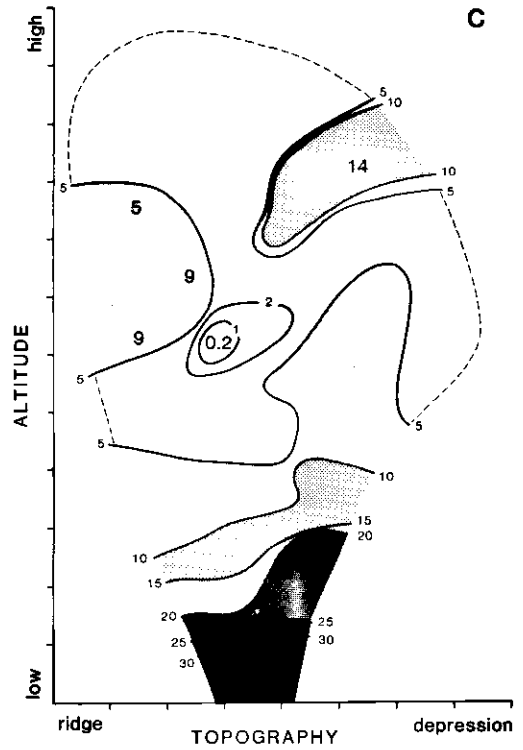


Fig. 5. Distribution of *C*-strategy prevalence scores (%) in the ordination space of Fig. 3. See text for explanation.

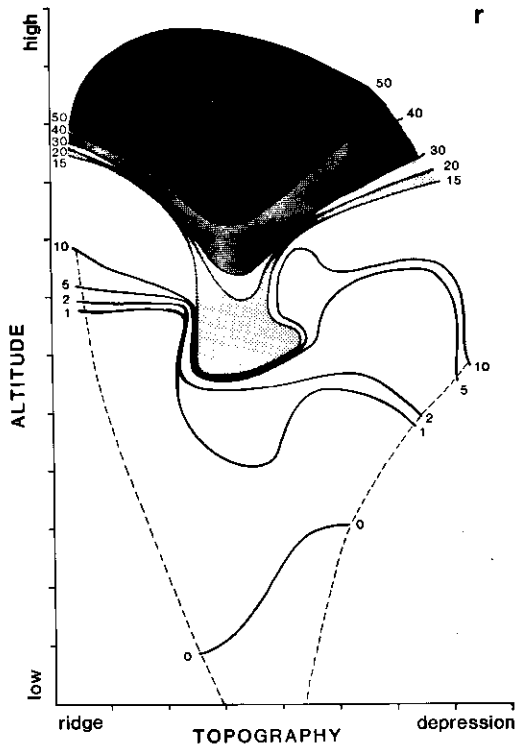


Fig. 8. Distribution of *r* strategy prevalence scores (%) in the ordination space of Fig. 3. See text for explanation.

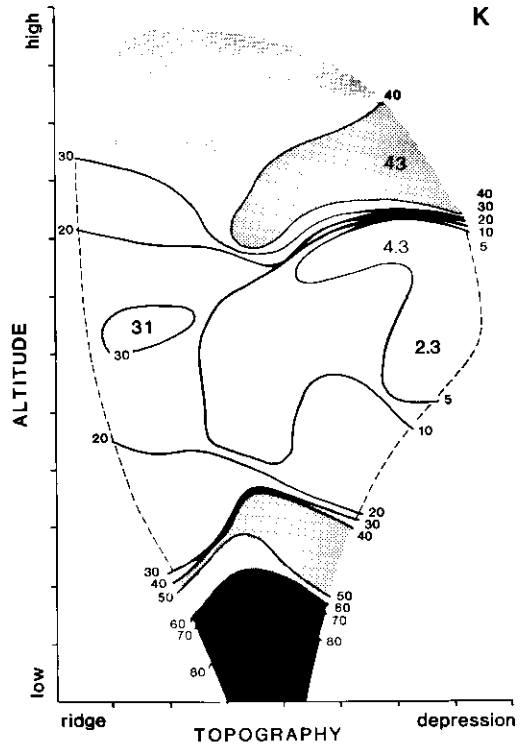


Fig. 9. Distribution of *K* strategy prevalence scores in the ordination space of Fig. 3. See text for explanation.

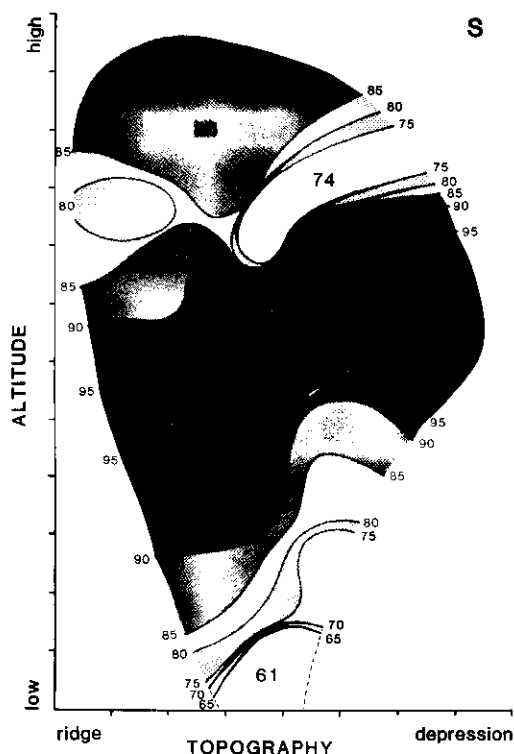


Fig. 6. Distribution of *S*-strategy prevalence scores (%) in the ordination space of Fig. 3. See text for explanation.

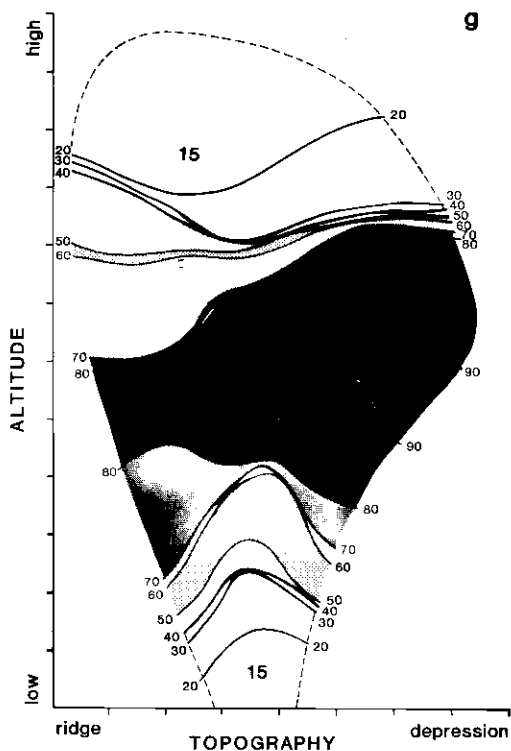


Fig. 10. Distribution of *g* strategy prevalence scores in the ordination space of Fig. 3. See text for explanation.

wind-exposed ridge sites, the maximum value remains somewhat below 90 and is reached at slightly lower altitudes. The slightly lower maximum in ridge habitats is partially due to the phenotypic flexibility of two dwarf shrubs (*Betula nana* and *Vaccinium uliginosum*), classified as *K*-strategists on the basis of their growth form in less extreme habitats. However, it is also possible that the divergence between selective pressures imposed by grazing and competition is at its smallest in wind-exposed ridge habitats (cf. Milchunas, Sala & Lauenroth 1988).

The same pattern also emerges from computations on vascular plants only (Fig. 7b). The main difference between the two computations is that the one based on vascular plants yields patterns which are cleaner and easier to interpret. From the most luxuriant forest communities to moderate snowbeds and ridge heaths, communities move along the left side of the triangle from the position $K\% = 80$, $g\% = 20$ (community 01) to the position $K\% = 2$, $g\% = 95$ (community 25). From there, the extreme ridge heaths move back along the same side of the triangle, whereas the communities in the boulder-field zone (with pronounced physical disturbance) move primarily towards the *r*-strategy pole.

Conclusions

With respect to the lower half of the gradient, Grime's scheme and the MacArthur-Fretwell scheme perform about equally well. However, the changes in the vegetation and flora from middle altitudes to upper alpine boulder fields are difficult to reconcile with the predictions of Grime (1977, 1979, 1988). Conversely, the combination of the MacArthur-Fretwell scheme and the theory of exploitation ecosystems (Fretwell 1977; Oksanen et al. 1981) yields predictions which conform to observed patterns.

The differences between the performances of the two approaches only become obvious when the sampling is extended to really extreme habitats. Modern gradient analyses tend to stop where continuous vegetation ceases and thus do not yield evidence of the reversal (see e.g. Nilsson & Wilson 1990).

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App. 1 follows on next page

App. 1. Distribution of the quantitatively most important species in the 25 community types arranged in five main groups. All species are included which attained a cover of at least 1% in at least one type. Figures are cover % values; +: < 1%.

Species	Strategy	Forest			Heath				Snowbed low						Ridge heath					Snowbed high		Ridge, plateau high						
		Grime	MAF	01	02	03	11	12	13	14	21	22	23	24	25	26	31	32	33	34	35	41	42	51	52	53	54	55
Phanerogams																												
<i>Alchemilla alpina</i>	CS	K	-	-	-	+	-	-	-	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Anthoxanthum odoratum</i>	CSR	gg	-	-	-	-	-	-	-	2	+	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Arctostaphylos alpina</i>	S	gD	-	-	-	-	1	-	1	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-
<i>Betula nana</i>	CS	K	1	+	+	3	4	12	5	+	-	-	-	-	-	8	1	-	-	-	-	-	-	-	-	-	-	-
<i>Calamagrostis lapponica</i>	CSR	gg	-	-	-	1	2	1	2	-	+	-	-	-	-	1	1	1	+	-	-	-	-	-	-	-	-	-
<i>Cardamine bellidifolia</i>	CSR	K	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	
<i>Carex bigelowii</i>	CSR	gg	-	-	-	-	+	-	+	-	1	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	
<i>C. lachenalii</i>	CSR	gg	-	-	-	-	-	-	-	-	-	-	2	+	-	-	-	-	-	-	-	1	-	-	-	-	-	
<i>Cassiope hypnoides</i>	S	ge	-	-	-	-	-	-	-	8	1	3	+	3	-	-	+	2	-	4	1	1	6	4	-	6	-	
<i>C. tetragona</i>	S	ge	-	-	-	-	-	-	-	-	-	-	-	+	-	1	1	2	-	-	-	-	-	-	+	5	1	
<i>Cornus suecica</i>	C	K	31	14	4	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Deschampsia flexuosa</i>	CR	gg	4	+	+	10	2	+	+	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Diapensia lapponica</i>	S	ge	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2	+	-	-	-	-	-	-	-	-	-	
<i>Empetrum hermaphroditum</i>	S	ge	4	15	25	17	10	15	23	5	1	-	-	-	-	22	13	8	3	-	-	-	-	-	-	-	-	
<i>Festuca ovina + vivipara</i>	CSR	gg	+	+	-	-	-	-	+	-	2	-	+	+	-	-	-	-	-	-	-	-	-	-	-	2	-	
<i>Gnaphalium supinum</i>	S	gD	-	-	-	-	-	-	-	+	1	-	+	2	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Gymnocarpium dryopteris</i>	C	K	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Huperzia selago</i>	S	ge	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	
<i>Juncus trifidus</i>	CSR	gg	-	-	+	-	+	-	-	7	-	-	-	-	-	+	-	1	-	-	-	-	-	-	-	-	3	
<i>Loiseleuria procumbens</i>	S	ge	-	-	-	-	-	-	+	+	-	-	-	-	-	1	+	+	-	-	-	-	-	-	-	-	-	
<i>Luzula confusa</i>	SR	r	-	-	-	-	-	-	-	-	+	+	-	2	-	+	-	2	-	4	19	16	10	6	26	21	-	
<i>Oxyria digyna</i>	CR	K	-	-	-	-	-	-	-	-	+	2	+	-	-	-	-	-	-	3	-	-	-	-	-	-	-	
<i>Phyllodoce coerulea</i>	S	ge	3	-	-	+	+	-	+	+	1	-	+	+	-	-	-	+	+	+	-	-	-	1	-	-	1	
<i>Poa alpina</i>	CSR	gg	-	-	-	-	-	-	-	-	+	+	1	1	-	-	-	-	-	-	-	-	-	-	+	-	-	
<i>Polygonum viviparum</i>	CSR	gg	-	-	-	-	-	-	-	1	5	1	+	2	-	-	-	-	-	-	-	-	-	-	+	-	-	
<i>Ranunculus glacialis</i>	C	K	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	2	13	1	3	9	4	3	
<i>R. nivalis</i>	C	K	-	-	-	-	-	-	-	-	-	-	1	-	+	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Salix herbacea</i>	S	gD	-	-	-	2	5	-	1	19	25	35	25	43	3	1	3	14	14	9	8	-	6	8	1	1	5	
<i>Saussurea alpina</i>	C	K	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-		
<i>Saxifraga oppositifolia</i>	S	K	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	+	-	-	-	2	-	-	-		
<i>Trisetum spicatum</i>	CSR	gg	-	-	-	-	-	-	-	-	-	+	2	+	1	-	-	-	-	+	2	-	-	-	-	-	-	
<i>Vaccinium myrtillus</i>	CS	K	15	12	8	31	18	11	7	9	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
<i>V. uliginosum</i>	CS	K	3	+	1	+	1	+	2	-	-	-	-	-	-	3	3	2	-	-	-	-	-	-	-	-		
<i>V. vitis-idaea</i>	CS	K	5	4	3	-	2	6	3	-	-	1	-	-	-	5	5	2	+	13	-	-	-	-	-	-		
<i>Viola biflora</i>	CS	K	-	-	-	-	-	-	-	2	5	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-		
Cryptogams																												
<i>Alectoria nigricans</i>	S	ge	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	1	-	-	-	+	1	2		
<i>A. ochroleuca</i>	S	ge	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	+	-	+	-	-	-	1	5		
<i>Cetraria ericetorum</i>	S	ge	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	1	1	-	-	1	5	1	-		
<i>C. islandica</i>	S	ge	-	-	-	+	+	+	+	+	+	1	-	+	-	+	+	-	-	-	-	1	1	7	-	-		
<i>C. nivalis</i>	S	ge	-	-	-	-	-	-	-	-	-	-	-	-	-	+	1	1	1	5	-	-	1	-	10	17		
<i>Cladonia bellidiflora</i>	S	r	-	-	+	-	+	+	+	+	+	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-		
<i>C. coccifera coll.</i>	S	r	-	-	+	-	+	+	+	+	+	1	1	-	2	+	+	+	2	+	+	1	-	-	-	-		
<i>C. crispata</i>	S	ge	-	-	+	+	+	+	+	+	+	+	+	-	-	-	+	+	-	-	-	-	1	5	1	-		
<i>C. gracilis v. nigripes</i>	S	ge	-	-	+	+	+	+	+	+	+	+	+	-	-	+	+	+	-	-	-	-	1	-	-	-		
<i>C. mitis</i>	S	K	-	+	1	-	-	-	-	1	4	1	-	+	-	1	1	3	+	-	-	-	-	-	-	-		
<i>C. uncialis</i>	S	ge	-	-	+	-	+	+	1	+	1	2	+	-	-	+	1	1	-	-	-	-	-	-	-	-		
<i>Conostomum tetragonum</i>	S	ge	-	-	-	-	-	-	-	-	-	-	3	1	8	-	-	-	-	7	-	1	-	2	-	-		
<i>Cornicularia spp.</i>	S	ge	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	3	-		
<i>Dicranum fuscescens</i>	S	ge	-	-	9	5	25	2	18	26	13	11	3	1	-	15	19	22	7	1	-	-	-	-	-	-		
<i>D. scoparium</i>	S	ge	1	6	6	3	1	5	2	3	1	+	1	-	-	1	+	+	-	-	-	-	-	-	-	-		
<i>Drepanocladus uncinatus</i>	S	ge	-	-	-	-	-	-	-	-	1	-	6	+	-	-	-	-	-	-	1	-	2	-	-	-		
<i>Hylocomium splendens</i>	S	K	22	22	11	1	5	19	5	-	1	-	1	-	-	6	+	-	-	-	1	-	-	-	-	-		
<i>Kiueria spp.</i>	S	ge	-	-	-	-	-	-	-	1	+	2	9	22	17	-	-	-	-	-	-	-	1	-	1	-		
<i>Nephroma arcticum</i>	S	K	3	7	4	2	21	19	10	3	1	+	-	-	-	1	-	3	-	-	-	-	-	-	-	-		
<i>Ochrolechia spp.</i>	S	ge	-	-	-	-	+	-	1	1	5	20	23	+	24	11	26	17	46	29	41	13	45	33	13	8		
<i>Orihocaulis spp.</i>	S	ge	2	2	+	21	2	1	4	3	14	8	12	16	19	-	-	-	-	-	4	2	-	-	-	-		
<i>Peltigera rufescens</i>	S	K	-	2	1	-	1	+	1	+	+	+	-	-	-	-	-	-	-	1	5	-	-	-	-	-		
<i>Pleurozium schreberi</i>	S	K	12	11	10	4	4	3	5	-	+	-	-	-	-	5	2	1	-	-	-	-	-	-	-	-		
<i>Pohlia nutans</i>	S	r	-	-	-	-	-	-	-	-	-	1	1	3	11	-	-	-	-	-	-	-	-	1	1	1		
<i>Polytrichum alpinum</i>	S	K	1	+	1	1	+	+	+	+	1	+	-	-	-	-	+	+	-	-	-	-	-	-	-	-		
<i>P. hyperboreum + piliferum</i>	S	ge	-	-	-	-	+	-	-	1	1	-	-	-	-	2	+	3	8	1	-	-	17	+	3	1		
<i>P. juniperinum</i>	S	ge	-	+	+	-	1	-	+	4	1	+	-	3	-	+	3	2	-	-	-	-	-	-	-	-		
<i>P. norvegicum</i>	S	K	-	-	-																							