

Predation, Herbivory, and Plant Strategies Along Gradients of Primary Productivity

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I. Vegetation Processes in Benign and Stressful Environments: Variations on the Same Theme?

Plant ecologists have divergent ideas on the impact of stress on vegetation processes. One view can be traced to Darwin's (1859) statement that, for organisms inhabiting extreme environments, the struggle for existence is almost exclusively against the "elements," not between different organisms. This view has a strong foothold in British animal and plant ecology (Southwood, 1977; Grime, 1977, 1979; Callaghan and Emman-

uelsson, 1985). In Central Europe, struggle between organisms is often regarded as important, even in extreme environments. Environmental stresses are chiefly seen in the role of external constraints that determine which characteristics of plants are most competitive in a given environment (Walter, 1964, 1968; Ellenberg and Mueller-Dombois, 1974; Ellenberg, 1978), although the possibility that environmental stresses directly exclude superior competitors is accepted. A still less compromising view of competition as the organizing principle of plant communities prevails in northern Europe, dominated by Cajander's (1909) view of site-specific community types that consist of those plants that are maximally competitive in the habitat and utilize resources in sufficiently different ways to permit competitive coexistence. For Cajander, distributional limits in both local and global scale are always products of changes in the competitive balance between different species. Major vegetational transitions represent similar changes in the competitive balance between different types of plants. A similar view of competition and community structure has spread to American plant ecology, when researchers with roots in the zoological tradition of Gause (1934), Lack (1954), and MacArthur (1972) have become interested in plants (Cody, 1986; Tilman, 1982, 1984, 1985, 1987, 1988a).

In the inevitable clash between Grime's school and what could be called the Cajander-Tilman school (Thompson, 1987; Tilman, 1988b), the logical position of the latter school is stronger. Grime's (1979) idea that a single plant type would be a superior competitor under all circumstances is in conflict with the principle of allocation (Tilman, 1988a), with well-known ecophysiological facts (e.g., photosynthetic responses of different plants to moisture, light, and temperature; see Kershaw, 1975; Lechowicz, 1978; Bazzaz, 1979) and with the existence of a tradeoff between short-term and long-term competitiveness (Smith, 1976). It is also difficult to see how stress could reduce the importance of competition. In every habitat, there is some limit for the plant biomass that the resource basis can support. When this level is approached, competition seems inevitable.

Tilman (1988a) showed that a large part of global vegetational patterns can be explained on the basis of changing terms of competition. In arid areas where water is a minimum factor and canopy never gets dense enough to create substantial competition for light, the size and shape of the root system largely determines the competitiveness of the plant. Plants allocating many resources to roots and only little to stems can thus outcompete plants with an opposite allocation pattern. Also, in early successional habitats and in cold areas, where mineral nutrients are often in short supply, competition can mainly take place in the soil, favoring plants with low shoot/root ratios (Chapin and Shaver, 1985; Tilman,

1987). In cold and windy habitats with lots of bare ground, thermal conditions can further increase the advantages of low stature (Billings and Mooney, 1968; Walter, 1968; Ellenberg, 1978).

Although many types of environmental stresses may favor high allocation of resources to roots, it is difficult to explain the transition from forests to steppes and arctic or alpine tundras solely as a consequence of changing terms of competition. These transitions occur in areas where the vegetation is still closed and competition for light has by no means ceased to exist. Yet, typical tundra and steppe plants do not differ from trees just by having different allocation patterns. Typically, these plants are herbaceous and have leaf-producing meristems close to the ground, and even the woody ones are characterized by weak apical dominance, so that the above-ground shoot system remains much shorter than would be possible with the prevailing level of allocation to shoots (see Walter, 1964, 1968; Knapp, 1965; Ellenberg, 1978). If competition were equally important in stressful and benign environments, it would seem more advantageous to make the allocation to shoots in the form of an erect woody stem. In a few years, such a stem would overtop the shoots of herbaceous plants and prostrate dwarf shrubs. Winter ecology can explain a part of this enigma: plants extending above the snow cover must cope with extremely hostile thermal and moisture conditions in late winter and early spring (Tranquillini, 1957, 1970). However, most tundra plants are either herbaceous or have much lower stature than could be explained by winter ecology alone. Thermal advantages of staying close to the ground do not explain prostrateness, either: robust cushion form (i.e., tight packing of erect shoots) is an equivalent, possibly even superior way of maximizing the warming effect of direct solar radiation (Gauslaa, 1984). Also, explanations based on the superiority of the fibrous root system of graminoids (Walter, 1964, pp. 280–292) or their superior ability to recycle nutrients (Jonasson and Chapin, 1985) are problematic, because they presuppose that erect woody plants could not evolve functionally similar root systems or recycling mechanisms.

Although the transition from forests to steppes and tundras does not quite fit the implications of the Cajander–Tilman competition approach, it does not fit Grime's theory either. If arid and arctic timberlines represented cases where superior competitors become directly excluded by environmental stresses, the timberlines should be abrupt. As pointed out by Ellenberg (1978, p. 522), where one tree can grow, so could another one too. Thus, in the absence of disturbance, the site should become a closed forest. However, parklands with scattered trees are typical for transitions from forests to steppes and tundras from equatorial to (McNaughton, 1985) subarctic (Norin, 1961) areas, with just two notable exceptions. One consists of subarid temperate areas without fire-resis-

tant trees, where fire prevents the development of savanna-like formations (Walter, 1968). This does not qualify as an example of an undisturbed timberline. The other one consists of islands without native herbivores (e.g., Hawaii and New Zealand; see Cockayne, 1958; Connor, 1965; Knapp, 1965; Mark, 1955; Burrell, 1965; Mueller-Dombois, 1967; Walter, 1968; Williams, 1975). On these islands, timberlines in the normal sense do not exist at all. In their natural state, the gradients of increasing aridity on Hawaii and New Zealand are characterized by forests grading into scrublands with successively lower stature, whereas graminoid-dominated vegetation has only occurred on disturbed sites. (Even there, the graminoids are functionally more like shrubs than like northern hemisphere grasses: leaves are extremely robust and sit on 1–2 m tall perennial pedestals.) On the mountains of Hawaii, rain forests directly grade into alpine barrens with rosette trees. On New Zealand, undisturbed altitudinal gradients consist of forests grading to successively lower scrublands and, finally, to barren crests dominated by robust cushion plants. Consequently, Ellenberg's point implies that undisturbed timberlines are practically nonexistent: either there is some form of disturbance or the transition from the dominance of upright woody plants to the prevalence of prostrate or semiprostrate plants is replaced by some continuous gradient where plants change their allocation patterns but retain an erect growth form.

In conclusion, the Cajander–Tilman approach is logically sound but its premises seem to be inapplicable to the rapid or sharp transitions from forests and closed scrublands to typical steppe and tundra communities. Grime, in turn, may be right in proposing that increasing stress sometimes implies lower intensity competition but cannot explain why this should happen. The enigma can be solved by assuming that stress is inevitably accompanied by disturbance (Tilman, 1988a, pp. 140–145; Tilman, 1988b, pp. 313–318). The aberrant vegetational patterns of grazer-free islands (Oksanen, 1988) suggest that grazing vertebrates are a central source for this disturbance, although fire can sometimes be an important contributing source. What remains to be explained is why a certain intensity of stress and intense grazing by vertebrates inevitably go together.

II. Trophic Dynamics and Primary Productivity

A theory which connects stress and grazing was outlined by Fretwell (1977). He found the hypothesis of Hairston *et al.* (1960) on trophic dynamics and population regulation to be appealing, but could not apply it to grassland ecosystems. According to Hairston *et al.*, the world is green

(i.e., plant biomass is abundant) because predators regulate herbivores at a level where only a small fraction of primary production is consumed by grazers. However, this did not seem to apply to North American short-grass plains. There, plant biomass is not strikingly plentiful, and historical evidence suggests that this is not a man-made situation. Studies from similar but still undisturbed ecosystems suggest that grazers are resource-limited (Sinclair, 1977, 1985) and have strong impact on the vegetation (McNaughton, 1979, 1985). Moreover, the native plants of the plains are clearly adapted to intense grazing pressure (Stebbins, 1981). Fretwell's solution was to accept the general view of Hairston *et al.*, that consumers can regulate their resources, but to reject the specific point that carnivores always limit herbivore populations and prevent depletion of forage. Fretwell suggested that trophic dynamics depend on primary productivity: the hypothesis of Hairston *et al.* applies to relatively productive habitats, whereas in more barren areas, grazers are resource-limited and the vegetation is subjected to intense natural herbivory.

Fretwell's (1977) idea was formally analyzed by Oksanen *et al.* (1981). They assumed that the equation for the growth of plant biomass contains a term representing the potential gross primary productivity of the habitat, and that both herbivores and carnivores are capable of regulating the abundances of their resources (Sih *et al.*, 1985). On both trophic levels, interactions between consumers are chiefly indirect, taking place via shared resources. The potential primary productivity of the habitat determines how much plant biomass it can maximally sustain and the density of grazers needed to keep the plant biomass at any fixed level smaller than the maximum. With these assumptions, one can construct a phase space with biomasses of plants, grazers, and carnivores as its axes and find zero isoclines (actually: isosurfaces) where consumption and growth are equal for each of the three components. As three-dimensional isocline models are somewhat cumbersome to work with, it is fortunate that the ecologically relevant conclusions for plants can be presented as a two-dimensional projection, corresponding to the simple models of Rosenzweig and MacArthur (1963).

Figure 1 represents a set of such two-dimensional isocline graphs for habitats with vast differences in primary productivity. In all habitats, the plant isocline is arch-shaped, but the archs differ in size and curvature. The isoclines corresponding to extremely barren environments are very close to the origin, whereas those for more productive habitats have higher and wider archs. As consumers are not directly affected by the factors which regulate the growth of plants, their isoclines are assumed to be identical for all habitats. In the absence of carnivores, the herbivore isocline is a pure consumer isocline, i.e., a straight vertical line: the short-term well-being of the grazers depends only on the amount of forage

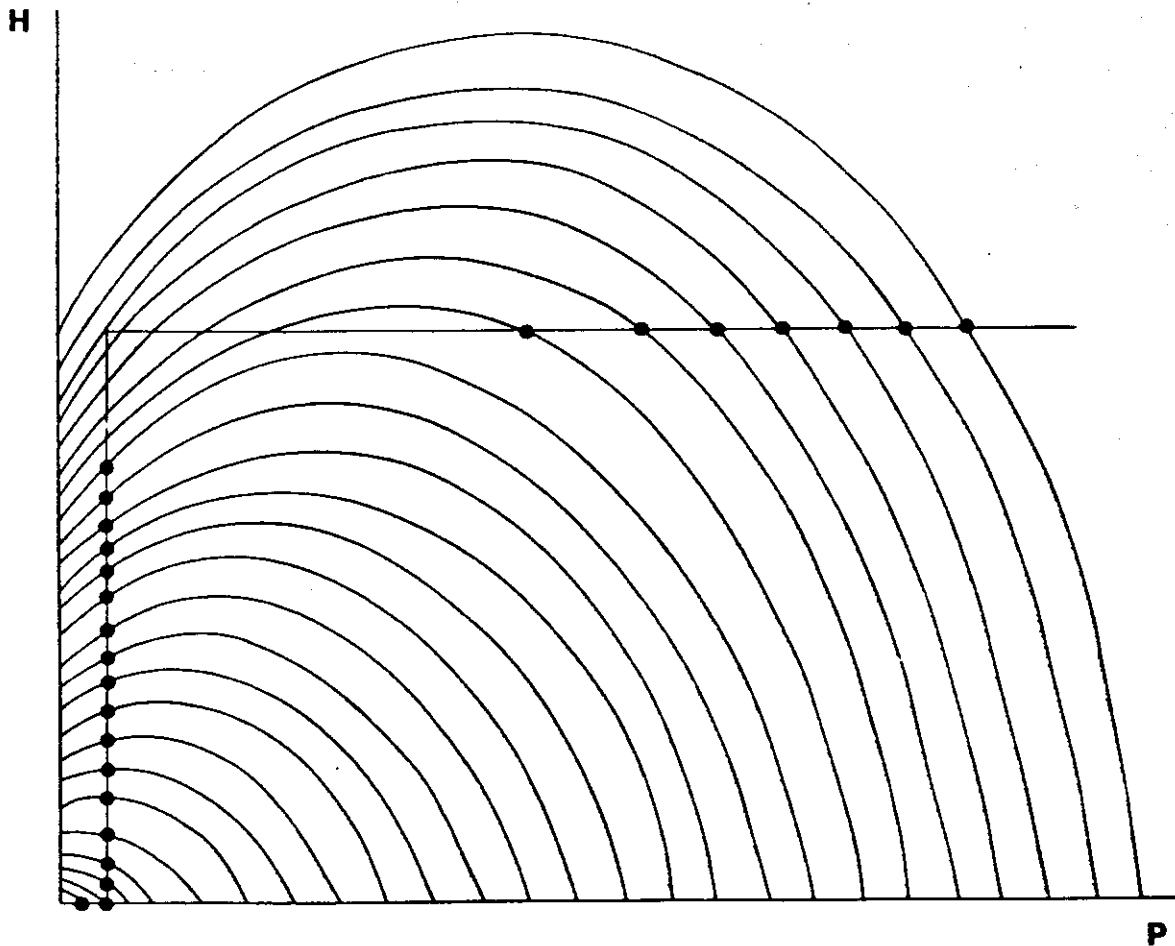


Figure 1 An isocline model of a herbivore (H)-plant (P) exploitation system with the impact of carnivores implicitly included. Archs, plant isoclines for habitats with different primary productivities; rectangle, herbivore isocline; dots, equilibrium points for each herbivore-plant system.

and is independent of the density of grazers (see Noy Meir, 1975; Rosenzweig, 1977; Caughley and Lawton, 1981). In the presence of carnivores, the herbivore isocline becomes complicated (Rosenzweig, 1973; Oksanen *et al.*, 1981), but we can get around this problem by noticing that, in laissez-faire exploitation systems, a top consumer limits the density of its resources to some constant level. Consequently, the effect of carnivores on grazer-plant dynamics can be mimicked by making the herbivore isocline consist of a vertical piece (the herbivore isocline in the absence of carnivores) and a horizontal piece which actually represents the carnivore isocline.

The isocline analysis of Fig. 1 shows that increasing primary productivity is accompanied by qualitative changes in the dynamics of the grazing chain. In extremely barren habitats, plant and herbivore isoclines do not meet at all. Consequently, the equilibrational community is predicted to be free of grazers and increasing productivity is predicted to increase the equilibrational plant biomass. In somewhat more productive habitats, plant

and herbivore isoclines meet in the vertical section of the herbivore isocline. Consequently, the equilibrium community consists of plants and grazers. In this productivity interval, the herbivore–plant system exhibits a phenomenon dubbed as the “Paradox of Enrichment” by Rosenzweig (1971): increased primary productivity only increases the equilibrium densities of grazers, whereas accessible (i.e., above-ground) plant biomass remains constant. The next qualitative shift occurs when the environment becomes so productive that the plant isocline meets the horizontal section of the herbivore isocline (actually: the carnivore isocline). From this point onward, Paradox of Enrichment shifts to the interaction between carnivores and herbivores, and plant biomass starts to increase again in response to increasing primary productivity.

In order to have labels for ecosystems with different dynamics in the grazing chain, Fretwell (1977) called the three productivity zones where the model predicts qualitatively different trophic dynamics “one link,” “two link,” and “three link” ecosystems. This terminology creates the impression that food chains are predicted to be shorter in less productive habitats, which is debatable (Pimm, 1982; Pimm and Kitching, 1987). Excluding transients and those predators which exploit temporary outbreaks generated by a locally unstable grazer–plant equilibrium, this impression is in a way correct. Notice, however, that what has been modeled is only a part of the grazing chain. The model is restricted to animals which move on the land in their search of food and are active throughout the year or have high costs of dormancy, i.e., to vertebrates. Typical invertebrate grazing systems have many features (low mobility of herbivores, predictable association between the herbivore and the food plant, low costs of dormancy) which make it unlikely that their part of the grazing chain reacts to changes in primary productivity. Moreover, the carnivores that isocline models deal with are only a part of the carnivore trophic level—those capable of killing healthy prey. There are also carnivores adapted to search for weak prey (and carrion) and the presence of such carnivores (e.g., wolverines, jackals) in two-link ecosystems is not in conflict with the isocline model (see Oksanen and Ericson, 1987a).

How the predicted changes in trophic dynamics influence the life of the plants can be visualized by plotting the predicted equilibrium phytomass against the potential primary productivity of the habitat (Fig. 2a). The distance between the phytomass in the absence of grazers (dashed line) and the predicted equilibrium (solid line) represents the intensity of natural grazing. The plant ecological implications become still more tangible when the information is rearranged by counting the predicted percent difference between maximum and equilibrium biomass. This represents the intensity of natural grazing pressure from the point of view

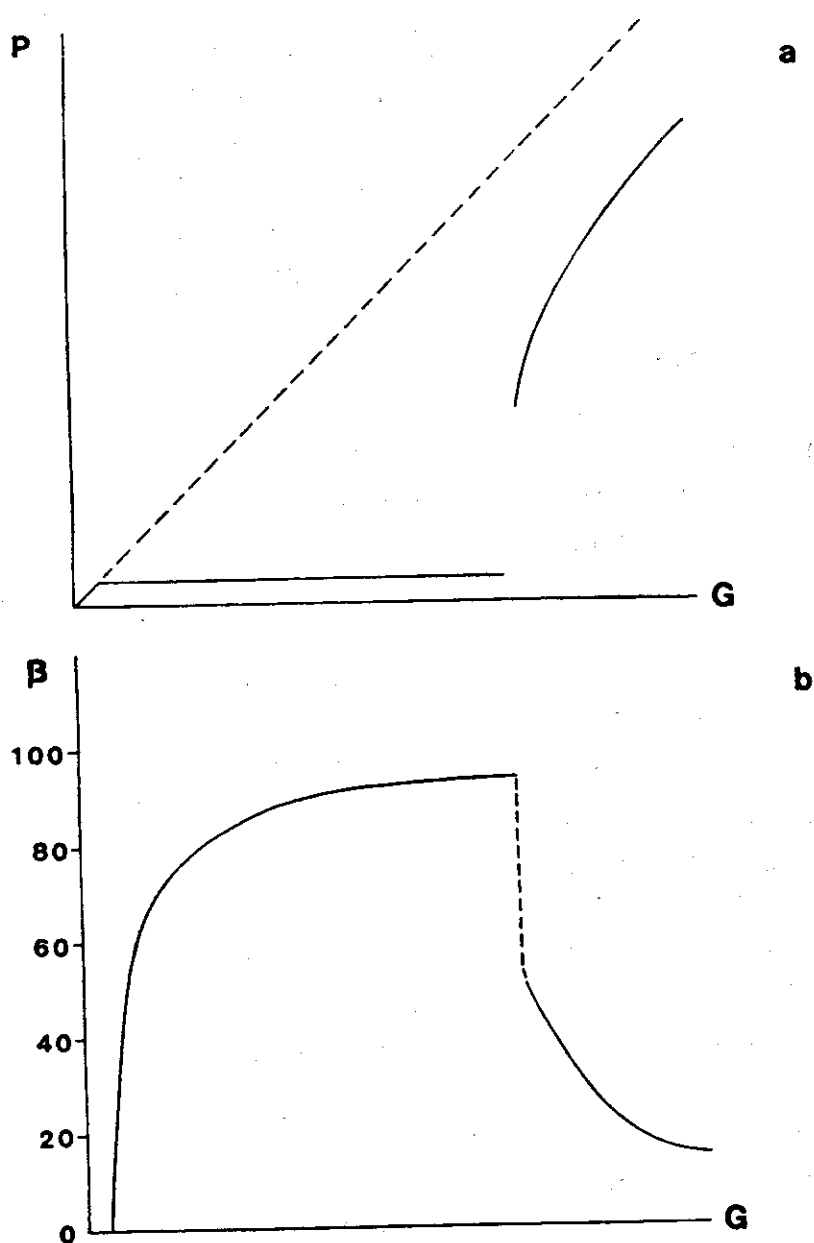


Figure 2 Predictions on phytomass and grazing pressure generated by Fig. 1. (a) Predicted relation between gross primary productivity (G) and above-ground phytomass (P) in the absence (dashed line) and presence (solid line) of grazers. (b) Predicted percent reduction of above-ground phytomass due to natural grazing pressure (β) as a function of gross primary productivity (G).

of plants. Focusing on this measure (β , Fig. 2b), we see that the productivity interval of two-link ecosystems stands out as a distinct zone with much higher natural grazing pressure than in other parts of the productivity cline.

The predicted relationship between primary productivity and natural grazing pressure is not especially sensitive to deviations from the assumption of strictly laissez-faire consumer–resource dynamics. Interference among herbivores would tilt the plateau part of Fig. 2a upward, but the impact on Fig. 2b would be very slight. Interference among carnivores would have still less influence: the increase in equilibrial phytomass

in the right-hand part of Fig. 2a would become a bit more gradual, but only extreme levels of interference would produce notable changes in Fig. 2b. However, the plant predictions of the isocline model are sensitive to deviations from two assumptions, which are not yet stated. The isoclines are drawn so that grazers are assumed to be able to survive on very scanty vegetation, whereas carnivores are assumed to require relatively high grazer densities in order to break even. Converse assumptions would reduce two-link ecosystems to a marginal phenomenon at the transition from one-link to three-link ecosystems, and if both herbivores and carnivores were assumed to survive on a very scanty resource basis, the predictions would change so that practically all ecosystems would have three-link dynamics (which I think is the case in arthropod grazing chains). With regard to vertebrate grazers, my assumption is based on observations of semidomesticated reindeer, which are able to survive on ranges with very low biomasses of food plants. (A similar observation could be obtained, for example, by looking at goats and camels in the Middle East semideserts.) With regard to carnivores, I rely on studies showing that efficient pursuers of vastly different body sizes indeed require quite high prey densities (Schaller, 1972; Erlinge, 1974).

The central message of Fig. 2 is that what Grime (1977, 1979) proposes to be the stress-tolerant strategy might actually represent adaptations to intense grazing pressure. Facts and logics seem to support this reinterpretation (Tilman, 1988a). British heathlands play a central role in Grime's (1979) discussion on "stress tolerators," and this type of vegetation is indeed a product of long-lasting grazing (Gimingham, 1972). Moreover, Grime's (1979; Table 6) list of characteristics of supposed stress tolerators is easily reinterpreted as a catalogue of grazing-tolerant features. Low palatability is a clear antigrazer adaptation; small, leathery and needlelike leaves are more grazing-resistant than broad and mesomorphic ones; prevalence of vegetative reproduction is adaptive in heavily grazed habitats where inflorescences tend to be consumed (McNaughton, 1979; Oksanen and Ericson, 1987b; Tihomirov, 1959). Long life span of leaves makes heavy investments in defense more feasible, and low maximum growth rate is an inevitable consequence of such investments.

There is a straightforward way to test the relative merits of the two interpretations of Grime's stress-tolerant strategy. If the strategy really represented adaptations to environmental stresses, there should be a monotonous trend of increasing amount of stress-tolerant features along a gradient of increasing environmental stress. If, in turn, natural grazing pressure is the crucial factor, the so-called stress tolerators should be absent from the extremely stressful habitats (Fig. 2b). These contrasting predictions can be tested with ordination data of Oksanen and Ranta

(1989) on the vegetation of a mountain chain in Norwegian Lapland (Oksanen, 1980), rising from birch forests to eternal snow. In Table 1, 15 species with extremely high, middle, and extremely low scores on the first ordination axis (i.e., altitude) are compared to those morphological, reproductive (see Söyrinki, 1939), and chemical characteristics with which Grime (1979) predicts unambiguous differences between his competitive and stress-tolerant strategies (Table 1). The supposedly stress-tolerant features are relatively common at middle altitudes, but the high-alpine element is again characterized by features which Grime regards as competitive. This is not a peculiarity of this particular mountain chain: *Ranunculus glacialis* holds the altitudinal record throughout the Scandinavian mountains (Gjaerevoll and Jörgensen, 1952) and the European Alps (Ellenberg, 1978) and is the dominating constituent of Scandinavian high-alpine vegetation (Nordhagen, 1927, 1943; Gjaerevoll, 1956). *Oxyria digyna* has wide circumpolar distribution in high-alpine habitats

Table 1 Occurrence of Grime's Competitive (C) and Stress-Tolerant (S) Features in the High-, Middle-, and Low-Altitude Plants of Iddonjårga Mountains*

	1	2	3	4	5	6	7	8	Score C-S
High-altitude plants									
<i>Cardamine bellidifolia</i>	C	C	C	C	C	C	C	C	8-0
<i>Cerastium cerastiodes</i>	S	S	S	C	S	C	S	C	3-5
<i>Carex lachenalii</i>	—	S	S	S	C	C	S	C	3-4
<i>Luzula confusa</i>	—	S	S	C	S	C	S	C	3-4
<i>Oxyria digyna</i>	C	C	C	C	C	C	C	C	8-0
<i>Poa alpina</i>	—	S	S	C	C	C	S	C	4-3
<i>Ranunculus glacialis</i>	C	C	C	C	C	C	C	C	8-0
<i>Ranunculus nivalis</i>	C	C	C	C	C	C	C	C	8-0
<i>Saxifraga aizoides</i>	C	S	S	C	S	C	S	S	3-5
<i>Saxifraga caespitosa</i>	S	S	S	C	S	C	S	C	3-5
<i>Saxifraga cernua</i>	C	C	C	C	C	C	C	S	7-1
<i>Saxifraga oppositifolia</i>	S	S	S	S	S	S	S	C	1-7
<i>Saxifraga rivularis</i>	C	C	C	C	C	C	C	C	8-0
<i>Saxifraga tenuis</i>	S	S	C	C	S	C	S	C	4-4
<i>Trisetum spicatum</i>	—	S	S	C	C	C	S	C	4-3
Score for S features	4	9	8	2	6	1	9	2	75-41
Middle-altitude plants									
<i>Alchemilla alpina</i>	C	C	C	S	C	C	C	C	7-1
<i>Anthoxanthum odoratum</i>	—	S	S	C	C	C	S	C	4-3
<i>Carex bigelowii</i>	—	S	S	S	C	C	S	S	2-5
<i>Calamagrostis lapponica</i>	—	S	S	S	C	C	S	S	2-5
<i>Diapensia lapponica</i>	S	S	S	S	S	S	S	C	1-7
<i>Euprasia frigida</i>	C	C	S	C	C	C	C	C	7-1

(continued)

Table 1 (Continued)

	1	2	3	4	5	6	7	8	Score C-S
<i>Festuca ovina</i>	—	S	S	S	S	C	S	C	2-5
<i>Hieracium alpinum</i>	S	S	C	C	C	C	C	C	6-2
<i>Juncus trifidus</i>	—	S	S	S	S	C	S	C	2-5
<i>Luzula frigida</i>	—	S	S	S	S	C	S	C	2-5
<i>Loiseleuria procumbens</i>	A	S	S	S	S	S	S	C	1-7
<i>Phyllodoce coerulea</i>	S	S	S	S	S	S	S	C	1-7
<i>Pyrola minor</i>	S	S	C	S	S	S	S	S	1-7
<i>Ranunculus acris</i>	C	S	C	C	C	C	C	C	7-1
<i>Silene acaulis</i>	S	S	S	S	S	S	S	C	1-7
Score for S features	6	13	11	11	8	5	11	3	46-68
Low-altitude plants									
<i>Betula pubescens</i>	C	C	C	C	C	C	C	C*	8-0
<i>Cornus suecica</i>	C	C	C	C	C	C	C	S	7-1
<i>Deschampsia flexuosa</i>	—	S	S	C	S	C	S	S	2-5
<i>Gymnocarpium dryopteris</i>	C	C	C	C	C	C	C	S	7-1
<i>Equisetum arvense</i>	—	S	S	S	C	C	S	S	2-5
<i>Equisetum pratense</i>	—	S	S	S	C	C	S	S	2-5
<i>Juniperus communis</i>	C	S	S	S	S	S	S	C*	2-6
<i>Linnaea borealis</i>	S	S	S	S	S	C	S	S	1-7
<i>Luzula pilosa</i>	—	S	C	C	S	C	S	C*	4-3
<i>Lycopodium annotinum</i>	S	S	S	S	S	S	S	S	0-8
<i>Pedicularis lapponica</i>	C	S	S	C	C	C	C	S	5-3
<i>Salix caprea</i>	C	C	C	C	C	C	C	C*	8-0
<i>Salix myrsinifolia</i>	C	C	C	C	C	C	C	C*	8-0
<i>Salix phylicifolia</i>	C	C	C	C	C	C	C	C*	8-0
<i>Trientalis europaea</i>	C	C	C	C	C	C	C	S	7-1
Score for S features	2	8	7	5	5	2	7	9	71-45
χ^2 -tests ^b									
High vs. low altitude	—	—	—	—	—	—	—	*1	—
High vs. middle altitude	—	—	—	*2	—	—	—	—	*3
Middle vs. low altitude	o ⁴	—	—	o ⁵	—	—	—	o ⁶	*7

^a (1) Life form: C, tree, upright shrub, or ordinary herb; S, cushion plant, rosette plant, or trailing dwarf shrub; —, graminoid or *Equisetum* (relation to Grime's categories unclear). (2) Shoot structure: C, leaves well differentiated and apically attached to an upright stem or elevated by a stem-like petiole; S, photosynthesizing organs with wide vertical spreading or entirely basal position. (3) Leaf shape: C, robust and mesomorphic; S, small or narrow and needle-like. (4) Leaf texture: C, soft; S, tough and leathery. (5) Leaf longevity: C, short (deciduous); S, long (evergreen). (6) Palatability: C, high, moderate, or low due to small amounts of acute toxins; S, very low, due to large concentrations of secondary compounds. (7) Perennation: C, specialized buds or seeds; S, stress-tolerant leaves or roots. (8) Reproduction: C, generative reproduction has a significant role in the life cycle; S, reproduction overwhelmingly vegetative; C*, little or no generative reproduction in Söyrinki's (1939) material but substantial generative reproduction in more southern areas (i.e., generative reproduction belongs to the strategy of the plants but cannot be executed under subarctic conditions), combined with C in the calculation of the C-S score. Life form has been ignored in the tests of total C-S scores because of its positive correlation with shoot structure.

^b *, $p < 0.05$; o, $p < 0.1$; —, not significant. (1) $\chi^2 = 5.17$, (2) $\chi^2 = 8.69$, (3) $\chi^2 = 13.90$, (4) $\chi^2 = 3.31$, (5) $\chi^2 = 3.34$, (6) $\chi^2 = 3.47$, (7) $\chi^2 = 8.41$.

(see Mooney and Billings, 1961; Billings and Mooney, 1968). Also, the high-alpine saxifrages of Table 1 (and their morphologically similar congeners) are a dominating element in the boulderfield flora of arctic, boreal, and temperate mountains (see Nordhagen, 1927, 1943; Böcher, 1933, 1954; Braun-Blanquet, 1948–1950; Gjaerevoll, 1956; Reisgl and Pitschmann, 1958; Komarková, 1978).

However, just changing the label of Grime's stress-tolerant strategy to "grazing-tolerant strategy" is not sufficient for relating broad vegetational patterns to the predictions of the isocline model. Grime's catalog is not derived from first principles but represents summary of observations, and comparing observation-based generalizations to further observations creates a risk of circular reasoning. With regard to such a key characteristic as stature, Grime refrains from making any clear statements. Moreover, graminoids, which are a prominent constituent of many tundra and steppe communities, show less than perfect fit to the list of features that Grime regards as stress-tolerant (see Table 1).

An attempt to connect Fig. 2b to broad vegetational patterns thus requires that two questions be answered. First, the impact of grazing on stature must be analyzed. Second, one must find out when grazing will favor plants that Grime regards as stress tolerators—with slow growth rate and a large quantity of resources allocated to the production of secondary chemicals—and when will graminoid-type plants with low defensive investment and an ability to recover rapidly be favored. In both issues, my approach is to apply the general theory of Evolutionarily Stable Strategies (ESS; see Maynard Smith, 1974) and to turn attention to patterns in nature only after predictions have been derived from first principles.

III. Grazing and the ESS Foliage Height of Plants

The main reason for plants to grow tall is competition for light, which makes it advantageous to divert resources from leaf surfaces to erect stems. If there is enough competition for light to favor any vertical growth at all, woody plants should normally have an advantage over herbs and grasses (see above). Conversely, if there is no selective pressure for tall stature in herbs, there is hardly any point in producing erect, woody stems. Thus, an analysis of the ESS foliage height in herbs also tells a good deal about the relative advantages of woody and herbaceous habits.

In a purely competitive situation, the foliage height ESS of herbs represents a balance between two factors. On one hand, it is always advantageous to be slightly taller than the neighbors. On the other hand,

the taller the herb, the greater fraction of available resources must be allocated to support structures. This balance summarized below, has been analyzed by Givnish (1982) in an ingenious way. Let $f(h)$ represent the amount of resources available to leaves as a function of foliage height and $g(\Delta h)$ be the photosynthetic rate per unit of leaf area as a function of the difference between the foliage height of the plant and the average foliage height in the vegetation. If the function $f(h)$ and the value and first derivative of $g(\Delta h)$ at $\Delta h = 0$ are known, the ESS foliage height can be found as the value of h that satisfies the equation

$$-f'(h)/f(h) = g'(0)/g(0) \quad (1)$$

The reason is that the photosynthetic performance of a plant depends on the product $f(h)g(\Delta h)$. A product increases as long as the relative decrease rate of one factor [$f(h)$] is slower than the relative increase rate of the other factor [$g(\Delta h)$]. The ratio of the first derivative to the function represents these relative rates; the minus sign on the left is needed because we compare a decrease to an increase [i.e., $f'(h) < 0$].

Givnish (1982) argued that $g(\Delta h)$ is a sigmoid function, steepest at $h = 0$. The denser the vegetation, the further down is the lower asymptote of the $g(\Delta h)$ curve which represents the net photosynthetic rate of below-canopy leaves. With regard to the $f(h)$ function, Givnish was a bit inconsistent. He assumed linearly decreasing $f(h)$, which was compatible with his data (where scatter prevents firm conclusions about the form of $f(h)$ from being drawn). However, his equations showed that $f(h)$ must be strongly upward convex, as h appears in fourth power (Givnish, 1982; Eq. A9), and also common sense says this. Because of mechanical constraints, height increments of a given magnitude must require greater investments of raw materials if the shoot is tall to begin with. This point has an important corollary: even if the plant cover is sparse and, consequently, $g'(0)/g(0)$ has a low value, prostrateness will not easily be an ESS for herbs in a purely competitive situation, because of the low marginal costs of raising leaves slightly above the ground (see Fig. 3). As an erect, woody stem in a few years lifts leaves higher up than a herbaceous stem produced by corresponding annual investment, we can conclude that undisturbed competition favors erect, woody plants even in habitats where competition for light is only a minor factor and optimally allocating plants invest most of their resources in roots.

The model of Givnish (1982) is based on the tacit assumption that tissue losses either do not occur or they are independent of shoot height. In grazed systems, these premises are unrealistic. Leaf tissues have some positive mortality rate (m) due to grazing, and this rate is a function of foliage height: pieces of foliage which are so close to the ground that it is difficult for the grazer to get them will have a much lower mortality rate

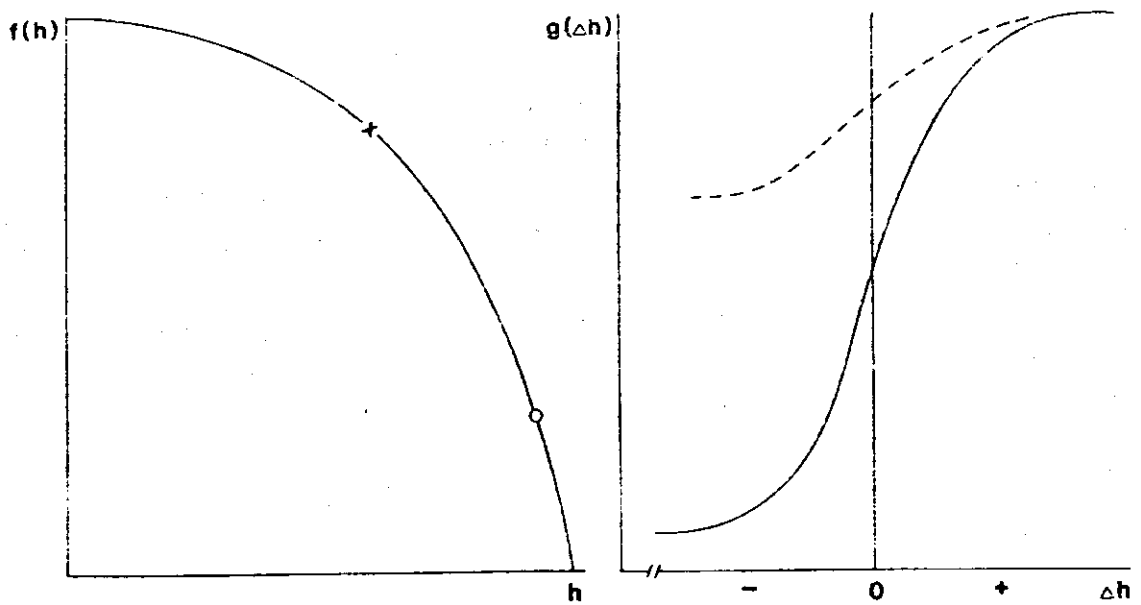


Figure 3 Amount of resources available for foliage (f) as a function of foliage height (h) and photosynthetic rate per unit of foliage (g) as a function of the difference (Δh) between the foliage height of the plant and the average foliage height of the vegetation. Dashed line, sparse vegetation; solid line, dense vegetation. Corresponding ESS foliage heights are marked by \times and \circ , respectively.

than more elevated pieces of foliage. The simplest plausible form for $m(h)$ is a sigmoidally increasing function of h (Fig. 4). However, other forms are also possible. Small grazers especially can have problems with handling tall leaves of herbaceous plants. In that case, $m(h)$ will be hump-backed, with a negative slope at high values of h .

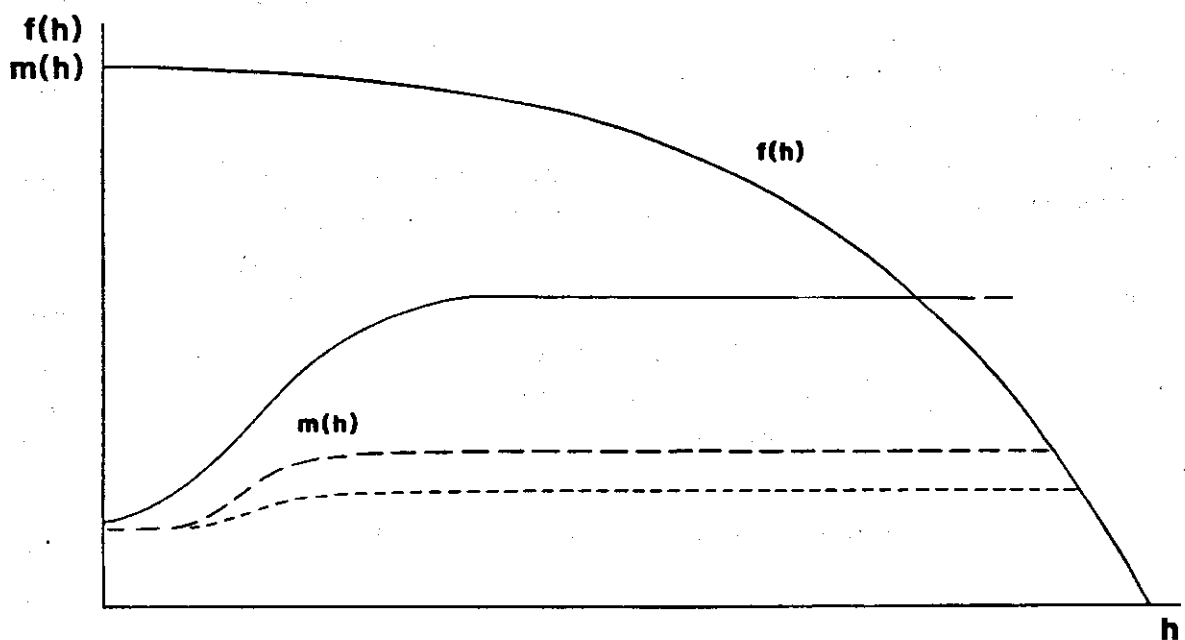


Figure 4 Amount of resources available to foliage (f) and rate of tissue loss (m) as functions of foliage height. Solid m curve, intense grazing; dashed line, moderate grazing; dotted line, light grazing.

With a constant instantaneous rate of grazing, leaf tissues produced at the time $t = 0$ disappear in a negative exponential manner, with the amount of remaining leaf tissues (L) after time t being

$$L = e^{-mt} \tag{2}$$

The contribution of leaves produced at $t = 0$ to the energy balance of the plant can be obtained by multiplying the instantaneous contribution rate, i.e., $f(h)g(\Delta h)$, by the area between Eq. (2) and the time axis, which represents the effective lifetime (T) of the leaves. Integrating Eq. (2) from $t = 0$ to $t = \infty$ yields the simple result that $T = 1/m(h)$. By noting $f(h)/m(h) = z(h)$, we can directly apply the results of Givnish (1982): a given foliage height is an ESS if it satisfies the equation

$$-z'(h)/z(h) = g'(0)/g(0) \tag{3}$$

There are two ways to proceed further: to construct the $z(h)$ curve dividing $f(h)$ by $m(h)$ point by point and to perform a graphical analysis comparable to Fig. 2. The result (Fig. 5) shows that, in most cases, weak or moderate grazing pressure has no impact on the foliage height ESS. When grazing pressure becomes high enough to have any impact at all, the impact is drastic at once: the ESS foliage height “jumps” from high to very low, and is thereafter only little affected by further increases in the intensity of grazing. The grazing pressure which is intense enough to cause this shift depends on the density of the vegetation, but the abrupt

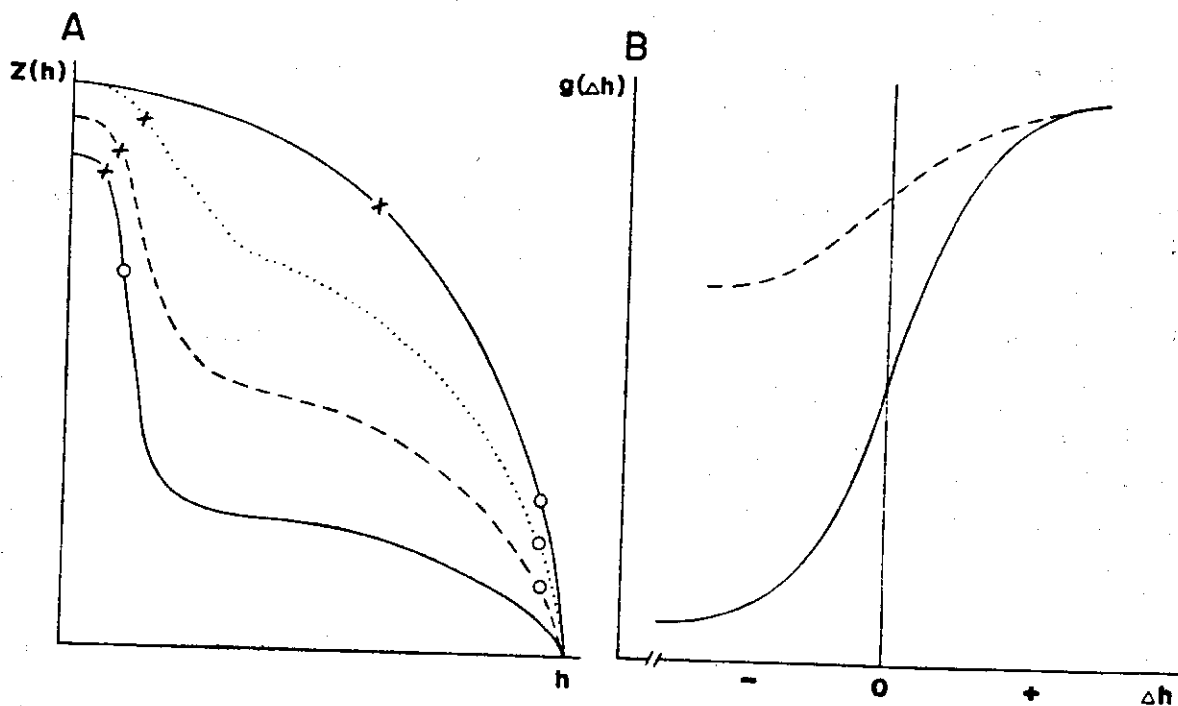


Figure 5 An ESS analysis corresponding to Fig. 3, but with $f(h)$ replaced by $z(h)$, obtained by dividing $f(h)$ for the appropriate $m(h)$ values. (A) solid line (top), $z(h)$ for no grazing [= $f(h)$]; dotted line, light grazing; dashed line, moderate grazing; solid line (bottom), intense grazing. For each $z(h)$ curve, ESS heights for sparse and dense vegetation have been marked by \times and \circ as in Fig. 1. (B) As described in Fig. 3.

nature of the shift does not. A hump-backed $m(h)$ curve would further aggravate the abruptness of this shift. In that case, the impact of weak grazing pressure is to favor plants that are taller than the foliage height ESS for the purely competitive situation provided that this ESS is greater than the foliage height for the hump of the $m(h)$ curve; sufficiently high grazing pressure again favors prostrate plants.

An analytical approach clarifies the situation. Substituting $z(h) = f(h)/m(h)$ and doing some rearrangements yields

$$-f'(h)/f(h) + m'(h)/m(h) = g'(0)/(g(0)) \quad (4)$$

If the $m(h)$ function is sigmoid, $m'(h) \approx 0$ for a wide range of h values (Fig. 4), including the neighborhood of the purely competitive ESS for practically all conceivable $g(\Delta h)$ curves (see Fig. 2). In the neighborhood of the competitive ESS, Eq. (4) thus degenerates to Eq. (1). If the $m(h)$ curve is hump-backed and the vegetation is at least moderately dense, $m'(h)$ is negative in the neighborhood of the competitive ESS, thus low grazing intensities will indeed increase foliage height ESS. Whether the $m(h)$ function is sigmoid or hump-backed, the foliage height ESS will shift to a very low value when the rising part of the $m(h)$ curve becomes steep enough to satisfy Eq. (4).

The above analysis presupposes that all plants have the same photosynthetic response to changed light intensities. Under this premise, foliage heights below the ESS level are always suboptimal and probably even lethal if the vegetation is dense. However, a pronounced shade plant could readily invade plant communities consisting of tall plants. For an invading shade plant, even weak grazing pressure would represent strong selection for low stature. Being well below the average foliage height of the dominants, a shade plant is in a situation where $g'(\Delta h)/g(\Delta h)$ is very small; consequently, fairly low maximum values of $m'(h)/m(h)$ can suffice to make $m'(h)/m(h)$ alone greater than $g'(\Delta h)/g(\Delta h)$. Plants with an intermediate shoot height between the canopy and the handling threshold of grazers get the worst of both worlds by being too low to compete for light but yet too tall to escape grazing.

The all-or-none impact of grazing on the foliage height ESS gets especially interesting in systems with substantial fluctuations in the intensity of grazing which, indeed, is more the rule than the exception in areas grazed by mobile herds of ungulates (McNaughton, 1979, 1985), fluctuating populations of microtine rodents (Fuller *et al.*, 1977; Černjavskij and Tkačev, 1982; Andersson and Jonasson, 1986) or both (Batzli *et al.*, 1980). Even if the average grazing pressure were high enough to favor prostrate plants, they might go extinct in years of low grazing intensity. Conversely, even if erect woody plants were favored on the average, they might never manage to reach safe size before becoming grazed and

trampled by an ungulate herd or bark-gnawed to death by rodents. As long-term fitness in a fluctuating environment depends on the product of annual fitnesses (Levins, 1968; Schaffer, 1974), it is imperative for a plant to hedge its bet and to make sure that its fitness in the worst year will not be zero (see Stearns, 1976). Typical basal-leaved graminoids can be regarded as masters of the trade of coping with fluctuating intensity of grazing. They can flexibly increase leaf height if grazers remain absent and competition for light becomes intense. Yet, they hold the most valuable tissues out of the reach of grazers. After grazing they can first produce leaves that lie flat on the ground. Later on, these pieces of foliage can be lifted up by producing vertical leaf segments which start to function like petioles.

IV. Grazing and the ESS Level of Plant Defenses

Natural selection does not reward a plant for damaging or killing grazers but for directing herbivory from oneself to one's neighbors (Moran and Hamilton, 1980). Thus, the level of defense that represents an ESS can be studied with the same method that has above been applied to the study of foliage height ESS. Assuming that a plant has a fixed amount of reduced carbon available and an allocation pattern between different plant organs which is independent of the allocation of carbon to defense, the amount of photosynthetically active leaf tissues (f) that a plant can construct is a decreasing function of their concentration of defensive compounds (d). As structural tissues and defensive compounds are two alternative ways of allocating reduced carbon, the relation can be specified as $f(d) = 1/(d + 1)$ (see Fagerström, 1989). The rate of net energy accumulation, $p(d)$, must be closely related to $f(d)$. If plants did not respire and if reduced carbon were a limiting resource for the construction of photosynthetically active tissues, $p(d)$ would be directly proportional to $f(d)$, so that the two would be interchangeable with appropriate scaling of units. However, respiration will inevitably consume some reduced carbon. A simple way to model this is to assume that respiratory costs are independent of the allocation between productive tissues and defensive compounds, in which case, carbon-limitation implies

$$p(d) = f(d) - c = 1/(1 + d) - c \quad (5)$$

where c stands for respiratory costs. The assumption of constancy can indeed be criticized, but the deduction given below is quite robust with respect to deviations from a constant c . The main thing is that c is positive for all values of d , as it indeed has to be.

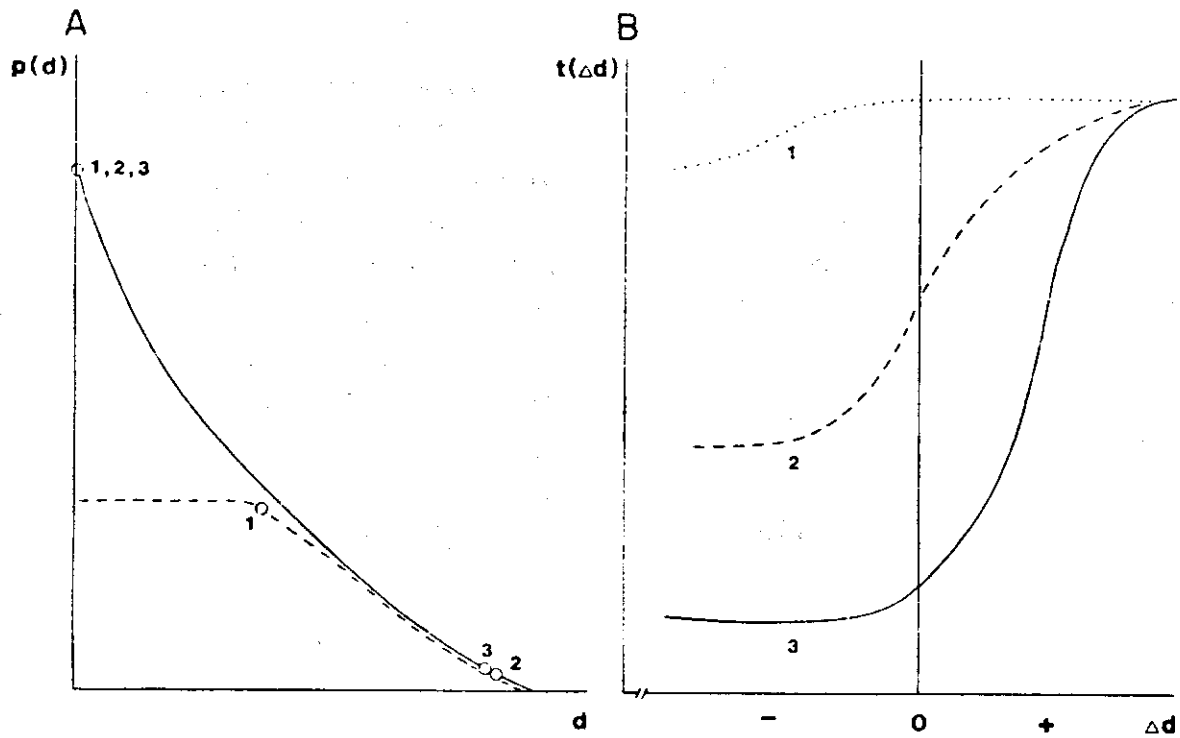


Figure 6 (A) Amount of photosynthetic parenchyma (p) as a function of the level of defense (d) in a nutrient-rich (solid line) and nutrient-poor (dashed line) habitat. (B) The effective production time of the leaves (t) as a function of the difference between the ambient level of defense and the level of defense in the plant (Δd) for lightly grazed (1, dotted line), moderately grazed (2, dashed line), and intensely grazed (3, solid line) habitat. The corresponding ESS levels of defense are marked by circles that are numbered as the $t(\Delta d)$ curves.

Equation (5) generates a downward convex $p(d)$ curve (Fig. 6, solid line); which should be realistic for nutrient-rich sites. In nutrient-poor sites, the values for $p(d)$ for low levels of d will be less than predicted by Eq. (5): even if plants do not allocate anything to defense, nutrient shortage prevents them from using all available reduced carbon for making photosynthetically active leaf tissues. Consequently, the leftmost part of the $p(d)$ curve will be almost flat (see Tuomi *et al.*, 1984), and Eq. (5) becomes relevant first when all surplus carbon has been channeled to defensive compounds. The resulting $p(d)$ curve (Fig. 6, dashed line) will thus be sigmoidally decreasing.

The rate of tissue loss (m), in turn, will be a sigmoidally decreasing function of the difference between the level of defense in the plant and the average level of defense in the vegetation [$m(\Delta d)$]: plants that are much less palatable than average are rejected, those which are more palatable are preferred. Small differences in the level of defense matter most for plants which are at the limit of being included in the diet. The rate of tissue loss for rejected plants will be low regardless of the intensity of grazing, whereas the loss rate of preferred plants must be an increasing function of the intensity of grazing. According to the theory of opti-

mal foraging (Krebs, 1978), the level of defense where m is maximally sensitive to small changes in Δd depends on the availability of high-quality forage. In lightly grazed environments where high-quality items (e.g., reproductive organs; see Tast and Kalela, 1971) abound, only the best will be good enough. When the grazing pressure is intense and there is acute shortage of subsistence food, only the worst food items will be rejected (see Thomas and Edmonds, 1983). Consequently, increasing grazing pressure will both increase the steepness of the $m(\Delta d)$ curve by raising its upper asymptote and shift the steepest part rightward (from $\Delta d < 0$ to $\Delta d > 0$). With a rate of tissue mortality m , the effective production time (t) of the foliage will be $1/m$ (see previous section). As the inverse of a sigmoidally decreasing function, $t(\Delta d)$ will be a sigmoidally increasing one (Fig. 6).

The contribution of the leaves to the energy balance of the plant is their production rate, $p(d)$, times their effective lifetime, $t(\Delta d)$. Thus, the results of Givnish (1982) can be directly applied. The level of defense is an ESS if it satisfies

$$-p'(d)/p(d) = t'(0)/t(0) \quad (6)$$

For situations where $p(d)$ and $f(d)$ curves match (i.e., plants are carbon-limited), we can substitute $p(d) = 1/(d + 1) - c$. After rearrangements, this gives

$$1/[1 - c + (1 - 2c)d - cd^2] = t'(0)/t(0) \quad (7)$$

Three predictions immediately emerge from Fig. 6 and Eq. (7). First, zero level of carbon-based chemical defense is practically never optimal in nutrient-poor habitats. As long as mineral nutrients limit the construction of photosynthetically active leaf tissues, defense is so cheap that even slight grazing pressure favors increasing levels of defense, up to the point where reduced carbon becomes a limiting resource. Second, if grazing will ever favor allocation of "costly" carbon to defense, moderate intensities will do it already. At high grazing pressures, $t'(0)$ starts to be a decreasing function of grazing intensity, because grazers cannot be choosy. Although this is to some extent compensated by decreasing $t(0)$, the result is still that $t'(0)/t(0)$ reaches a maximum at moderate grazing intensity. Third, provided that respiratory costs are not overwhelmingly high ($c < 0.5$), the marginal costs of defense are a decreasing function of d for low and moderate levels of defense. Consequently, it is unlikely that an ESS could be found at low allocations of costly carbon to defense. If the left-hand side of Eq. (7) is smaller than the right-hand side at $d = 0$ or when all "surplus carbon" has become allocated to defense (i.e., at the lowest value of d where Eq. (7) becomes relevant), there will be runaway selection to higher and higher levels of defense, until the second-order

term in the denominator of the left-hand expression starts to dominate. This has an interesting corollary. Because nutrient limitation pushes the region of applicability of Eq. (7) rightward where marginal costs of allocating costly carbon to defense are not as forbiddingly high as at $d = 0$, moderate nutrient shortage increases the likelihood of runaway selection to high levels of defense. However, this does not apply to extreme levels of nutrient shortage: then the plateau of the $p(d)$ curve extends to high values of d and, consequently, the second-order term dominates immediately when Eq. (7) becomes relevant, making runaway selection impossible.

In less technical terms, the above predictions can be summarized as follows. Allocation of surplus carbon to defense is part of a defense ESS almost regardless of the intensity of grazing. In relatively nutrient-poor habitats, it is likely that moderate intensities of grazing shift the ESS to high levels of carbon-based chemical defense, and it is possible that extremely high grazing intensity shifts the ESS back to the use of surplus carbon only. In nutrient-rich habitats, the ESS level of purely carbon-based chemical defense is likely to remain zero regardless of the intensity of grazing. Instead, plants will opt for rapid recovery or forms of defense which yield better marginal gains at $d = 0$ (nitrogen-containing toxins, spines). These predictions are not especially novel: rather similar ideas have been deduced from observations by, for example, Bryant *et al.* (1983), Coley *et al.* (1985), and van der Meijden *et al.* (1988). However, the model shows that these ideas follow from first principles, and that reference to the somewhat confusing concept of compensatory growth (see Belsky, 1986) is not needed. The essential issue is the relation between marginal gains and marginal costs of defense, not the direct reaction of plants to grazing.

V. Graminoid, Ericoid, and *Dryas* Strategies

From Sections III and IV we can conclude that, depending on conditions, grazing will favor one out of three broad adaptational syndromes. If the habitat is nutrient-rich and grazing is both intense and frequent, prostrate plants will be favored. These should have morphological and reproductive features which improve grazing tolerance (small, narrow, or finely lobed leaves, either chiefly vegetative reproduction or many inflorescences, each with a small number of small seeds which ripen quickly), and they should have structures which decrease their attractiveness to grazers (hairs, thick cuticle). However, there should not be accumulations of defensive chemicals above the level of carbon surplus. This combination of characteristics is found in many short grasses, but also in

many arctic–alpine dicots. To emphasize that this syndrome is by no means restricted to monocots, I have chosen to call it the *Dryas* strategy, after mountain avens. In nutrient-poor habitats, constant and relatively high intensity of grazing will favor plants which differ from the *Dryas* strategy by having high levels of strictly carbon-based chemical defense. This combination of traits should usually go together with evergreen leaves, which make it more easy to achieve high concentrations of defensive chemicals with a feasible annual investment. Thus, the syndrome becomes practically identical to what Grime (1977, 1979) called the stress-tolerant strategy. I call the syndrome the ericoid strategy after the dicot group for which this combination of traits is especially typical.

Fluctuating intensity of grazing will favor plants that share most characteristics of the *Dryas* strategy but differ from it by having a capacity for rapid vertical growth by means of basal intercalary meristems or an apical bud at ground level. I call this combination of traits the graminoid strategy, as the majority of plants with these characteristics are graminoids (members of families Poaceae, Cyperaceae, and Juncaceae). However, dicots with rosettes of erect, finely lobed leaves (e.g., *Geum rossii* of Rocky Mountains) represent this strategy, whereas tall grasses, tussock grasses, and obligately prostrate graminoids do not.

Data on global and continental vegetation patterns (Walter, 1964, 1968; Knapp, 1965; Ellenberg, 1978) and on the vegetation of well-studied mountain, tundra, and steppe–desert areas (Nordhagen, 1927, 1943; Böcher, 1933, 1954; Kalliola, 1939; Braun-Blanquet, 1948–1950; Whittaker and Niering, 1965; Bliss, 1975; Komarková, 1978; Olsvig-Whittaker *et al.*, 1983) suggest that moderately barren ecosystems are consistently dominated by one of the three variants of the grazing-tolerant strategy. The *Dryas* strategy is especially typical for dry but at least moderately nutrient-rich tundras. The ericoid strategy is characteristic for nutrient-poor oceanic tundras (continuously chilly weather, strongly leached soils) and arid regions with Mediterranean-type climate, where favorable thermal and moisture conditions do not coincide and soils get leached by winter rains. There are some peculiar types of grasslands in habitats which are even more nutrient-poor than the areas where typical representatives of the ericoid strategy prevail [e.g., the tussock tundra of nonglaciated parts of Alaska and northern USSR (see Wein and Bliss, 1974; Chapin and Shaver, 1985) and grasslands in interior Australia (see Winkworth, 1967)]. However, these formations are dominated by tussock graminoids which have little to do with the graminoid strategy as defined above but seem rather to represent cases where high levels of defense arise automatically, as a consequence of the extreme nutrient shortage of the habitat. Genuine representatives of the graminoid strategy—herbaceous plants with basal growth points and narrow or finely

lobed leaves—prevail in at least moderately nutrient-rich arid, alpine, and arctic habitats with strongly pulsatory primary production which inevitably makes grazing intermittent.

If the vegetational patterns of tundra, steppe, and semidesert environments were caused by changes in environmental constraints on classical competition, the vegetation of extremely barren environments should be either basically similar or represent a continuation of the same trend. However, extreme deserts are dominated by tall shrubs or low trees and by annuals with relatively “mesomorphic” looks (Walter, 1964, 1968). Extreme high-altitude barrens of temperate and boreal mountains are dominated by mesomorphic perennial herbs like *Ranunculus glacialis* (see Table 1). The dominant of polar deserts, *Papaver radicum*, has basically similar morphology, and the distinctive feature of polar deserts (as opposed to semideserts) is the rarity of graminoids and trailing dicots (Bliss *et al.*, 1984). On tropical mountains, rosette trees represent the ultimate high-alpine life form: they occur above alpine grasslands (Troll, 1941; Smith and Young, 1987) and seem to be limited downward by herbivory (Kofford, 1957; Mulkey *et al.*, 1984).

Further evidence can be obtained from herbivore enclosure experiments. A large-scale experiment with temperate steppe vegetation was inadvertently performed when a remnant of the Ukrainian steppe was protected against grazers. The immediate result was an expansion of shrubs and tall grasses at the cost of the original dominants (*Stipa*, bunch grasses). Later on, the area was invaded by Scots pines (Walter, 1968, p. 602). A controlled long-term enclosure experiment has been run on the lowland tundra at Barrow, Alaska, since the 1950s. The general result has been a pronounced decline in the abundance of typical tundra graminoids. Tall grasses have flourished in favorable habitats and a gradual build-up of moss banks has taken place in less favorable ones (Batzli *et al.*, 1980). The enclosure experiments in arid plains of the Serengeti, Tanzania, have resulted in an even quicker and more complete replacement of short grasses by tall grasses (McNaughton, 1979). In my tundra enclosures on Finnmarksvidda, Norwegian Lapland, changes in plant cover have been equally dramatical (Oksanen, 1988). During the first 3 years, there was a pronounced expansion of the blueberry (*Vaccinium myrtillus*) on lichen–moss tundra and almost total disappearance of mosses (Oksanen and Oksanen, 1981). In the other two habitats (snowbed and low herb meadow), changes proceeded at a more uneven pace. After 8 years, however, the results were clear in all habitats: the plants that were closest to the *Dryas* strategy were suffering heavy losses, whereas the tallest and most broad-leaved ones were favored (Fig. 7). Age structure differences between blueberry twigs in enclosures and on open plots (Fig. 8) support the interpretation that

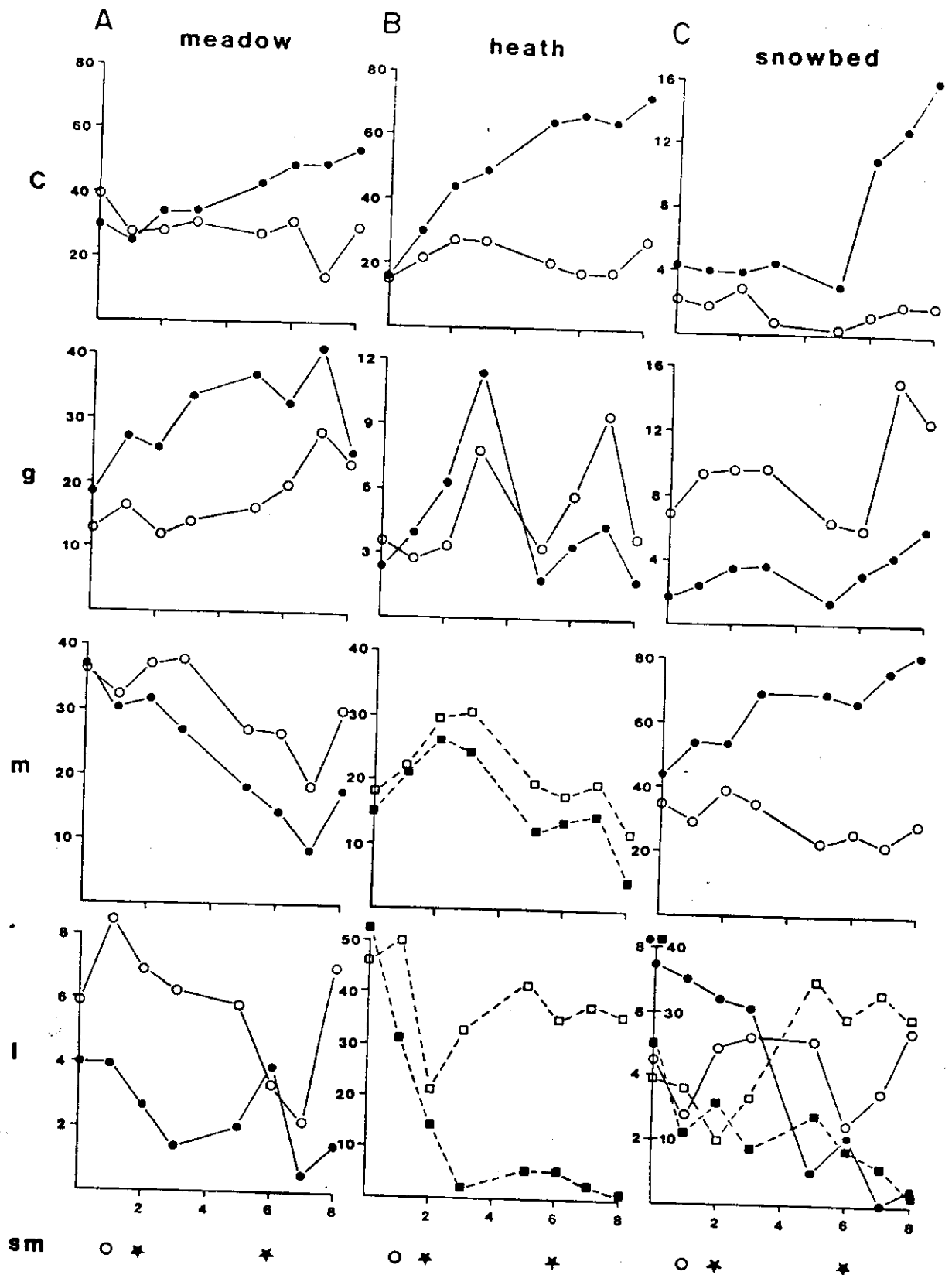


Figure 7 Changes in the relative abundance of pronounced competitors (c), typical graminoids (g), medium-sized plants (m), and low plants (l) in exclusions (solid symbols) and on open plots (open symbols) in the following different tundra habitats: (A) shrubby meadow (c are broad-leaved shrubs and dwarf shrubs and tall grasses, m are herbs with foliage heights from 5 to 15 cm, l are smaller herbs), (B) lichen-moss heath (c are broad-leaved shrubs and dwarf shrubs, m are fruticose lichens, l are low mosses and hepatics), and (C) dry snowbed (c are the tallest herbs and grasses, m are dwarf willows, goldenrods, and dandelions, l are prostrate herbs, low mosses, and hepatics). Squares and dashed lines refer to cryptogams, dots/circles and entire lines to vascular plants.

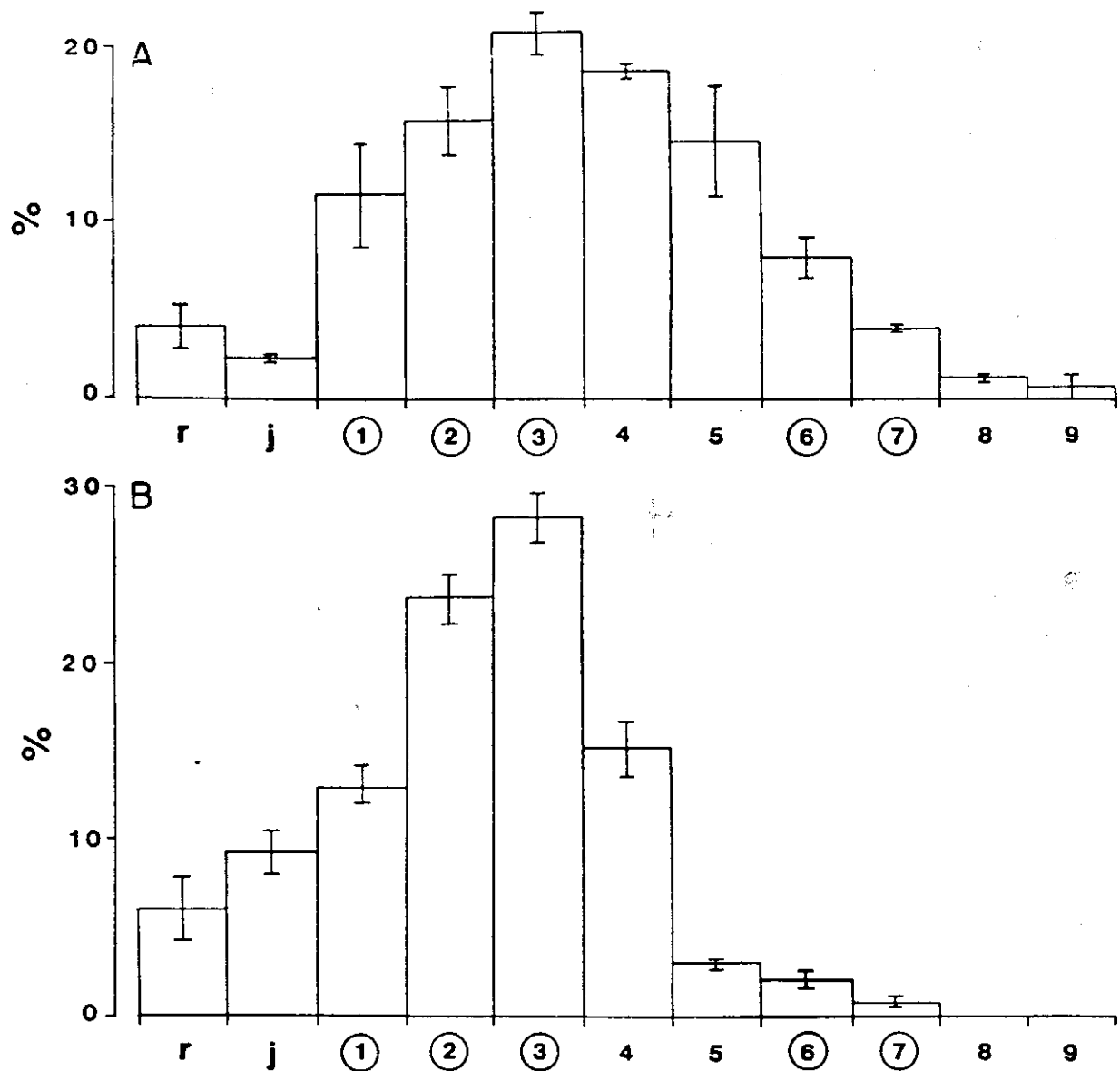


Figure 8 Age structures of (A) enclosure and (B) open plot populations of *Vaccinium myrtillus* on the lichen–moss heath. r is a horizontal runner without an above-ground part; j is a juvenile shoot without overwintered above-ground parts; numbers 1 through 9 refer to the number of overwintered annual above-ground segments, which are circled if the oldest segment grew up under high or moderate vole density. Vertical bars refer to standard errors.

differences in survival rates during vole peaks account for the observed vegetational changes.

VI. Concluding Remarks

My chapter has focused on presenting a view of steppes, arctic–alpine tundras, and tropical alpine grasslands as the rangelands of the nature, where grazing and grazer-mediated indirect interactions (apparent competition; see Holt, 1977) are overridingly important for structuring plant communities. This must, however, be seen in proper perspective. The

model of Oksanen *et al.* (1981) implies that natural herbivory is *not* important in ecosystems with primary productivity greater than $700 \text{ g/m}^2/\text{yr}$ dry matter, except for such parts of the vegetation which receive very little resources and disproportionately much herbivory, and is even less important in extremely barren habitats such as polar deserts, alpine boulderfields, and arid deserts. When it comes to explaining the structure of these plant communities which cover most of our globe, I am a firm advocate of the Cajander–Tilman approach. In the present chapter, I have focused on plant communities and vegetation processes which I regard as exceptional in a global perspective, because that is where I have found new challenges and unexplained patterns.

VII. Summary

A model of population dynamics in the grazing chain predicts that the importance of natural herbivory is small in productive habitats because predators prevent the persistence of excessively high grazer densities, and in extremely barren areas, where grazers only occur at transients. In areas with intermediate productivity, natural grazing pressure is predicted to be intense, because moderate herbivore densities are sufficient to consume the relatively meager production of the vegetation. Consequently, classical resource competition should be an overridingly important vegetation-structuring process in productive and in extremely barren areas, whereas, in areas with intermediate primary productivity, i.e., arctic and alpine tundras, steppes, arid savannas, and the grassland belts of tropical mountains, grazing and grazer-mediated indirect interactions between plants should play a correspondingly central role. Traits of morphology and life history in dominating plants of these habitats fit the idea that the native grazers play a central role in structuring their vegetation. This hypothesis is also supported by the results of experimental exclusions of grazers and by the aberrant vegetational patterns of grazer-free islands.

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In the fieldwork on the tundra, the help of Tarja Oksanen and Aslak Lukkari has been indispensable. Section IV on plant defenses was substantially revised in response to the comments of Torbjörn Fagerström, who showed that marginal cost of defense can be a decreasing function of d , and David Tilman, who pointed out the need to incorporate respiratory costs in the model. Useful comments were also provided by Don Alstad and two anonymous referees. The work has been supported by a grant from NFR (Swedish Council For Natural Sciences).

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