

ADAPTATION TO DISTURBANCE AS A PART OF THE STRATEGY OF ARCTIC AND ALPINE PLANTS

Perspectives for Management and Restoration

LAURI OKSANEN^{1,2} and RISTO VIRTANEN¹

¹*Department of Biology
University of Oulu
FIN-905 70 Oulu
FINLAND*

²*Department of Ecological Botany
University of Umeå
S-901 87 Umeå
SWEDEN*

1. Introduction

According to the traditional view, arctic and alpine tundras are extremely vulnerable ecosystems, where even minor disturbances can produce major damage from which recovery is slow [78]. Interactions between plants are supposed to be predominantly mutualistic [16, 39]. Hence, destruction of the plant cover does not open competition-free space for colonists but merely increases the hostility of the stressful environment. Moreover, seed production in arctic and alpine plants is supposed to be erratic and hazardous [9] and the predominating plants are thought to substitute sexual reproduction for vegetative spread through rhizomes or stolons [5, 8, 10]. Consequently, lack of seeds is presumed to slow down the colonization of disturbed habitats. All forms of damage and tissue removal in these stressful areas are considered to lead to the 'forbidden combination' of stress and disturbance, which no plants can survive [40].

The above view of arctic and alpine tundras contains some undeniable wisdom. Low temperature is indeed inevitably associated with low recovery rates [7], because all rate-related processes tend to scale with temperature [60, 109]. In the Arctic, permafrost makes the tundra physically vulnerable, as any change in the insulating properties of the plant cover may have a rapid self-sustaining impact on drainage conditions. In alpine areas disturbance of vegetation can influence physical processes, such as the frequency of avalanches, the speed of solifluction and the rate of soil deflation on wind-exposed ridges. The current increase in all kinds of human activity in tundra areas - oil and hydroelectric development, plus mining in the Arctic, downhill skiing in alpine areas, and motorized terrain traffic in all tundra areas with even moderate density of human population - raises warranted concern [70]. Air pollution is an acute threat on many

subarctic and subalpine timberline forests, especially in areas where evergreen conifers prevail. Global warming provides an entirely different kind of threat to the tundra. In the short term, it can improve the resilience of arctic and alpine vegetation to disturbance, but in a longer perspective, it can threaten the very existence of these ecosystems by allowing the expansion of more competitive boreal plants [17, 23, 24]. In continental areas, where the mass balance of glaciers depends primarily on winter precipitation and is only marginally influenced by increases in winter temperatures, global warming could even result in glaciation of current tundra areas.

Although there are many good reasons to be concerned about the impacts of various kinds of man-made disturbance on arctic and alpine ecosystems, we argue that the traditional temperate-zone-oriented view of arctic and alpine ecosystems as extremely vulnerable to all kinds of disturbance is based partially on false generalizations. Similarly, the concept that arctic plants are unable to invade disturbed sites by means of sexual reproduction is also open to question. These false generalizations can lead to unnecessary defeatism in restoration problems and to unwarranted restrictions in the use of the tundra for grazing, which can be detrimental to biological diversity [32, 46]. Worst of all, arctic ecologists can be accused of having cried wolf where no danger exists which can reduce professional credibility, when the arctic environment faces real threats.

2. The Importance of Sexual Reproduction in the Arctic

The first comprehensive and systematic study on the role sexual and vegetative reproduction in a tundra landscape was performed by Söyrinki [110, 111] on Petsamontunturi (Pechenga Tundra). This relatively small area (15 by 17 km) lies close to the arctic timberline, but is surrounded by subarctic woodlands and has a slightly alpine character (the highest point is 632 m. a.s.l., the general altitude is 400-500 m.). Today, the area is heavily polluted by the smelters of the mining city of Nikel [117] although the area was pristine when the first study was conducted. Moreover, the area was only relatively lightly grazed by reindeer. Consequently, typical tundra heaths of this relatively continental area were covered by a continuous lichen carpet, dominated by *Cladina stellaris*. On moderately wind-exposed ridges *Cetraria nivalis* abounded, and even the most extreme deflation sites were characterized by an abundance of fruticose lichens [57].

As the material of Söyrinki [110, 111] is somewhat difficult to utilize due to its awkward presentation, the main results are summarized below. Table 1, presents the mean densities of floral shoots and seedlings in different habitat categories. These data show an immense variation in seedling numbers which can only partially be attributed to variation in floral shoot density. Typical low arctic heaths and tall fern meadows are characterized by virtual absence of seedlings, whereas seedlings abound in nutrient-rich habitats from scrublands to ridge heaths and snowbeds. Moreover, seedlings are relatively abundant on wind-blown ridges and in snowbeds, regardless of nutrient availability.

In addition to gathering a wealth of habitat-specific data, Söyrinki [111] studied the reproduction of every species encountered on this tundra. He took qualitative notes on the intensity of flowering, studied the germinability of the seeds and searched for seedlings in sites where the plants grew. Moreover, he dug up specimens and studied whether their shoot structure indicated capacity for vegetative reproduction. The

information of this impressive work is summarized in Table 2, where the plants of different habitats are assigned to four categories on the basis of their capability to reproduce sexually and to a further four categories on the basis of their ability to reproduce vegetatively. In the case of sexual reproduction, category 3 includes plants which were noted to flower profusely, to produce ripe and viable seeds dependably, and from which seedlings were common. Category 2 includes plants which produce seeds and seedlings in the area but which either flower sparsely or have difficulties with producing ripe seeds on the tundra. Thus, their seedlings were only sporadically observed. Category 1 consists of species for which seedlings were only seldom encountered, and category 0 refers to species for which seedlings were not found on this tundra. As for vegetative reproduction, category 3 consists of creeping dwarf shrubs and herbaceous plants with horizontal rhizomes whose internodes are typically at least 5 cm long. These plants must also produce strong adventitious roots, allowing different parts of the clone to become physiologically independent individuals. Category 2 consists of herbs with horizontal or oblique rhizomes with typical internodal lengths between 1 and 5 cm and of creeping dwarf shrubs with weak adventitious roots. Category 1 consists of herbs with relatively vertical rhizome (internodal lengths of horizontal parts normally less than 1 cm) and of creeping dwarf shrubs with only occasional formation of weak adventitious roots. Plants assigned to category 0 have only a taproot. (Vegetative reproduction by means of bulbils, recorded in four species only, is not included in Table 2.)

The species were also assigned to six habitat groups on the basis of the first habitat mentioned by Söyrinki, except that plants were assigned to oligotrophic heaths if this species-poor habitat category was mentioned at least as one of the typical habitats. Plants which primarily grow below and south of the timberline and which Söyrinki had only occasionally encountered on this piece of tundra were excluded from the data base.

The species-specific data show that luxuriant low arctic scrublands and wetlands are occupied by plants representing a broad spectrum of reproductive strategies, which is also typical for corresponding temperate habitats [45]. Among the few species thriving on nutrient-poor low arctic heaths, vegetative reproduction prevails. Conversely, the majority of the species growing primarily on nutrient-rich *Dryas* dominated heaths, ridges, rock faces or snow beds are characterized by successful sexual reproduction in these habitats, whereas their capacity for vegetative reproduction is limited. Summaries where all species are treated as equal can be misleading as the most successful species of a given habitat weighs as much as rare species, which barely appear in some special micro-sites. Fortunately, the vegetation of Petsamontunturi has been subjected to a detailed study by Kalliola. Moreover, descriptive studies of mountain vegetation in northern Scandinavia [36, 48, 91] and northern Russia (Virtanen, Oksanen and Wiklund, unpublished) provide an opportunity of examining the success of these plants in more extreme alpine habitats and in typical lowland tundra. Table 3 presents data on the vegetative and sexual reproduction of those species, which are noted as dominants or co-dominants in at least one common arctic-alpine habitat in northern Europe. (In the case of high alpine scree, the concept of dominant was interpreted loosely, including all plants which are frequently encountered above the altitudinal limit of continuous vegetation).

Table 1. Densities of floral shoots and seedlings in different habitat categories of Petsamontunturi. Habitat categories where floral shoots were not counted are denoted as n.c. Source: Söyrinki [105], Tab. 12; cases where our categories consist of several different entities in Söyrinki's material are denoted by an asterisk; the numbers refer to unweighted averages.

Plant community	Floral shoots per m ²	Seedlings per m ²
Herb-rich scrubland *	55	2054.0
Tall herb meadow*	106	640.0
Tall grass meadow	n.c.	44.0
Tall fern meadow	0	0.6
Bog scrubland*	20	267.0
Mesic scrubland	25	25.0
Mesic heath, eutrophic	105	153.0
Mesic heath, oligotrophic	n.c.	2.0
Dry heath, oligotrophic	n.c.	0.2
Ridge heath, eutrophic	26	45.0
Ridge heath, oligotrophic	0	0.0
Extreme ridge heath	n.c.	39.0
Early snowbed, eutrophic	188	2410.0
Early snowbed, oligotrophic*	113	289.0
Late snowbed, eutrophic	n.c.	370.0
Late snowbed, oligotrophic*	n.c.	49.0
Dwarf shrub bog	36	126.0
Graminoid bog*	204	52.0

Table 2. Per cent occurrence of different levels of sexual (G0-G3) and vegetative (V0-V3) reproduction in the plants of six habitat categories of Petsamontunturi, according to Söyrinki [106]. The category 'luxuriant meadows' includes also herb-rich willow scrublands. The category 'eutrophic heaths' (*syn. Dras* heaths) includes low herb meadows without any clear snowbed characters. Snowbeds include several community types referred to as 'heath meadows' (Heidenwiesen) by Söyrinki. n = number of species in the category.

Plant communities	G 3	G 2	G 1	G 0	V 3	V 2	V 1	V 0	n
Luxuriant meadows	46	8	27	19	50	12	27	12	26
Wetlands, shores	42	26	13	19	65	13	13	10	31
Nutrient-rich heaths	65	17	17	0	39	17	22	22	23
Nutrient-poor heaths	25	25	33	17	67	17	17	0	12
Ridges and rock faces	80	12	8	0	16	20	24	40	25
Snowbeds	75	10	8	8	15	23	43	20	40

Table 3. Success in sexual and vegetative reproduction in the dominating plants of major arctic-alpine habitat categories, according to Söyrinki 1939. Numbers in parentheses refer to vegetative reproduction by bulbils.

Species	Sexual reproduction	Vegetative reproduction
Luxuriant habitats		
<i>Salix glauca</i> s. lat.	3	3
<i>Salix phylicifolia</i>	0	3
<i>Salix lanata</i>	3	3
<i>Trollius europaeus</i>	3	1
<i>Filipendula ulmaria</i>	0	3
<i>Geranium sylvaticum</i>	3	1
<i>Cirsium helenioides</i>	1	3
<i>Cicerbita alpina</i>	0	3
Wetlands		
<i>Arctagrostis latifolia</i>	1	3
<i>Eriophorum angustifolium</i>	2	3
<i>Carex aquatilis</i>	0	3
<i>Carex rotundata</i>	2	3
<i>Rubus chamaemorus</i>	3	3
Eutrophic heaths		
<i>Carex rupestris</i>	1	3
<i>Salix reticulata</i>	3	3
<i>Silene acaulis</i>	3	0
<i>Dryas octopetala</i>	3	0
<i>Astragalus alpinus</i>	3	2
Oligotrophic heaths		
<i>Betula nana</i>	3	3
<i>Empetrum hermaphroditum</i>	2	3
<i>Phyllodoce coerulea</i>	3	1
<i>Vaccinium myrtillus</i>	1	3
<i>Vaccinium vitis-idaea</i>	1	3
Ridge heaths		
<i>Festuca ovina</i>	3	2
<i>Loiseleuria procumbens</i>	3	1
<i>Arctostaphylos alpina</i>	3	3
<i>Diapensia lapponica</i>	3	0
Snowbeds		
<i>Anthoxanthum odoratum</i>	3	1
<i>Phleum alpinum</i>	3	2
<i>Agrostis mertensii</i>	3	1
<i>Deschampsia flexuosa</i>	3	2
<i>Trisetum spicatum</i>	3	1
<i>Phippsia algida</i>	3	1
<i>Poa alpina</i>	3	0
<i>Carex bigelowii</i>	2	3
<i>Salix herbacea</i>	2	3
<i>Salix polaris</i>	1	3
<i>Polygonum viviparum</i>	0	(3)
<i>Ranunculus nivalis</i>	3	1
<i>Ranunculus acris</i>	3	1
<i>Sibbaldia procumbens</i>	3	2
<i>Cassiope hypnoides</i>	3	3
<i>Gnaphalium supinum</i>	3	2
High alpine scree		
<i>Cardamine bellidifolia</i>	3	0
<i>Oxyria digyna</i>	3	0
<i>Saxifraga cespitosa</i>	3	0
<i>Saxifraga tenuis</i>	3	1

Table 3. shows that the dominating plants of low arctic wetlands do indeed reproduce mainly or exclusively vegetatively, which is a normal situation in sedge-dominated wetlands even in the boreal zone [50, 103]. On the other hand, the dominants of low arctic heaths use both reproductive modes in concert. One of them (*Phyllodoce caerulea*) relies primarily on sexual reproduction, while the predominantly

boreal *Vaccinium* spp. have low success in sexual reproduction, which is also normally the case in the taiga [61]. Sexual reproduction prevails among the dominating plants of nutrient rich *Dryas* heaths and among the dominants of snowbeds and wind-exposed ridges. The characteristic plants of high alpine scree reproduce only sexually. Indeed, many high arctic and high alpine plants are missing from Söyrinki's [110, 112] material because their occurrence in northern Fennoscandia is restricted to the Scandinavian mountain chain [53]. On the basis of inspected field and herbarium specimens and the drawings in Lid [64], it could be asserted that the pattern would have become accentuated if the study had been conducted in an area with a richer arctic-alpine flora. The missing species are almost exclusively sexually reproducing herbs and graminoids with a taproot or a more or less vertical rhizome or trailing dwarf shrubs with no or only weak adventitious roots. Indeed, the characteristic plants of high alpine areas, *Ranunculus glacialis* [28, 36], and of polar deserts *Papaver polare* and *P. radicum (sensu lato)* [2, 104], are herbs with showy inflorescences and depend on sexual reproduction [74, 96]. The reason for the prevalence of sexual reproduction in high arctic and high alpine environments can be derived from Dahl's [27] discussion on the relationships between *Vaccinium myrtillus* and *Phyllodoce caerulea* on the low alpine heaths of Rondane, southern Norway. Dahl noted that the prolific vegetative reproduction of *V. myrtillus* makes it competitively superior to *P. caerulea* in habitats with stable soils. However, this growth form creates difficulties in sites subjected to solifluction, because different parts of clones move at different speeds. Such movement damages *V. myrtillus* clones and sometimes even causes uprooting. *P. caerulea*, which spreads vegetatively along the ground, but only forms weak adventitious roots [111] retains the central advantages of clonal growth but is much less vulnerable to solifluction, because uprooting is restricted to a minor part of the root system. The same argument applies e.g. to *Cassiope tetragon*. The strategy of *Phyllodoce caerulea* and *Cassiope tetragona* is especially successful in habitats with relatively weak soil movements, because the damage to adventitious roots is only moderate and the soil is covered by a continuous moss and humus layer, making sexual reproduction undependable. Where soil movements are more intense, conditions are more stressful for plants with any kind of adventitious rooting and more favourable for sexual reproduction [33]. Thus, semi-clonal dwarf shrubs are replaced by single-shoot graminoids and herbs and by woody plants with a central taproot only [54, 55, 101]. Among graminoids, viviparous (i.e. bulbil-forming) species are indeed common in high arctic and high alpine environments, but as a parallel trend cannot be seen in flowering dicots, it seems reasonable to attribute this phenomenon to the pollination problems of anemophilous plants in sparsely vegetated habitats.

It is easy to share Murray's [74] embarrassment over the ill-founded dogma that dependence on vegetative reproduction and apomixis would be typical for arctic plants. Rather, it seems that arctic plants are subject to similar trade-offs as are the perennial plants in other areas [96]. Murray was probably also correct in his claim that the dogma has persisted at least partially due to the fact that much of arctic ecology has been produced by researchers living in warm-temperate areas, who are prone to overemphasize the harshness of the Arctic.

The concept of the importance of clonal reproduction in the Arctic cannot, however, be shrugged off as a misconception. Even Söyrinki's data [110] from 1938 suggest that nutrient-poor low arctic habitats with undisturbed soils are exceptionally unfavourable habitats for sexual reproduction. Plants adapted to these habitats may or may not produce substantial amounts of viable seeds, but they seldom achieve any

return for this investment, because the cold, raw humus provides unfavourable conditions for seedlings, which can be made even worse by a continuous cryptogam layer [110]. It is thus no wonder that natural selection can create there plants like *Carex bigelowii* and *Calamagrostis lapponica*, with low seed viability, and why boreal forest floor plants like *Vaccinium myrtillus*, *V. vitis-idaea* and *Cornus suecica* can flourish in low arctic habitats, where current climate seldom allows for the production of a good berry crop.

Even those plants of oligotrophic low arctic heaths and wetlands, which normally produce viable seeds, appear to invest exceptionally little energy in flowering. The common low arctic habitats, such as lichen-dwarf shrub heaths and the tussock tundra, are not popular places for flower-lovers, and this is not due just to the frequency of wind pollinated species. Söyrinki [111] notes that the dominating low arctic dwarf shrub, *Betula nana*, flowers there relatively sparsely. The catkins bore, on average about 50 seeds only while elsewhere the average annual seed production of a dwarf birch shrub was about 940 seeds. The dominating plant of the tussock tundra, *Eriophorum vaginatum*, was noted to flower sparsely and to be entirely sterile in some sites. Ecologists working along the gradient from temperate to low arctic habitats can thus easily conclude that the importance of vegetative reproduction increases with increasing latitude. However, the trend is reversed at higher latitudes and altitudes, both in Europe (see above) and in North America [47, 74]. Moreover, sexual reproduction prevails even in nutrient-rich low arctic habitats. This can depend in part on the fact that soil movements counteract leaching. Thus, the availability of nutrients correlates positively with the intensity of cryoperturbation [54, 56, 91]. Moreover, good availability of nutrients also increases the speed of the decomposition process [107] [107], thus counteracting the formation of thick layers of raw humus.

3. Natural Grazing Pressure on the Tundra

The classical concept of the tundra as an extremely sensitive ecosystem, where plants fight against the rigours of the physical environment and do not tolerate any form of disturbance, was long ago attacked by Russian ecologists. Tihomirov [116] pointed out that graminoid-rich mesic tundra habitats are practically turned upside down every few years by brown lemmings (*Lemmus* spp.) and that the periodic low fertility of graminoids in these habitats can be a direct consequence of consumption of floral buds [see also 86]. The underlying observations were largely qualitative, but results of quantitative studies support Tihomirov's argument [4, 19, 73, 81]. Woody plants of low arctic heaths, in turn, are intensely grazed by collared lemmings (*Dicrostonyx* spp.). In Fennoscandia, the niche of collared lemmings is taken over by grey-sided voles (*Clethrionomys rufocanus*), which lack digging claws and are thus not especially well adapted to cope with the hard tundra snow. Nevertheless, they can profoundly influence the vegetation, especially in habitats with at least some scattered shrubs [3, 16, 89].

In addition to lemmings, the tundra vegetation of the Old World is profoundly influenced by reindeer (*Rangifer tarandus*). Tihomirov [116] noted that strong impacts on the vegetation are observed in areas where most of the grazing is done by wild reindeer. In North America, the low arctic caribou populations were severely decimated by firearm-equipped Indians before any censuses and studies on their impact upon natural vegetation were conducted, and they were still regarded as threatened by overhunting in the 1960's [59]. Thereafter, caribou and their predators have recovered and appear to

have reached an equilibrium density at least in eastern Canada [22, 25, 26]. This natural equilibrium state is characterized by a strong impact of caribou on the vegetation of low arctic heaths [69], comparable to the impact of domesticated reindeer on corresponding plant communities in northern Fennoscandia [91].

The central role of herbivores in arctic plant ecology is supported by enclosure studies and by vegetation patterns encountered in grazer-free arctic islands. In relatively productive tundra habitats, removal of herbivores leads to increased dominance of erect woody plants or tall herbs [72, 82, 87], whereas bank-forming cryptogams take over in less productive tundra habitats [4]. Prostrate herbs and small cryptogams are eliminated. Basal-leaved graminoids can increase initially [83], but in the long run, even this plant category appears to lose ground. On Jan Mayen and Bear Island, where herbivorous mammals do not occur, the most favourable sites support herbfields, while moss banks prevail in more extreme sites [66, 105, 121]. Arctic-alpine sedges and grasses are widespread on Jan Mayen, but they only form a subordinate component of the vegetation and appear to be restricted to disturbed sites [63, 105, 122] (also *pers. obs.*). On the geologically more stable Bear Island, some grasses are encountered in habitats grazed by migratory geese, but sedges are floristic rarities, with only a few known localities on the island [30].

One possible explanation for the profound importance of grazing vertebrates on the plant cover of the tundra is provided by the hypothesis of exploitation ecosystems [34, 35, 80, 82]. Briefly, the hypothesis states that herbivores of productive areas are regulated by their predators [49]. However, predators with a capacity for killing healthy prey need high feeding rates in order to maintain their muscular bodies. Consequently, the potential regulation from predation cannot be realized in unproductive habitats, where relatively low grazer densities suffice to deplete the vegetation. Predators can indeed also be periodically numerous in typical tundra habitats [98], but only as exploiters of outbreak populations, which are in any case doomed to crash.

The central assumptions of the hypothesis are, that plants are vulnerable to grazers and that trophic guilds can be treated as if they were single populations. Both assumptions are currently intensely debated [1, 99, 100, 115]. However, even the critics of the hypothesis admit that it has some validity in the arctic and alpine zones of boreal mountains, where the diversity of plant growth forms is low and where three resident species of grazers - the reindeer/caribou, the brown/Norwegian lemming and the collared lemming - can be regarded as keystone herbivores of the three major categories of winter resources provided by the tundra (lichens, mosses and twigs of woody dicots). The situation with the alpine tundra at middle latitudes is basically similar; there the overwintering grazer guild normally consist of one browsing ovid, (e.g. in truly alpine areas the ibex *Capra ibex* or the mountain goat *Oreamnos americanus*) one harvesting lagomorph (the pikas, *Ochotoma spp.*), one hibernating marmot, and, in areas with deep soils, normally even one 'gopher' (burrowing herbivore). The issue of herbivore regulation in arctic and alpine areas thus clearly refers to a few species with largely non-overlapping wintering niches. Moreover, there is clear empirical evidence on the absence of resident carnivores from the tundra, except for the most productive low arctic habitats such as herb-rich willow thickets [85, 88, 92].

4. Disturbance, Stress and Strategies of Arctic and Alpine Plants

On the basis of the arguments summarized in the preceding sections, we conclude that the traditional view of the tundra as a static ecosystem, where plants help each other in the combat against the rigours of the physical nature, is in conflict with both logical argument and empirical evidence. One kind of disturbance - intense grazing by resource-limited herbivores - is ubiquitous in relatively unproductive arctic and alpine habitats, and another - intense cryoperturbation - is typical for middle and high arctic areas and common in high alpine habitats as well. Oksanen and co-authors [83, 84, 90] have argued that the entire morphological and reproductive syndrome described by Grime [39, 40] 'stress tolerant strategy' represents adaptations to intense herbivory and has no direct connection to environmental stress *per se*. (For a similar approach to benthic algae, see Steneck and Dethier [113], but see also Grime [44]).

The core of the argument is that grazing selects for entirely different kinds of traits than devastating physical disturbance, which leaves no survivors *in situ*. Loss of above-ground tissues obviously selects for high root to shoot ratios and for vegetative reproduction by means of horizontal rhizomes, especially if the loss is caused by grazers, which prefer nutrient-rich floral shoots [31, 86, 116]. Moreover, herbivory selects for tough and narrow, finely lobed or scale-like leaves and against broad, mesomorphic leaves, because partial consumption of mesomorphic leaves creates long wounds, exposing the remaining tissues to desiccation and parasitic fungi. The advantages of low palatability in herbivory-controlled vegetation are obvious, so is the use of stress-tolerant leaves and roots as perennation organs. (Discrete winter buds or compact rhizomes would form easily accessible energy and nutrient packages for wintering herbivores.)

A closer look at the evolutionary stable defence strategies of plants [4, 15, 51] reveals that plants have two strategies to withstand grazers. They can either invest large amounts of reduced carbon in defensive compounds, which inevitably results in low growth rates, or they can defend themselves solely by means of freely available inorganic substances (e.g. silica) or by means of mechanical deterrents (e.g. thick cuticles, thorns), which are relatively efficient even at low investment levels [93]. The result of Oksanen's [83] *Evolutionary Stable Strategy* (ESS) analysis was that chemical defence is selected in nutrient-poor environments, where growth is slow and where reduced carbon is a relatively cheap commodity. Conversely in nutrient-rich habitats grazing should select for rapidly growing plants with structural or silica-based defence, as had been earlier proposed [6, 15, 93]. The two main ways of surviving intense grazing were called ericoid and graminoid strategies by Oksanen [83] [83]. Moreover, he pointed out that the main advantage of typical graminoids - their ability to produce erect leaves rapidly from basal intercalary meristems - is lost in habitats with persistent, intense grazing, where shoot competition never becomes intense. Such a situation favours entirely prostrate plants [52, 71, 95]. This solution was referred to as the *Dryas* strategy by Oksanen.

On the basis of the above arguments, Oksanen [83] and Oksanen and Ranta [90] presented their own triangular ordination of plant strategies. One corner of the scheme was K-strategy or competitiveness *sensu* Tilman [118, 119], i.e. a suite of morphological, physiological and reproductive traits which enables plants to complete their life cycles in an environment, where critical resources are depressed to a low level by these plants. Another pole is the classical r-strategy, which can be regarded as identical to Grime's [38-40] R or ruderal strategy. Grime's competitors or C-strategists,

adapted to transient dynamics in resource-rich environments where interference competition prevails, are regarded as intermediate between K- and r-strategists, as proposed by Grace [37]. The third pole is formed by g-strategists, adapted to frequent but small losses of above ground tissues. The ericoid, graminoid and *Dryas* strategies are seen as subsets of the more general concept of g-strategy.

The results of exclosure experiments [72, 82, 83] and studies on vegetation patterns on grazer-free arctic islands [66], by and large, support the plant strategy scheme of Oksanen [83]. However, there are some notable exceptions. Supposed representatives of the *Dryas* strategy are common and locally even abundant on the grazer-free Jan Mayen Island, where dwarf willows (*Salix herbacea*) grow amongst moss banks and hepatics abound on snowbeds at high altitudes. Moreover, *Dryas octopetala* itself appears to be relatively sensitive to grazing and trampling by reindeer [106]. Although persistent, intense grazing can select for prostrate plants, it seems thus to be incorrect to pool them into a single functional category.

The basic problem with the approach of Oksanen and collaborators [83, 84] was that, apart from the concept of a triangular plant strategy scheme, they did not see anything positive in Grime's approach. They argued that competition must be equally important in all undisturbed habitats and regarded Grime's S-strategy as grazing tolerance misinterpreted. In the debate on plant competition, they took Tilman's [118] view entirely and insisted that there was no point in discussing competitiveness without reference to specified limiting resources. However, even Tilman's [119] analysis implies that stress constrains the allocation patterns of plants by reducing the amount of non-photosynthetic tissues that can be maintained. In the competition issue, experimental evidence [18] and logical arguments [43] make it untenable to maintain that Grime's view of competition would be simply wrong. Before the strategy schemes of Oksanen and his co-workers can be offered as alternatives to Grime's triangular model, the above problems must be addressed.

A solution for the competition problem was outlined by Grace [37]. His argument can be further clarified by explicit references to animal ecological literature, where it has been long ago noticed that competition is a composite term, encompassing two fundamentally different processes [67]. Interference competition arises when two animals try simultaneously to capture the same resource item or establish a territory on the same piece of habitat. Because the outcome of interference depends on physical strength, competitiveness in this context can be defined without reference to resources and animals can be arranged into competitive hierarchies [97]. Exploitation competition, in turn, emerges from the diffuse impact of consumption on resource levels. In pure exploitation competition, two consumers need never meet and the negative interactions between them are entirely mediated via impacts on limiting resources. Consequently, competitiveness depends entirely on the ability of animals to maintain positive energy balance in a resource-poor environment (i.e. on their stress-tolerance), and in discussions on competitive interactions and their consequences it is essential to specify the characteristics of limiting resources. Grime defines competition as interference, whereas Tilman works on exploitation competition. Both concepts are useful but in different time scales.

For example, consider a forest burn or an abandoned field in the boreal zone. It is quickly invaded by willows, birches, alders and aspens, which rapidly exploit the abundant light and mineral resources by extending their crowns and roots laterally. Light levels on the ground decrease rapidly, and in the soil environment, pockets of high nutrient availability are likely to be depleted. Successes in competition for light

resources and soil resources are likely to re-enforce each other, as argued by Grime [43] and quick growing species - especially willows - rapidly gain dominance. A few spruce seedlings may also appear in the habitat, but they are not especially competitive in this situation. Their rigid architecture prevents flexible exploitation of light gaps and their slow rate of vertical growth makes them losers in the contest for space and light. Due to their low rate of energy capture, their growth rate in the soil environment is also low. The competitive superiority of second-growth deciduous trees in these conditions is a major economic concern, making the control of deciduous second growth an essential ingredient in the forestation of abandoned fields. However, spruces survive in the depletion zones created by willows and other second-growth species, and furthermore they keep growing vertically, whereas the vertical growth of willows stagnates, due to their energetic inefficiency and their vulnerability to snow breaks. Other second-growth deciduous trees face the same fate at a later stage in succession [108]. After a few decades, spruces start to overtop second-growth deciduous trees, which cannot survive in the shade of the spruces. A few aspens sometimes survive as emergents, but only spruce can reproduce successfully in the shaded and nutrient-poor environment created by the spruces themselves. Thus, competition has changed its nature from interference to exploitation, and competitiveness now depends on the ability of the plant to tolerate low resource levels, as argued by Tilman [118, 119].

The trends described above have been recurrently discussed by Grime [39-42], who maintains that secondary succession in moist and nutrient rich habitats leads from the dominance of ruderals via the dominance of competitors to the dominance of stress-tolerators. Consistent with this approach, Grime and his co-workers [45] classified typical climax trees of Great Britain as stress-tolerators. Unfortunately, this approach generates a very heterogeneous category, and the characteristics of temperate climax trees is in conflict with the morphological and reproductive attributes which Grime regards as typical for stress-tolerators. Moreover, practically all boreal and temperate forest plants adapted to intense interference competition have many ruderal features (relatively short life span, early age of first reproduction, copious production of small, easily dispersed seeds). Conversely, the ruderals, which dominate early stages of secondary succession in burned forest and on abandoned fields (e.g. fireweed, *Epilobium angustifolium*, various annual and biennial herbs) have the highest growth rates immediately after disturbance [see also 46] and are thus good interference competitors in a short time interval, when they easily overtop willow seedlings. As emphasized by Smith [108] secondary succession is characterized by a trade-off between speed and efficiency. The quick ruderal species are not only good colonizers but also good interference competitors in a short time frame. Grime's competitors are mid-successional species, combining high capacity for interference competition over a moderate time interval with good dispersal ability. These species are indeed dominants of fertile temperate habitats of Britain [45], but only because of heavy and relatively recent disturbance. As pointed out by Tilman [119], undisturbed secondary succession would lead to the development of broad-leaved deciduous forest, where Grime's interference competitors would be replaced by exploitation competitors.

Grime and his co-workers have succinctly analyzed the mechanisms of interference competition and demonstrated its ability to create absolute competitive hierarchies in a short time period, but the hierarchies do change when the time frame is changed. Consequently, we regard it as natural to emphasize time-independent attributes and to define competitiveness as the ability of plants to persist in the habitat over several generations and to gain numerical dominance by modifying the environment so that

other plants cannot persist there in equally high numbers. This is a basically the approach of Tilman, where Grime's competitors are regarded as intermediate between competitors and ruderals. Our approach makes stress-tolerance an integral part of competitiveness. It is thus justifiable to ask to what extent competition and stress due to external constraints select for different attributes. With regard to competition for light, the answer is easy. Competitiveness requires tall stature, whereas maximum tolerance of shaded conditions is achieved by prostrate plants, which need not maintain heterotrophic above-ground organs. The same principle applies even if the stress is caused by low temperatures or lack of water. Stems are superfluous if light is not a limiting resource [120], and plants with low photosynthesis rates for whatever reason cannot afford heterotrophic above-ground tissues. Below-ground tissues can be maintained, if they pay back their costs by boosting the rate of photosynthesis by providing more water.

When the direct impact of stress is integrated to the strategy scheme [90], the triangular strategy representation is replaced by a tetrahedron, where adaptational syndromes selected by competition, stress, herbivory and devastating physical disturbance form the corners (Fig. 1). The new dimension, to be referred to as s-strategy has only one general attribute: lack of erect above-ground stems (Table 4). In cold environments, s-strategy first expresses itself in the form of semi-prostrateness and low root to shoot ratios [68, 114] and then by the replacement of vascular plants by cryptogams. However, trade-offs between competitiveness and colonization ability occur even in Antarctic mosses [20, 29, 65]. The polar variant of s-strategy consists of crustose lichens and prostrate hepatics.

The dominating components of undisturbed plant communities along the gradient from relatively productive temperate and boreal habitats to high arctic and high alpine habitats form a path on the K-g-s face of this tetrahedron (Fig. 2). The dominants of temperate and boreal forests lie in the K-strategy corner. Along the gradient from forests to typical low arctic tundra, we are moving towards the direction of g-strategy. Indeed, elements of s-strategy also start to appear, but as the rate of photosynthesis in these habitats well exceeds the maintenance costs of foliage, the s-strategic elements have a subordinate role in the overall adaptational syndrome of low arctic plants. On extremely oceanic mountains, where cryoperturbation is curtailed by the copious snow cover and mild winters, the gradient from low arctic or low alpine to higher elevations can be depicted as a path towards the s-strategy corner (Fig. 2, solid line). Even on relatively oceanic mountains, this gradient is normally interrupted by cryoperturbation, favouring plants with r-strategic features. On the mountains of Fennoscandia, the break of the gradual trend is traditionally regarded as the boulder field limit (*Blockenmeeresgrenze*). The dominating plants of the high alpine scree areas above the boulderfield limit, *Ranunculus glacialis* and *Luzula arcuata* (*sensu lato*) [27, 28, 76, 91] are characterized by relatively high investments in sexual reproduction and surprisingly tall stature; i.e. they combine r- and K-strategic features, whereas the elements of s-strategy are surprisingly weak. Consequently, the boulder field limit must lie well below the altitudes, where stress would constrain severely the allocation patterns of plants. In our plant strategy tetrahedron, the boulder field limit represents a sharp turn away from g-strategy and towards the K-r-s face of the tetrahedron (Fig. 2., dashed line).

Table 4. Central attributes of the four primary strategies of the proposed tetrahedral plant strategy

	Strategy				
	K	r	g graminoid variant	g ericoid variant	s
Stature	Normally tall ⁽¹⁾	relatively low	low	low	low
Shoot:root ratio	variable ⁽²⁾	high	low	high	normally high ⁽³⁾
Maximum growth rate	low	high	high	low	low
Tolerance to low resource levels	high	low	variable	high	high
Reproduction	sexual + vegetative	sexual	primarily vegetative	primarily vegetative	variable
Resource allocation per offspring	high	low	variable	variable	variable
Leaf texture	soft	soft	tough	tough	variable
Leaf shape	broad	variable	narrow	narrow	variable
Palatability	high	high	intermediate	low	variable

(1) low if light is not limiting

(2) dependent on relative roles of nutrient and light limitation

(3) can be low in arid areas

Along gradients of increasing latitude, cryoperturbation is normally intense already in the middle Arctic, favouring plants which combine elements of r-strategy and g-strategy. Polar deserts are subjected to intense cryoperturbation and dominated by relatively pure r-strategists, which possess only a modest display of s-strategic features. Arctic vegetation gradients can thus be represented as a path which disappears to the direction of r-strategy and never reaches the vicinity of the s-strategy corner, because high intensities of environmental stress are always accompanied by intense disturbance (Fig. 2., dotted line).

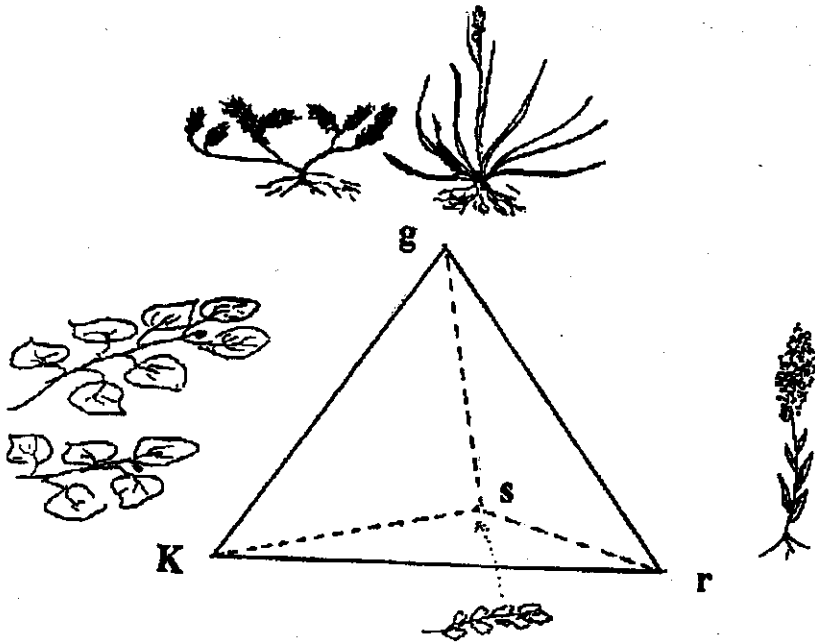


Figure 1. A tetrahedral modification of the triangular plant strategy scheme of Oksanen and Ranta (1992). Three primary strategies (K, r and g) are illustrated on the face of the tetrahedron. For g-strategy both the graminoid and the ericoid variants are depicted. The s-strategy dimension lies behind this front pane, and is characterized by decreasing allocation to support tissues and other heterotrophic above ground organs. The extreme s-strategist is represented by a hepatic, i.e. an all-leaf plant totally devoid of heterotrophic tissues.

5. Management Perspectives

An ecologist facing questions about the vulnerability of arctic ecosystems and strategies for their restoration has to ask what kind of arctic ecosystems and what kind of disturbances are under investigation. The traditional view of extreme vulnerability is justified in the case of low arctic tussock tundras and low to middle Arctic, graminoid-dominated plains in respect of heavy physical disturbance as caused by vehicle traffic in summer. Damage to the vegetation and compression of the peat will inevitably initiate changes in the permafrost table, which in turn changes drainage conditions. The initial disturbance will thus trigger a chain of secondary changes, which are likely to persist for centuries. If the damaged area is large, re-establishment of any kind of closed vegetation will be slow, due to the weak sexual reproduction of the dominating plants. However, this aspect should not be over-emphasized. Some arctic wetland plants (e.g. *Eriophorum scheuchzeri*) are characterized by prolific seed production and strong capacity for

vegetative spread [111] and could be used in restoration of disturbed low and middle arctic wetlands.

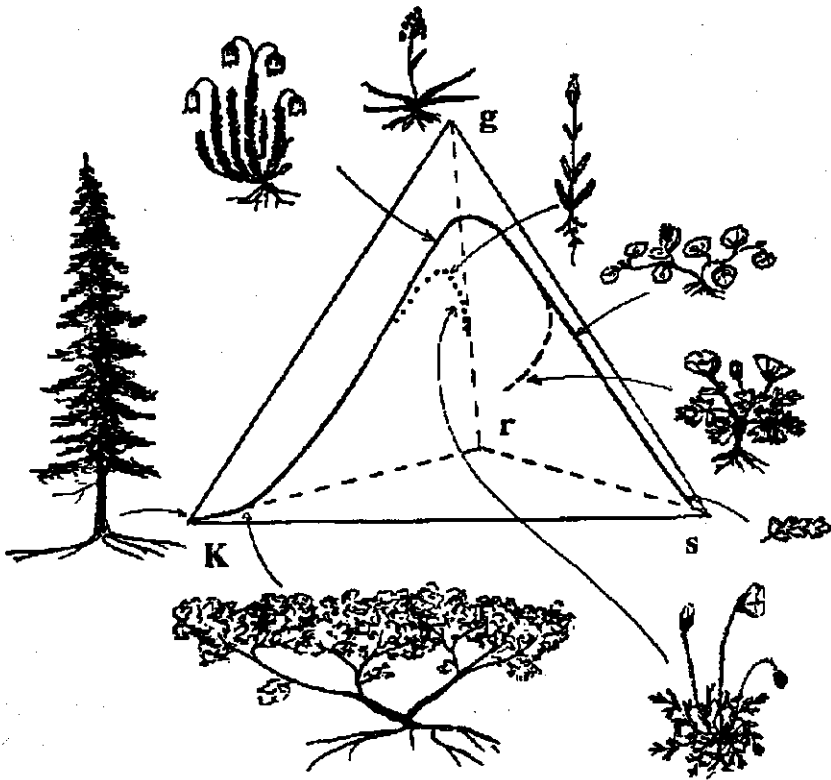


Figure 2. Main vegetational patterns along the gradient from northern boreal forests to high arctic and high alpine scree areas, depicted in the plant strategy tetrahedron of Fig. 1., which has now been rotated so that the K-g-s plane is to the front. Characteristic plants along the gradient are depicted in the insert figures. The solid line refers to the gradient from boreal forests to high alpine snowbeds on extremely oceanic mountains, where cryoperturbation remains modest at all altitudes. The dashed line refers to typical gradients of moderately oceanic mountains (e.g. the northern Scandes), where cryoperturbation becomes intense at highest altitudes and sets the limit of continuous vegetation. Above this limit, physical disturbance causes a shift towards r-strategy, but pre-emptive competition for favourable micro-sites can be also locally important. Thus, the characteristic plants combine r- and K-strategy elements with a moderate expression of s-strategy. The dotted line refers to typical latitudinal gradients, where cryoperturbation becomes intense already south of the limit of continuous vegetation, favouring plants which can survive the combination of intense grazing and severe physical disturbance. In the polar desert, physical disturbance is overwhelmingly important and the dominating plants have pronounced r-strategy (ruderal) characteristics.

In formerly glaciated precambrian shield areas, tussock tundra occurs only locally in bog margins, while the dominating habitats are tundra heaths, underlain by glacial till

[13, 14, 62, 91]. Anybody who has participated in the construction of a reindeer fence across such a landscape must have realized that permafrost is normally just a minor issue, as bedrock is normally only a few decimetres below the soil surface. Occasionally glacial till can be of such a depth that the deepest till layers are permanently frozen. However, this form of permafrost has little impact on drainage conditions in a hilly shield landscape. Thus, vehicle tracks on heathlands do not initiate any dramatic secondary changes. They do not become quickly vegetated, either, because of the relatively low rate of primary production, the low seed production of the dominating vascular plants and the sensitivity of lichens to mechanical damage. Thus, there is need to be careful with the management of this kind of landscape, but the need to restrict terrain traffic is not as urgent as in low arctic wetlands and tussock tundra areas. Moreover, there are several plants with dependable seed production and an ability to establish on bare mineral soil e.g. *Festuca ovina*, *Juncus trifidus* and *Luzula spicata*, [111], which can be used in restoration of disturbed low arctic heaths. If the important issue is not to restore the original vegetation, liming with dolomite and seeding with plants from nutrient-rich low arctic habitats can be recommended. Plants like *Astragalus alpinus* and *Dryas octopetala* vigorously invade disturbed habitats such as roadsides and railroad banks in nutrient-rich North Fennoscandian tundra areas, and even several floristic rarities (e.g. *Arenaria pseudofrigida*, *A. humifusa*, *Braya purpurascens*, *Papaver lapponum* subsp. *scandinavicum* and *Silene furcata* subsp. *angustifolia*) can be locally abundant in such sites [75, 120] (also *pers. obs.*). This approach offers an aesthetically attractive alternative to the use of roadside grasses and can be recommended at least for chronically disturbed areas, where the original vegetation cannot be restored.

In the middle and high Arctic, heavy man-made disturbances will inevitably interact with permafrost-related soil processes. The magnitude of secondary impacts can vary, depending on drainage conditions and the texture and depth of the soil. As the dominating plants are disturbance adapted and characterized by relatively high reproductive effort, colonization after the relaxation of the disturbance should not be a serious problem, although the process will inevitably be slow in the unproductive high Arctic. If the disturbed area is large, colonization could be speeded up by transplanting patches of intact vegetation in the interior parts of the disturbed area.

Another aspect of the supposed vulnerability of the tundra refers to its use for the production of reindeer meat. Overgrazing problems on the Swedish tundra are intensely debated in major national newspapers, and an equivalent, though less voluminous, debate also takes place in Finland and Norway. If our view of the ecology of the arctic and alpine habitats is correct, the concepts of natural and overgrazed state are meaningless in the context of the tundra. The natural death of an arctic-alpine grazer is starvation and so-called overgrazing is an essential part of the natural state of the tundra. Moreover, the floristic rarities of Fennoscandia (and other primarily low arctic or low alpine areas) are middle and high arctic plants, adapted to the combination of intense grazing and severe cryoperturbation. Judged on the basis of their gross morphology and reproductive biology, these plants can be expected to be very vulnerable to competition and to the closing of the cryptogam layer [120]. Depletion of the plant cover, exposition of mineral soil by the trampling reindeer herds and the erosion which often follows, can in the short term reduce the aesthetic value of the tundra and the immediate impact of such disturbance is likely to be negative for all plants [32]. However, these events may be essential for the floristic long-term diversity of the tundra.

There can indeed be local situations where reindeer numbers are higher than would be optimal for the maintenance of the diversity of tundra vegetation, and summer

grazing of lichen heaths is a potential problem for both nature protection and reindeer husbandry [79, 94]. However, reindeer density corresponding to the carrying capacity of the ranges, should be higher than the reindeer density which gives maximal meat production (calving and growth rates of animals decline when carrying capacity is approached). There should thus be no basic conflict between the use of the tundra for meat production and preservation of the diversity and beauty of its vegetation. In some areas, reindeer numbers have been boosted by the use of hay for winter food (although there have also been reductions in winter resources, due to hydroelectric construction projects and forestry). However, the availability of hay for reindeer is a consequence of the decline in the traditional transhumance activity (*sæter* and *sheiling* settlements), with summer production of meat, milk and wool on the mountains. Areas with high density of *sæter* settlement and high intensity of grazing used to be characterized by high biodiversity [77] and their disappearance is a major concern for nature conservation. We should therefore be glad that reindeer herding has at least partially taken over the role of sheep and cattle husbandry in traditional outback-country, which was so labour-intensive that it could only survive when the standard of living was low and labour was cheap.

6. Conclusions

The traditional view of the Arctic as a stress-influenced ecosystem with high sensitivity to disturbance and low capacity of recovery is only partially true. It applies primarily to poorly drained low and middle arctic grass-sedge tundras, where physical disturbance initiates secondary changes via its impact on permafrost and where the total seed production of the plant community is low. However, most arctic habitats are naturally highly disturbed, and adaptations to different kinds of disturbance are an essential part of the life history strategy of typical arctic plants. Tundra areas with continuous vegetation have been shaped by intense predator-prey interaction between plants and grazing mammals. Middle arctic tundras are naturally subjected to both grazing pressure and physical disturbance. The characteristic plants of these habitats are single shoot herbs and graminoids, which have small, basely attached leaves and which rely on sexual reproduction. Plants with these characteristics are quickly eliminated from grazer exclosures, because of over-topping by taller plants, build-up of a compact moss layer, and the consequent absence of germination sites. Polar deserts lack grazers, but are even more influenced by soil movement. The characteristic plants of polar deserts occur as fugitive species in strongly disturbed low arctic habitats and could be used there in restoration projects, along with middle arctic plants.

Vegetation processes and plant strategies in the Arctic can, by and large, be understood in the light of the triangular strategy scheme of Oksanen and Ranta, where the main trade-offs are between competitiveness and adaptation to different combinations of frequency and intensity of disturbance. In the most extreme habitats, however, it is essential to consider also the direct impacts of stress, which constrains the allocation patterns of plants between foliage and non-photosynthetic organs. On the basis of this consideration, a tetrahedral plant strategy scheme is proposed, where the poles are K-strategy (competitiveness), r-strategy (ruderality), g-strategy (adaptation to grazing) and s-strategy (adaptation to intense stress).

Acknowledgements

The authors record their sincere thanks to the editor and an anonymous referee for constructive criticism, which encouraged the development of the tetrahedron plant life strategy.

References

1. Abrams, P.A. (1993) Effect of increased productivity on the abundance of trophic levels, *Amer. Nat.* **141**, 351-371.
2. Aleksandrova, V.D. (1988) *Vegetation of Soviet polar deserts*, Cambridge Univ. Press.
3. Andersson, M. and Jonasson, S. (1986) Rodent cycles in relation to food resources on an alpine heath, *Oikos* **46**, 93-106.
4. Batzli, G.O., White, R.G., Maclean Jr., S.F., Pitelka, F.A. and Collier, B.D. (1980) The herbivore-based trophic system, in J. Brown, P.C. Miller, L.L. Tieszen and F.L. Bunnell (eds.), *An arctic ecosystem*, Dowden, Hutchinson & Ross, Stroudsburg, Pennsylvania.
5. Bell, K.L. and Bliss, L.C. (1980) Plant reproduction in high arctic environment, *Arctic and Alpine Res* **12**, 1-10.
6. Bell, R.H.V. (1982) The effect of soil nutrient availability on community structure in African ecosystems, in B.J. Huntley and B.H. Walker (eds.), *Ecology of tropical savannas*, Springer-Verlag, Heidelberg, 193-216.
7. Benninghoff, W.S. (1974) Macrobiology and ecology in polar deserts, in T.H. Smiley and Zumberge (eds.), *Polar deserts and modern man*, University of Arizona Press, Tucson, 91-97.
8. Billings, W.D. and Mooney, H.A. (1968) The ecology of arctic and alpine plants, *Biol. Rev.* **43**, 481-529.
9. Bliss, L.C. (1962) Adaptations of arctic and alpine plants to environmental conditions, *Arctic* **15**, 117-144.
10. Bliss, L.C. (1971) Arctic and alpine plant life cycles, *Annual Rev. Ecol. Syst.* **2**, 405-438.
11. Bliss, L.C. and Peterson, K.M. (1992) Plant succession, competition and the physiological constraints of species in the Arctic, in F.S. Chapin, III, R.L. Jefferies, J.F. Reynolds, G. Shaver and J. Svoboda (eds.), *Arctic ecosystems in a changing climate: an ecophysiological perspective*, Academic Press, San Diego, 111-136.
12. Bliss, L.C. and Wein, R.W. (1972) Plant community responses to disturbances in the western Canadian Arctic, *Canadian Journal of Botany* **50**, 1097-1109.
13. Böcher, T.W. (1954) Oceanic and continental vegetation complexes in southwest Greenland, *Meddr. Grønland* **148**, 1-336.
14. Böcher, T.W. (1963) Phytogeography of Middle West Greenland, *Meddr Grønland* **148**, 1-289.
15. Bryant, J.P., Chapin, F.S., III and Klein, D.R. (1983) Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory, *Oikos* **40**, 357-358.
16. Callaghan, T.V. and Emanuelsson, U. (1985) Population structure and processes of tundra plants and vegetation, in J. White (eds.), *The population structure of vegetation*, Dr. W. Junk, Dordrecht, 399-439.
17. Callaghan, T.V., Sonesson, M. and Sømme, L. (1992) Responses of terrestrial plants and invertebrates to environmental change at high latitudes, *Philosophical Transactions Roy. Soc. London B.* **338**, 279-288.

18. Campbell, B.D. and Grime, J.P. (1992) An experimental test of plant strategy theory, *Ecology* **73**, 15-92.
19. Chernjavskij, F.B. and Tkachev, A.V. (1982) Populacionnye cikli lemmingov v arktike: ekologicheskie i endrokinnye aspekty, *Nauka, Moscow (in Russian)* ,
20. Convey, P. and Smith, R.I.L. (1993) Investment in sexual reproduction by Antarctic mosses, *Oikos* **68**, 293-302.
21. Cooper, D.J. (1986) Arctic-alpine tundra vegetation of the Arrigetch Creek Valley, Brooks Range, Alaska, *Phytocoenologia* **14**, 467-555.
22. Couturier, S., Brunelle, J. Vandal, D. and St. Martin, G. (1990) Changes in the population dynamics of the George River caribou herd 1976-87, *Arctic* **43**, 9-20.
23. Crawford, R.M.M. (1982) Habitat specialisation in plants of cold climates., *Trans Bot Soc Edin.* **44**, 1-12.
24. Crawford, R.M.M., Chapman, H.M., Abbott, R.J. and Balfour, J. (1993) Potential impact of climatic warming on Arctic vegetation, *Flora* **43**, 367-381.
25. Crête, M. and Huot, J. (1993) Regulation of a large herd of migratory caribou: summer nutrition affects calf growth and body reserves of dams, *Can. J. Zool.* **7**, 2291-2296.
26. Crête, M. and Manseau, M. (1996) Top-down and bottom-up forces in food webs: natural regulation of cervidae along a 1000 km latitudinal gradient, *Evol. Ecol.* **10**, 51-62.
27. Dahl, E. (1957) Rondane. Mountain vegetation in South Norway and its relation to the environment, *Skrifter Norske Videnskaps-Akad. Oslo. I. Matem.-Naturvidensk. kl.* **1956(3)** , 1-374.
28. Du Rietz, G.E. (1925) Die regionale Gliederung der skandinavischen Vegetation, *Svenska Vaxsoc. Sallsk. Handl.* **8**, 1-60.
29. During, H.J. (1992) Ecological classifications of bryophytes and lichens, in J.W. Bates and A.M. Farmer (eds.), *Bryophytes and lichens in a changing environment*, Calendron Press, Oxford,
30. Engelskjön, T. and Schweitzer, H.-J. (1970) Studies on the flora of Bear Island (Bjørnøya). I. Vascular Plants, in (eds.), *Astarte*, **3**, 1-36.
31. Ericson, L. and Oksanen, L. (1987) The impact of controlled grazing by *Clethrionomys rufocanus* on experimental guilds of boreal forest floor herbs, *Oikos* **50**, 403-416.
32. Evans, R. (1995) Impacts of reindeer grazing on soils and vegetation in Finnmark., *NORUT Informasjonsteknologi, Tromsø* ,
33. Freedman, B., Hill, N., Svoboda, J. and Hendry, G.H.R. (1982) Seed banks and seedling occurrence in a high-arctic oasis at Alexandra Fiord, Ellesmere Island, Canada, *Canadian Journal of Botany.* **60**, 2112-2118.
34. Fretwell, S.D. (1977) The regulation of plant communities by the food chains exploiting them, *Perspectives Biol. Med.* **22**, 169-185.
35. Fretwell, S.D. (1987) Food chain dynamics: the central theory of ecology?, *Oikos* **50**, 291-301.
36. Gjaerevoll, O. (1956) The plant communities of the Scandinavian alpine snow-beds, Kongel., *Norske Videnskabers Selsk. Skrifter* **1**, 1-405.
37. Grace, J.B. (1990) On the relationship between plant traits and competitive ability, in J.B. Grace and D. Tilman (eds.), *Perspectives on plant competition*, Academic Press, New York, 51-65.
38. Grime, J.P. (1974) Vegetation classification by reference to strategies, *Nature* **250**, 26-31.
39. Grime, J.P. (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory, *Amer. Nat.* **111**, 1169-1194.
40. Grime, J.P. (1979) *Plant strategies and vegetation processes*, John Wiley, Chichester.
41. Grime, J.P. (1987) Dominant and subordinate components of plant communities: implications for succession, stability and diversity, in A.J. Gray, M.J. Crawley and P.J. Edwards (eds.), *Colonization, succession and stability*, Blackwell Scientific Publications, Oxford, 413-428.

42. Grime, J.P. (1993) Stress, competition, resource dynamics and vegetation process, in L. Fowden, T. Mansfield and J. Stoddart (eds.), *Plant adaptation to environmental stress*, Chapman & Hall, London, 45-63.
43. Grime, J.P. (1994) The role of plasticity in exploiting environmental heterogeneity, in M.M. Caldwell and R.W. Pearcy (eds.), *Exploitation of environmental heterogeneity by plants*, Academic Press, New York, 1-19.
44. Grime, J.P. (1995) Functional types: a comment on Steneck and Dethier (1994), *Oikos* 73, 120-121.
45. Grime, J.P., Hodgson, J.G. and Hunt, R. (1988) *Comparative plant ecology*, Unwin Hyman, London.
46. Grime, J.P. and Hunt, R. (1975) Relative growth rate: its range and adaptive significance in a local flora, *Journal of Ecology* 63, 393-422.
47. Grulke, N.E. and Bliss, L.C. (1985) Environmental control of the prostrate growth form in two high arctic grasses, *Holarctic Ecology* 8, 204-210.
48. Haapasaaari, M. (1988) The oligotrophic heath vegetation of northern Fennoscandia and its zonation, *Acta Bot. Fennica* 135, 1-219.
49. Hairston, N.G., Smith, F. and Slobodkin, L. (1960) Community structure, population control and competition, *Amer. Nat.* 94, 421-425.
50. Heikkinen, R.K. and Kalliola, R.J. (1990) The vascular plants of the Kevo Nature Reserve (Finland): an ecological-environmental approach, *Kevo Notes* 9, 1-56.
51. Herms, D.A. and Mattson, W.J. (1992) The dilemma of plants: to grow or defend, *Quart. Rev. Biol.* 67, 283-335.
52. Hnatiuk, R.J., Woodwell, S.R.J. and Bourn, D.M. (1976) Giant tortoise and vegetation interactions on Aldabra atoll - part 2: coastal, *Biol. Cons.* 9, 305-316.
53. Hultén, E. and Fries, M. (1986) *Atlas of Northern European vascular plants*, 2, Koeltz Scientific Books, Königstein.
54. Jonasson, S. (1986) Influence of frost heaving on soil chemistry and on the distribution of plant growth forms, *Geogr. Ann.* 68A, 185-195.
55. Jonasson, S. and Callaghan, T.V. (1992) Root mechanical properties related to disturbed and stressed habitats in the Arctic, *New Phytologist* 122, 179-186.
56. Jonasson, S. and Sköld, S.E. (1983) Influences of frost-heaving on vegetation and nutrient regime of polygon-patterned ground, *Vegetatio* 53, 97-112.
57. Kalliola, R. (1932) Alpiinisesta kasvillisuudesta Kammikivialueella Petsamon Lapissa (in Finnish), *Ann. Bot. Soc. Vanamo* 2, 1-112.
58. Kalliola, R. (1939) Pflanzensoziologische Untersuchungen in der alpinen Stufe Finnisch-Lapplands, *Ann. Bot. Soc. Vanamo* 13, 1-321.
59. Kelsall, J.P. (1968) *The migratory barren-ground caribou of Canada*, Department of Indian Affairs and Northern Development. Bulletin No. 3, Canadian Wildlife Service, Ottawa.
60. Körner, C. and Larcher, W. (1988) Plant life in cold climates, in S.P. Long and F.I. Woodward (eds.), *Plants and temperature*, Plants and temperature, Symp. So. Exptl. Biology 42, 25-57.
61. Kujala, V. (1926) Untersuchungen über die Waldvegetation in Süd- und Mittel-Finnland. I. Zur Kenntnis des ökologisch-biologischen Charakters der Pflanzenarten unter spezieller Berücksichtigung der Bildung von Pflanzen-Vereinen A. Gefässpflanzen, *Comm. Inst. Forest, Finland* 10, 1-154.
62. Larsen, J.A. (1965) The vegetation of the Ennadai Lake area, N.W.T.: studies in subarctic and arctic bioclimatology, *Ecol. Monogr* 35, 37-59.
63. Lid, J. (1964) The flora of Jan Mayen, *Norsk Polar Institutt Skr* 130, 1-107.
64. Lid, J. (1979) *Norsk og Svensk Flora*, Det Norske Samlaget, Oslo.
65. Longton, R.E. (1988) Life-history strategies among bryophytes of arid regions, *J. Hatt. Bot. Lab.* 64, 15-28.

66. Lundberg, P.A., Virtanen, R.J., Oksanen, L. and Moen, J. (1996) Plant community structure on Arctic islands: absence of herbivores favours moss dominance, *MS (unpublished)* ,
67. MacArthur, R.H.G.e.H.R., New York. (1972) *Geographical ecology*, Harper & Rowe, New York.
68. Maessen, O., Freedman, B., Nams, M.L.N. and Svoboda, J. (1981) Resource allocation in high-arctic vascular plants of differing growth form, *Can. J. Bot.* **61**, 1680-1691.
69. Manseau, M., Huot, J. and Crête, M. (1996) Changes induced by summer grazing of caribou on arctic tundra communities, *Ecology (submitted)* ,
70. Matveyeva, N.V. (1988) Changes in tundra vegetation of Taimyr Peninsula under man's impact, *Flora* **180**, 1-6.
71. Merton, L.F.H., Bourn, D.M. and Hnatiuk, R.J. (1976) Giant tortoise and vegetation interaction on Aldabra atoll - part 1: inland, *Biol. Cons.* **9**, 293-304.
72. Moen, J. (1993) *Herbivory and plant community structure in a subarctic altitudinal gradient*. Dissertation, University of Umeå thesis, Department of Ecological Botany, University of Umeå, Sweden.
73. Moen, J., Lundberg, P.A. and Oksanen, L. (1993) Lemming grazing on snow-bed vegetation during a population peak, Northern Norway, *Arct. Alp. Res.* **25**, 130-135.
74. Murray, D.F. (1987) Breeding systems in the vascular flora of arctic North America, in K.M. Urbanska (eds.), *Differentiation in higher plants*, Academic Press, 239-262.
75. Nilsson, O. (1987) *Nordisk Fjällflora*, Bonniers, Stockholm.
76. Nordhagen, R. (1928) *Die Vegetation und Flora des Sylenegebietes. I. Die Vegetation*, Skrifter Norske Videnskaps-Akad. I-IX, I. Matem.-Naturvidenskapelig kl. 1927, Oslo.
77. Nordhagen, R. (1943) Sikilsdalen og Norges fjellbeiter. En plantesosiologisk monografi, *Bergens Mus. Skrifter* **22**,
78. Odum, E.P. (1971) *Fundamentals of ecology*, W.B. Saunders Comp, Philadelphia.
79. Oksanen, L. (1978) Lichen grounds of Finnmarksvidda, northern Norway, in relation to summer and winter grazing by reindeer, *Rep. Kevo Subarctic Res. Stat* **14**, 64-71.
80. Oksanen, L., Fretwell, S.D., Arruda, J. and Niemela, P. (1981) Exploitation ecosystems in gradients of primary productivity, *Amer. Nat* **118**, 240-261.
81. Oksanen, L. (1983) Trophic exploitation and arctic phytomass patterns, *The American Naturalist* **122**, 45-52.
82. Oksanen, L. (1988) Ecosystem organization: mutualism and cybernetics or plain Darwinian struggle for existence?, *Amer. Nat* **131**, 424-444.
83. Oksanen, L. (1990) Predation, herbivory and plant strategies along gradients of primary productivity, in J.B. Grace and D. Tilman (eds.), *Perspectives on plant competition*, Academic Press, San Diego, 445-474.
84. Oksanen, L. (1993) Plant strategies and environmental stress: a dialectic approach, in L. Fowden, T.A. Mansfield and J.L. Stoddart (eds.), *Plant adaptation to environmental stress*, Chapman and Hall, London, 313-333.
85. Oksanen, L., Aunapuu, M., Oksanen, T., Schneider, M., Ekerholm, P., Lundberg, P.A., Armulik, T., Aruoja, V. and Bondestad, L. (1996) Outlines of food webs in a low arctic tundra landscape in relation to three theories on trophic dynamics, in A. Gange (eds.), *Multitrophic interactions in terrestrial ecosystems*, Chapman and Hall, London, in press,
86. Oksanen, L. and Ericson, L. (1987) Concluding remarks: trophic exploitation and community structure, *Oikos* **50**, 417-422.
87. Oksanen, L. and Moen, J. (1994) Species-specific plant responses to exclusion of grazers in three Fennoscandian tundra habitats, *Ecoscience* **1**, 31-39.
88. Oksanen, L., Oksanen, T., Ekerholm, P., Moen, J., Lunderbg, P., Schneider, M. and Aunapuu, M. (1995) Structure and dynamics of arctic-subarctic grazing webs in relation to primary productivity, in G.A. Polis and K. Winemiller (eds.), *Food webs: integration of patterns and dynamics*, Chapman and Hall, New York, 231-242.

89. Oksanen, L., Oksanen, T., Lukkari, A. and Siren, S. (1987) The role of phenol-based chemical defence in the interaction between tundra populations of the vole *Clethrionomys rufocanus* and the dwarf shrub *Vaccinium myrtillus*, *Oikos* **50**, 371-380.
90. Oksanen, L. and Ranta, E. (1992) Plant strategies along vegetational gradients on the mountains of Iddonjarga - a test of two theories, *Journal of Vegetation Science* **3**, 175-186.
91. Oksanen, L. and Virtanen, R. (1995) Topographic, altitudinal and regional patterns in North Fennoscandian continental and suboceanic heath vegetation, *Acta Botanica Fennica* **153**, 1-80.
92. Oksanen, T., Oksanen, L. and Norberg, M. (1992) Habitat use of small mustelids in north Fennoscandian tundra: a test of hypothesis of patchy exploitation ecosystems, *Ecography* **15**, 237-244.
93. Owen-Smith, N. and Cooper, S.M. (1987) Palatability of woody plants to browsing ungulates in a South African savanna, *Ecology* **68**, 319-331.
94. Pegau, R.E. (1969) Effect of reindeer trampling and grazing on lichens, *Journal of Range Management* **23**, 95-97.
95. Pettersson, B. (1958) Dynamik och konstans i Gotlands flora och vegetation, *Acta Phytogeographica Suecica* **40**, 1-288.
96. Philipp, M., Böcher, J., Mattsson, O. and Woodell, S.R.J. (1990) A quantitative approach to the sexual reproductive biology and population structure in some arctic flowering plants: *Dryas integrifolia*, *Silene acaulis* and *Ranunculus nivalis*., *Meddelelser om Grønland: Bioscience* **34**, 3-60.
97. Pimm, S.L., Rosenzweig, M.L. and Mitchell, W. (1985) Competition and food selection: a field test of a theory, *Ecology* **66**, 798-807.
98. Pitelka, F. (1973) Cyclic pattern in lemming populations near Barrow, Alaska, *Arctic Institute of North America, Techn. Papers* **25**, 199-215.
99. Polis, G.A. and Strong, D. (1996) Food web complexity and community dynamics, *American Naturalist* (in press),
100. Power, M. (1992) Top-down and bottom-up forces in food webs: do plants have primacy?, *Ecology* **73**,
101. Raup, H.M. (1969) Observations on the relation of vegetation to mass-wasting process in the Mester's Vig district, Northeast Greenland, *Meddel. Grønland* **176**, 1-216.
102. Rønning, O.I. (1970) Synopsis of the flora of Svalbard, *Norsk Polar Institut Årbok* , 80-93.
103. Ruuhijärvi, R. (1960) Über die regionale Einteilung der nordfinnischen Moore, *Ann. Bot. Soc. Vanamo* **31**,
104. Scholander, P.F. (1934) Vascular plants from northern Svalbard, *Skifter om Svalbard og Ishavet* **62**,
105. Sheard, J.W. (1968) Vegetation pattern in a moss-lichen heath associated with primary topographic features on Jan Mayen, *Bryologist* **71**, 21-28.
106. Siekkinen, M. (1995) *Impact of reindeer grazing on mountain vegetation at Kilpisjärvi, N.W. Finnish Lapland (in Finnish)*. M.Sc thesis, Oulu.
107. Sjörs, H. (1971) *Ekologisk botanik*, Stockholm.
108. Smith, C.C. (1976) When and how much to reproduce: the trade-off between power and efficiency, *American Zoologist* **16**, 763-774.
109. Sørensen, T. (1941) Temperature relations and phenology of Northeast Greenland flowering plants., *Meddr. Grønland* **125**, 1-305.
110. Söyrinki, N. (1938) Studien über die generative und vegetative Vermehrung der Samenpflanzen in der alpinen Vegetation Petsamo-Lapplands. Allgemeine Teil, *Ann. Bot. Soc. Vanamo* **11**, 1-323.
111. Söyrinki, N. (1939) Studien über die generative und vegetative Vermehrung der Samenpflanzen in der alpinen Vegetation Petsamo-Lapplands. II Spezieller Teil, *Ann. Bot. Soc. Vanamo* **14**, 1-404.

112. Söyrinki, N. (1989) Fruit production and seedlings in *Polygonum viviparum*., *Memoranda Soc. Fauna Flora Fennica* **65**, 13-15.
113. Steneck, R.S. and Dethier, M.N. (1994) A functional group approach to the structure of algal-dominated communities, *Oikos* **69**, 476-498.
114. Stewart, J. and Freedman, B. (1994) Biomass allocation in ten *Saxifraga* species in the high Arctic, in J. Svoboda and B. Freedman (eds.), *Ecology of a polar oasis, Alexandra Fiord, Ellesmere Island, Canada*, Captus University Publications, Toronto,
115. Strong, D. (1992) Are all trophic cascades wet? The redundant differentiation in trophic architecture of high diversity ecosystems, *Ecology* **73**, 747-757.
116. Tichomirov, B.A. (1961) The relationship between animal and plant communities in the tundras of the U.S.S.R, (*Abbreviated English translation*) *Proc. Univ. Durham (USA) Phil. Soc* **13 Series A (Science)**, 231-240.
117. Tikkanen, E. and Niemelä, I. (1995) *Kola Peninsula pollutants and forest pollutants in Lapland*, Gummerrus Kirjapaino Oy, Jyväskylä, Finland.
118. Tilman, D. (1987) On the meaning of competition and the mechanisms of competitive superiority, *Functional Ecology* **1**, 304-315.
119. Tilman, D. (1988) *Plant strategies and dynamics and structure of plant communities*, Princetown University Press, Princetown, New Jersey.
120. Virtanen, R.J., Henttonen, H. and Laine, K. ((submitted)) Lemming grazing and structure of snowbed plant communities - a long-term experiment at Kilpisjärvi, N.W. Finnish Lapland, *Oikos* ,
121. Warren Wilson, J. (1952) Vegetation patterns associated with soil movement on Jan Mayen Island, *Journal of Ecology* **40**, 249-264.
122. Watson, E.V. (1964) An annotated list of the bryophytes of Jan Mayen Island, *Nytt Magasin for Botanik* **11**, 151-212.