

Natural grazing as a factor shaping out barren landscapes

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The rarity of undisturbed vegetation in barren areas

Ellenberg (1978) made a strong case for the idea that, in the absence of grazing and other disturbance, a gradient of increasing environmental stress should be characterized by forests merging into scrublands with successively lower stature, with prostrate plants prevailing only in environments without a continuous plant cover. If the vegetation is not extremely sparse and disturbance is not involved, competition should favour plants with elevated foliage (Givnish, 1982), and woody plants with their ability to accumulate height increments from year to year, should normally have an advantage over herbaceous plants. Ellenberg argued that any area where scattered trees or shrubs grow, but do not form a closed forest or scrubland, is either directly disturbed or a subclimax community, created and maintained by domesticated grazers.

Curiously, it is quite hard to find gradients of increasing drought or decreasing temperature where the vegetational patterns match Ellenberg's idea of an undisturbed vegetational gradient. Such clines exist in Hawaii where windward slope rainforests grade to arid leeward side scrublands without any distinct changes in the dominating life form. (Even the dominating species remains the same, see Knapp, 1965; Mueller-Dombois, 1987). Also rainforests that change to barren alpine areas in Hawaii are characterized by a gradual reduction in tree stature and, at the highest, by a replacement of regular trees with rosette trees (a life form which is typical of extreme alpine environments in the tropics). Rather similar gradients are also encountered in New Zealand, although an aberrant form of grass (extremely robust, with perennial pedestals of 1–2 m in height) plays a large role in the alpine vegetation of the leeward mountain slopes and was apparently dominating in some parts of the arid basins, too, even before the arrival of man (Cockayne, 1958; Burrell, 1965; Walter, 1968). Besides Hawaii and some other oceanic islands which never had native grazing vertebrates (e.g. Gough, *see* Wace, 1961) and New Zealand where this ecological group was only represented by a few species of flightless birds, almost all gradients of decreasing temperature or moisture are similar to the pattern which Ellenberg regarded as a consequence of grazing or other disturbance: forests become sparse and, while groups of trees, individual trees and erect shrubs still are able to grow and survive, the land becomes dominated by basal-leaved grasses, prostrate dicots, mosses, lichens or some mixture of these life forms (*see* e.g. Norin, 1960; Walter, 1964, 1968).

A possible solution to the enigma is that Ellenberg was right in his reconstruction of grazing-free vegetational gradients but his tacit assumption that only domesticated grazers count was erroneous. In fact, resource-limited populations of native herbivores should be even more detrimental to erect woody plants than sheep and cattle have been to sub-alpine trees and shrubs in Central Europe: while sheep and cattle spend the winter feeding on harvested hay, native grazers and browsers must find their food out of doors. As the above-ground organs of herbaceous plants have largely withered and their below-ground organs are difficult to get at (impossible if the ground is frozen), woody plants are likely to become

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utilized much more than they are in the summer (or wet season), when better forage abounds.

There are good grounds for assuming that grazing vertebrates of barren areas are indeed resource-limited. As pointed out by Fretwell (1977), the main alternative to be considered—predation—can regulate grazers at a level where ambush-type predators are barely able to break even. Data on various types of ambush predators, from lions (Schaller, 1972) to weasels (Erlinge, 1974) shows that the minimum prey density required for successful reproduction is fairly high and well above the levels observed e.g. on the dry shortgrass plains of the Serengeti (where young lions stray but have low survival, see Sinclair, 1977; Schaller, 1972) or on the tundra during non-outbreak years of small mammals (Batzli *et al.*, 1980; Oksanen & Oksanen, 1981, unpublished). The steppe and tundra vegetation seems to have so low an annual production that their carrying capacity is exceeded before the grazing populations have reached a density sufficient to make the area attractive for an ambush predator.

Grazer plant dynamics and coevolution in barren environments: a summary of theoretical viewpoints

A dynamic population model of a potential three-link grazing chain predicts that sufficient decrease in primary productivity causes a shift from three-link dynamics with predator-limited grazers and only light grazing pressure (corresponding to the perspective of Hairston *et al.*, 1960, see also Slobodkin *et al.*, 1967) to two-link dynamics, accompanied by intense natural grazing pressure (Oksanen *et al.*, 1981). With further decrease in primary production, natural grazing pressure will again gradually decrease and cease altogether in extremely barren environments where grazers cannot survive. The model predicts that both productive (three link) and extremely barren (one link) ecosystems are characterized by a linear or nearly linear relation between above-ground plant biomass and primary production, whereas the moderately unproductive (two link) ecosystems should have constant above-ground plant biomass, as grazers keep it down at their hunger threshold (Fig. 1, solid lines). A better idea of the predicted relation between primary production and natural grazing pressure can be obtained by dividing the predicted above-ground biomass by productivity: the biomass to productivity ratio will be constant in the absence of grazing, and the relative importance of grazing can be directly read from the distance from the maximal biomass to productivity ratio (Fig. 2, dotted line) to the predicted one (Fig. 2, solid line). Notice that the 'two-link' ecosystems, where intense natural grazing pressure is predicted, form a rather distinct zone, with an especially abrupt upper limit (because of overgrazing in the most productive 'two-link' ecosystems; see Noy Meir, 1975; Carpenter *et al.*, 1985). The steepness of the lower boundary is, in turn, a direct consequence of the behavior of the function $y = k/x$ when x (maximum biomass) increases and k (equilibrium biomass) remains constant.

At an early state of the development of the theory, C. C. Smith & E. Haukioja (pers. comm.) pointed out that our view of nature ignored a vast body of knowledge on chemical defense and plant-herbivore coevolution. Moreover, we tacitly assumed that those organism characteristics which are relevant for their consumers do not change in response to different levels of predation (grazing) pressure. Our critics suggested this assumption is erroneous: it seems likely that organisms living in environments where predation (grazing) is a major selective force evolve in such a way that their consumers will have a hard time capturing (or foraging on) them, and population dynamics will change accordingly. Our response was that consumers can respond by becoming better able to handle their food items, so that adaptations and counter-adaptations neutralize each other. Recent work on consumer-resource coevolution has not been sanguine to our tacit assumption of a dead arms race. The characteristics of consumers represent a trade-off between traits that are

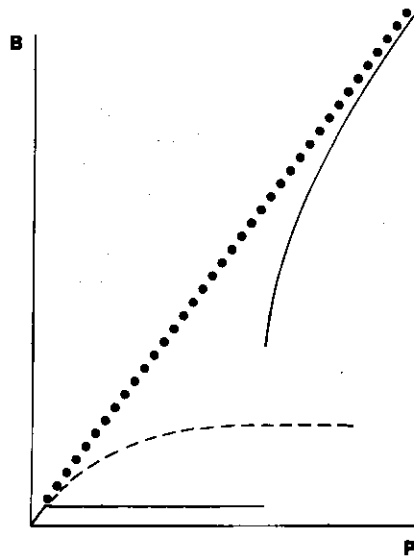


Figure 1. Relationship between potential primary productivity (P) and equilibrium above-ground plant biomass (B), assuming (1) that grazing is always unimportant (dotted line), (2) that the intensity of natural grazing varies along clines of primary productivity as predicted by Oksanen *et al.* (1981) (solid line) and (3) that the intensity of natural grazing varies as predicted by L. Oksanen (1988a) (solid line for at least moderately nutrient-rich habitats, dashed line for extremely nutrient-poor habitats).

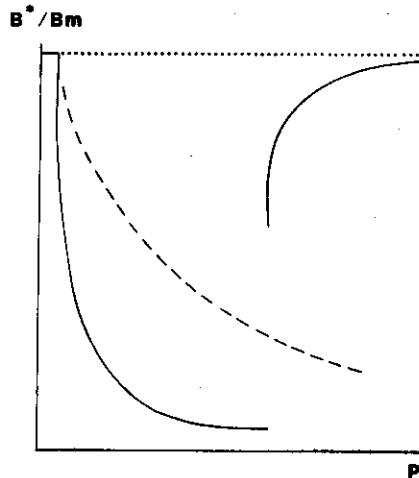


Figure 2. As Fig. 1, but the predicted biomasses under assumptions (1–3) have been divided by the predicted biomass under assumption (1) (no significant grazing pressure anywhere), to illustrate changes in the intensity of natural grazing pressure under assumptions (2) and (3).

useful for resource utilization and traits with other functions, and it is not true that this trade-off would generally change in favour of higher consumption efficiency when food becomes more difficult to get or to digest (Abrams, 1986). However, the position of our critics was not quite solid, either. Also, the assumption that whatever is bad for the consumer conveys selective advantage to the prey (forage) is flawed (Moran & Hamilton, 1980). Natural selection favours those traits which lead to a high ratio of the reproductive rate (or rate of vegetative expansion) to the rate of predation or grazing (Holt, 1977; Armstrong, 1979). At least for plants, it is probable that there is a negative correlation between features which reduce the rate of grazing and features which foster expansion. Depending on which influence is stronger, increasing grazing pressure may or may not favor plants with high levels of chemical or mechanical defense. Thus, the inclusion of an evolutionary perspective may or may not change the dynamic population predictions of Oksanen *et al.* (1981), and a rigorous analysis is needed before it is possible to tell whether or when changes in the model are necessary.

An ESS analysis of plant defense (Oksanen, 1989*a,b*) suggests that structural or quantitative chemical defense (Feeny, 1975) is unlikely to evolve in nutrient-rich environments, regardless of the intensity of grazing: the cost-gain balance for allocating small amounts of carbon to defensive compounds, when their prevailing level in the vegetation is close to zero is forbiddingly unfavorable. Qualitative defense (Feeny, 1975) only excludes herbivores that have no adequate detoxifying enzymes, while silica-based defense excludes herbivores with inappropriate teeth structure. However, neither form can be expected to have a major impact upon population dynamics of grazers with appropriate adaptations. In nutrient-poor habitats, moderate levels of carbon-based defense cost very little, because the construction of foliage is limited by shortage of nutrients. When this 'free' level of defense is high enough, it becomes advantageous to allocate even 'costly' carbon to defense. Once this is the case, there will be runaway selection to higher and higher defensive commitments, until cost factors other than sheer loss of reduced carbon (e.g. autotoxicity) start to count (L. Oksanen, 1989*a,b*). Basically, the reason for this runaway process is that allocation of a given amount of carbon from construction of tissues to defense increases the concentration of defensive compounds much more when the amount of structural material is low to begin with (Fagerström *et al.*, 1989).

High levels of chemical or mechanical defense will push the herbivore isocline to the region of relatively high plant density, as the herbivores must either be very selective feeders, focusing on the most palatable plant organs, or must resort to energetically costly methods of dealing with defensive substances (such as maintaining high pH in the digestive tract which prevents tannins from coagulating amino acids, *see* Berenbaum, 1980). Consequently, extremely nutrient-poor areas with low primary productivity should be characterized by much higher levels of plant biomass (Fig. 1, dashed line), lower grazing pressure (Fig. 2, dashed line), lower densities of herbivores than predicted by Oksanen *et al.* (1981), and the dominating plants should be extremely unpalatable (L. Oksanen, 1988*a,b*). Moreover, the transition from three- to two-link dynamic structure should take place at higher levels of primary productivity than predicted by Oksanen *et al.* (1981), and there is a distinct possibility of two alternative stable states in the vicinity of the critical productivity level.

Another essential limitation of the model of Oksanen *et al.* (1981) is that it ignores well-known attributes of landscapes. The model assumes that a habitat with a given primary productivity covers such vast areas that movements of herbivores and carnivores between habitats with different productivities do not influence local population dynamics. But arid and sub-arid landscapes are usually quite heterogeneous: the local primary productivity varies substantially in response to different soil conditions; and river beds (*wadis*) can harbor relatively luxuriant vegetation even in areas with very low precipitation (Olsvig-Whittaker *et al.*, 1983). The spatial heterogeneity of alpine environments is equally pronounced (*see* e.g. Nordhagen, 1927, 1943; Braun-Blanquet, 1948-50; Komarková, 1979; Komarková & Webber, 1978). Even on seemingly homogeneous tundra plateaux

the productivities of most luxuriant and most barren sites differ by an order of magnitude (Wielgolaski, 1975; Bliss, 1977; Bliss *et al.*, 1984; Miller, 1980). The scale of spatial variation in primary productivity is almost invariably so small that dispersal of animals from one habitat category to another must be easy. Quite frequently, the scale is small enough to imply that the home range of a single animal includes a large part of the spatial variation in primary productivity.

The impact of spatial heterogeneity upon the predictions of Oksanen *et al.* (1981) was recently analyzed by T. Oksanen (1989). Her chief results can be summarized as follows. (1) Habitat patches, small enough to form a fine-grained environment, have no independent dynamics at all; in such a habitat patchwork, the crucial variable is the average primary productivity of the home range of a herbivore. (2) When the patches are large enough to be experienced as a coarse-grained environment, then those which are much more productive than the prevailing habitat tend to have separate population dynamics, because optimal foraging concentrates consumption to the most rewarding patches, even if they are too small to include entire home ranges of consumers. (3) In coarse-grained environments where productive patches are abundant, they govern population dynamics in the whole complex. Even if consumers prefer more rewarding patches, there will be enough opportunistic foraging during transits through barren patches to change the local dynamics profoundly; in addition, territorial behavior can exclude individuals from productive patches and force them to live in the barren environment. Thus, productive habitats will subsidize the populations of barren habitats in two ways. The impact will be especially pronounced if the barren habitat provides enough resources for individual survival but not for reproduction.

In habitat complexes, the model of Oksanen *et al.* (1981) is thus applicable to the prevailing habitat type and to patches which are much more productive than the prevailing habitat, provided that the soil is not very nutrient-poor, but not to patches which are less productive than an abundant habitat type and not to nutrient-deficient habitats in general. Large expanses of extremely nutrient-poor and relatively unproductive habitat should have resource-limited herbivores, but lower densities of them than predicted by Oksanen *et al.* (1981), and the plant biomass should exceed their predictions by a wide margin. Small, barren patches should be only slightly different from their surroundings with regard to population dynamics. The relation between above-ground biomass and primary productivity in arctic and Scandinavian-alpine sites fits quite well with the predictions of Oksanen *et al.* (1981) (see Oksanen, 1983). The database does not include windblown ridges, subjected to especially severe wind erosion and leaching. (Small habitat patches with much lower productivity than in the surroundings are not represented, either.) However, the Austrian IBP-team (Larcher *et al.*, 1975) also studied nutrient-poor ridge habitats, dominated by an evergreen dwarf shrub with copious amounts of secondary chemicals. The above-ground biomasses of these relatively barren habitats (annual dry matter production 100–200 g/m²) were about 1 kg/m², which is an order of magnitude more than predicted by Oksanen *et al.* (1981).

The relevance of the landscape viewpoints of T. Oksanen (1989) can be illustrated by looking at the composition of plant and herbivore communities of different North Scandinavian habitats. In the low-alpine zone, habitats which are much more productive than prevailing tundra heaths are indeed dominated by competitive types of plants (tall herbs and willows; see Nordhagen, 1927, 1943; Kalliola, 1939; Oksanen, 1980). The herbivorous small mammal fauna of luxuriant meadow and thicket habitats is dominated by the root vole *Microtus oeconomus* (Viitala, 1977; Henttonen *et al.*, 1977; Oksanen & Oksanen, 1981) which is obviously more predation-adapted (fleet, strictly nocturnal, adapted to relatively high-quality forage; see Tast, 1966) than the dominating small mammals of heaths (the grey-sided vole, *Clethrionomys rufocanus*) and snowbeds (the Norwegian lemming, *Lemmus lemmus*). The activity of small mustelids is strongly concentrated to willow thickets, whereas tundra heaths are little utilized (Oksanen & Oksanen, 1981; T. Oksanen, unpublished). Conversely, extremely late low-alpine

snowbeds are dominated by the same vascular plants as less extreme snowbeds (dwarf willows, graminoids, prostrate herbs); they just occur in low densities. The palatable and relatively tall herbs, adapted to extreme snowbeds (the glacial buttercup, *Ranunculus glacialis*, and the mountain sorrel, *Oxyria digyna*) are restricted to higher altitudes where vast expanses of land are devoid of vegetation (Nordhagen, 1927). In the boreal zone where more habitats are relatively productive, even more barren habitat patches are dominated by erect woody plants (heather and pines); they harbor clearly predation-adapted small mammals (bank voles, *Clethrionomys glareolus*, and red voles, *C. rutilus*) and are utilized by predators with at least moderate intensity (Henttonen *et al.*, 1987; T. Oksanen, unpublished). Moreover, such patches do not seem to show any obvious devastation of the vegetation during small mammal peaks (Henttonen *et al.*, 1987), although preferred and grazing-sensitive plants seem to become damaged in relatively barren forest types (Elmqvist, 1987).

To summarize: inclusion of coevolutionary aspects changes the population dynamic predictions of Oksanen *et al.* (1981) for nutrient-poor unproductive habitats where quantitative impacts of natural grazers will be much less than predicted by Oksanen *et al.* (1981, compare solid and dashed lines in Figs 1 and 2), whereas qualitative effects upon the vegetation will be profound. Inclusion of landscape heterogeneity changes predictions for habitats which are adjacent to relatively large patches of substantially more productive habitat. For fine-grained environments, the average productivity of the home range of the grazer should determine the intensity of natural grazing pressure. Consequently, a gradient where the local primary productivity remains constant but the vegetation gets fragmented to successively smaller and smaller patches, further and further from each other, should show similar patterns in the intensity of natural grazing pressure, and in the composition of the vegetation, as gradients of decreasing local primary productivity.

Grazing by pikas (*Ochotona princeps*) and the alpine vegetation of Gore Range, Colorado: a case study on a gradient with increasing vegetational fragmentation

As test cases for the theory, gradients with increasing vegetational fragmentation are ideal, because the alternative explanation that the changes in the vegetation are caused by intensifying stress (Grime, 1979) can immediately be excluded. It is also advantageous to have a grazer with the habit of harvesting forage, because at least a part of its impact upon the vegetation can be directly measured. The vegetational gradients from timberline meadows to rock and talus in Rocky Mountains fulfil both criteria. True to their name, the Rockies are frequently devoid of continuous alpine mats (although such occur on smooth 'tails' of mountain chains such as the Niwot Ridge; see Komarková, 1979; Komarková & Webber, 1978). In many places, timberline meadows (sometimes even forests and sub-alpine meadows) give way directly to sheer rock and talus with only small patches of vegetation. The transition can be completed within a distance of a few hundred meters, and the altitudinal difference between continuous meadow and sheer rock is often negligible.

In the grazer fauna of the Rockies, two groups of small mammals seem to have a prominent role: the pocket gophers (*Geomys* spp.) which create copious disturbance in areas with continuous alpine mats (Thorn, 1982) and pikas (*Ochotona princeps*) which seem to maintain extremely stable populations in rocky areas (Southwick *et al.*, 1986), have a habit of hoarding forage for the winter (Broadbrooks, 1965; Orr, 1977), and are easy to study because of their diurnal activity and territorial behavior which includes loud vocalizations (Kawamichi, 1976; Svendsen, 1979).

Our study consisted of the following parts: (1) to search a suitable gradient where a timberline meadow got fragmented and gave way to rock and talus without substantial altitudinal difference, (2) to map the vegetational patterns in this gradient, (3) to document the mapped plant communities by means of relevés of 4 m², (4) to document the transition

from meadow-like to lawn-like vegetation by sampling eight plots of 1 m² on both sides of this transition, which were harvested in late July and above-ground biomasses of different species were determined, (5) to study the tiny fractions of vegetation deep in the rock and talus area by throwing a stick over the shoulder and recording the nearest species from its landing site (if any was in sight), its height and the moistness of the soil, until 100 records were obtained, (6) to map pika territories in the area, (7) to weigh three pika haypiles recurrently from late July to mid-August, (8) to weigh all pika haypiles that could be located in mid-August and (9) to mix each pile and to take a sample of about 30 g for determining species composition and a conversion factor from stack-dry weight to oven-dry weight (the rest of the pile was placed back to its original site).

The fieldwork was performed in July and early August 1981 in a glacial cirque in the north-eastern part of Gore Range, Colorado (between Eagle Nest Pk and Meridien Pk). This area was chosen because it was simultaneously fairly accessible (only 6 h walk from the road) and yet sufficiently far from roads and trails to minimize the risk of disturbance and loss of equipment. The cirque offered the kind of sharp gradient that we were looking for, and the plant communities in the cirque could be easily mapped from surrounding peaks.

The timberline meadows of mesic sites in the center of the cirque were very similar to those described by Hämet-Ahti (1978) from the continental parts of British Columbia. These had a much higher dominance of herbs and a lower abundance of woody plants than in corresponding vegetation of the Front Range, Colorado (Komarková, 1979), the tall herb *Erigeron peregrinus* being clearly the dominating species (Table 1). Closer to the edge of the rock and talus area, the abundance of this tall herb decreased, and *Geum rossii* (a herb with basal rosettes of finely lobed leaves) started to dominate. The change was a gradual one, and any border between *Erigeron*- and *Geum*-meadows would have been totally arbitrary. There was no dramatic change in the physiognomy of the vegetation, either: also, the plants of the *Geum*-meadows (including *G. rossii* itself) had erect leaves elevated by upright stems/petioles. About 10 m from the edge of the rock/talus, the vegetation changed abruptly. *G. rossii* remained the dominating species, but here its growth form was totally prostrate. Erect herbs and tall grasses which were still relatively abundant on the *Geum*-meadow were practically absent from this 'Geum-lawn', where the co-dominants were a herbaceous cushion plant, *Trifolium dasyphyllum*, and an evergreen one, *Silene acaulis*. The latter species is known to be very unpalatable, due to copious amounts of saponins in its leaves (Aleksandrova *et al.*, 1964). A shortgrass—*Festuca brachyphylla*—also became locally abundant, especially on unstable soils. Different variants of this lawn-like vegetation also prevailed on all vegetated patches within the rock and talus area which were large enough to be represented on the vegetation map (Fig. 3), usually with even greater dominance of *S. acaulis* than at the edge of the rock/talus. However, the smallest fragments of vegetation within the rock and talus had entirely different vegetation. In essence, they were patches of tall herb meadow, although the dominating species (mainly: *Senecio* spp, locally also *Aquilegia caerulea*) differed from the dominants of timberline meadows. Cushion plants were not encountered at all, and grasses were only recorded on unstable gravel; even there they were much less abundant than a broad-leaved rosette plant (*Claytonia megarhiza*).

The vegetational gradient of sites associated with running water was similar (Table 2). The wet timberline meadows were even more completely dominated by tall herbs than the mesic meadows. Closer to the talus, the abundance of the tallest herbs decreased, while the grass *Deschampsia caespitosa* became the dominant. Although *G. rossii* and *D. caespitosa* represent different major taxa, both have an essential morphological similarity: a combination of narrow and basally attached leaves which nevertheless can obtain fairly tall stature. Also on wet sites, a sharp border between meadows and lawn-like vegetation was found about 10 m from the edge of the rock/talus. At this border, the prostrate sedge *Carex pyrenaica* became the dominant of the community; *D. caespitosa* remained a co-dominant but changed its growth form from erect to prostrate, and taller herbs disappeared. The

Table 1. Dominance of plants on mesic meadows, lawns and on mesic-to-dry talus sites. Dominance on Geum-meadow and Geum-lawn are percentages of biomass values (standard errors in parentheses. 0.1 = from 0.15 to trace), underlining refers to significant biomass differences ($p < 0.05$, Mann-Whitney U-test) between meadow and lawn. Dominance on Erigeron-meadow are percentages of the sum of coverage-by-mean height products. Dominance on talus are percentages of frequency-by-mean height products (+ = trace). Plants are grouped on the basis of morphological attributes relevant for competitiveness and grazing-tolerance. Above-ground biomasses: Geum-meadow 38 g/m², Geum-lawn: 21 g/m²

Group/species	Erigeron meadow	Geum meadow	Geum lawn	Talus
<i>Tall and leafy herbs</i>				
Erigeron peregrinus	56	<u>1.2</u> (± 0.9)	0.0 (± 0.0)	0
Castilleja occidentalis	0	<u>6.8</u> (± 4.6)	0.7 (± 0.4)	0
Senecio fremontii	0	0.0 (± 0.0)	0.0 (± 0.0)	50
<i>Medium-sized herbs</i>				
Artemisia scopulorum	4	<u>4.2</u> (± 0.7)	0.7 (± 0.5)	0
Geum rossii	1	21.1 (± 12.8)	32.9 (± 15.3)	0
Polygonum bistortoides	1	<u>3.5</u> (± 1.0)	1.0 (± 1.0)	0
Erigeron melanocephalus	0	<u>9.9</u> (± 1.7)	3.4 (± 1.2)	0
<i>Dwarf shrubs</i>				
Vaccinium scoparium	5	18.3 (± 8.1)	6.8 (± 6.8)	0
Salix arctica	+	11.0 (± 8.9)	0.9 (± 0.6)	0
<i>Typical graminoids</i>				
Poa epipis	18	<u>5.1</u> (± 2.0)	0.1 (± 0.1)	0
Carex chalciolepis	0	1.5 (± 1.0)	3.2 (± 2.0)	3
<i>Short graminoids</i>				
Carex pyrenaica	0	4.6 (± 2.9)	0.9 (± 0.6)	3
Festuca brachyphylla	0	0.0 (± 0.0)	<u>0.5</u> (± 0.3)	5
<i>Cushion plants</i>				
Trifolium dasyphyllum	0	1.0 (± 0.7)	19.7 (± 6.4)	0
Silene acaulis	0	0.0 (± 0.0)	<u>18.1</u> (± 5.6)	0

only larger vegetation patch with wet soil in the rock and talus area was also occupied by a *C. pyrenaica*-*D. caespitosa*-lawn. However, in the records of small vegetation fragments from wet talus and rock, these two graminoids had a subordinate role only. The clear dominant was *Oxyria digyna*, a herb with roundish leaves, elevated by stem-like petioles. *Primula parryi* (another broad-leaved herb) was recorded on wet rock/talus and in wet timberline meadow but not in wet sites between these two extremes. The tallest herb in the whole material—*Angelica grayi*—was recorded on wet talus only.

The border between meadow and lawn communities coincided with the border of pika territories (Fig. 3), mapped in late July (i.e. when the haying period was just starting). Out of these territories, the two lawn communities covered, at the average, 270 m² (the rest was mainly sheer rock and stone; locally also dry ridge vegetation dominated by crustose lichens and *Dryas octopetala*). Assuming that the dry ridges had no value for summer grazing, the effective density of pikas per hectare with vegetation was thus 37, which should suffice to create quite intense grazing pressure (this density is similar to vole peaks at the taiga-tundra transition in northern Scandinavia; see Viitala, 1977; Henttonen *et al.*, 1987; Oksanen *et al.*, 1987; notice that the body weight of pikas is about five times that of grey-sided voles).

The average dry weight of pika haypiles in mid-August, after about 2 weeks of

Table 2. Dominance of plants on wet meadows and lawns and on wet talus. Calculations as in Table 1. Above-ground biomasses: Deschampsia-meadow: 38 g/m², Deschampsia-Carex lawn: 29 g/m²

Group/species	Arnica meadow	Deschampsia meadow	Deschampsia lawn	Talus
<i>Tall and leafy herbs</i>				
<i>Arnica mollis</i>	63	0.0 (±0.0)	0.0 (±0.0)	0
<i>Erigeron peregrinus</i>	14	0.8 (±0.5)	0.1 (±0.1)	0
<i>Caltha leptosepala</i>	8	8.2 (±6.1)	0.0 (±0.0)	0
<i>Primula parryi</i>	2	0.0 (±0.0)	0.0 (±0.0)	18
<i>Castilleja occidentalis</i>	0	3.6 (±1.3)	0.1 (±0.1)	0
<i>Oxyria digyna</i>	0	0.0 (±0.0)	0.1 (±0.1)	52
<i>Angelica grayi</i>	0	0.0 (±0.0)	0.0 (±0.0)	18
<i>Medium-sized herbs</i>				
<i>Ranunculus adoneus</i>	+	9.9 (±3.0)	0.3 (±0.2)	0
<i>Artemisia scopulorum</i>	0	5.1 (±2.0)	0.3 (±0.3)	0
<i>Polygonum bistortoides</i>	0	3.4 (±2.8)	0.0 (±0.0)	0
<i>Erigeron melanocephalus</i>	0	5.7 (±2.4)	8.3 (±1.9)	0
<i>Senecio dimorphophyllus</i>	0	5.3 (±1.3)	2.9 (±1.9)	0
<i>Typical graminoids</i>				
<i>Deschampsia caespitosa</i>	5	29.2 (±5.9)	15.4 (±4.8)	9
<i>Juncus drummondii</i>	1	1.6 (±0.6)	5.4 (±2.0)	0
<i>Prostrate graminoids & herbs</i>				
<i>Carex pyrenaica</i>	+	12.9 (±3.8)	59.9 (±4.9)	3
<i>Sibbaldia procumbens</i>	0	2.8 (±1.7)	2.6 (±1.7)	0

haymaking, was 1.6 kg. The rate of haymaking showed no sign of slowing down during our study period which suggests that the amount of forage harvested before the winter was of the order of 3 kg dry weight. There were profound individual differences in the amount of harvested forage: while most pikas had harvested forage worth about 1 kg dry weight, one overwintered female (no. 5 in Fig. 3) had managed to get haypiles with total dry weight of 6.8 kg. (This corresponds to the above-ground biomass of 180 m² of meadow.) The species composition of the haypiles (Tables 3 and 4) suggests that all pikas with an access to meadows also made their hay there and preferred the tallest out of the available grass and herb species (*Deschampsia caespitosa* on the wet meadow, *Castilleja occidentalis* on the mesic meadow). The pikas exploiting patches of lawn-like vegetation deep in the rock and talus area (no. 1, no. 8 and nos. 14-19) seemed to prefer grasses and woody plants and to shun cushion plants, at least while harvesting. Curiously, they had still managed to get 1.3 (± 0.2) kg hay (dry weight) which was close to the average for pikas with an access to meadows (1.7 ± 0.6 kg). Excluding the two apparently non-harvestable cushion plants, the amount of forage harvested by the pikas within the rocky area corresponded to the above-ground biomass of 100 m² *Geum*-lawn, i.e. more than a third of the total amount of forage available on their territories in late July.

The vegetational patterns from continuous timberline meadows to tiny fragments of vegetation within rock and talus recapitulated the patterns that can be observed on the Alps (Ellenberg, 1978) and on the Scandinavian mountains (Oksanen, 1980) where broad-leaved herbs dominate both on luxuriant sub-alpine sites and on the high-alpine boulder-fields, whereas alpine lawns and heaths in between are covered by prostrate plants. The current material shows that a pattern like this can be created by variations in the intensity of natural grazing pressure. The change from meadow to lawn at a distance of 10 m from rock/talus and the recurrence of tall herbs on the sheer mountain face, with northern

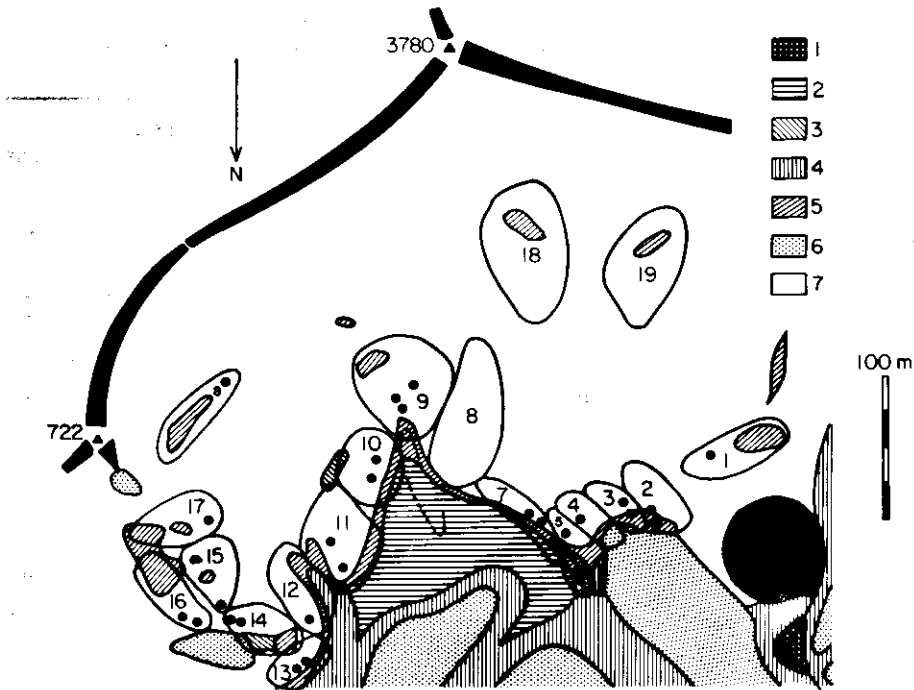


Figure 3. Distribution of different types of plant communities and pika territories in our study area. 1: marsh, 2: wet meadow, 3: wet lawn, 4: mesic meadow, 5: mesic lawn, 6: lichen-*Dryas* heath, 7: rock and talus. Ridges and peaks marked by thick lines and triangles (with altitudes in meters; altitude of the cirque floor about 3600 m). Pika territories and haypiles marked by solid lines and dots. Two territories are marked '8', because the right-hand one was vacated when the left-hand one was settled, suggesting dispersal. Territories 18 and 19 are only roughly mapped, because the area was unsafe to work in; these territories have been excluded from calculations of effective pika densities. The location of the last snowpach is marked by dashed lines; notice that it does not coincide with vegetational patterns.

exposition, would have been inexplicable without knowledge of pikas; these demonstrably exerted continuous intense grazing pressure on the lawn areas, extended their haying trips to adjacent pieces of meadow (see also Huntly *et al.*, 1986) but did not use meadow areas further away from talus and did not find it worthwhile to harvest tiny and widely spaced vegetation fragments on the mountain face.

The importance of pikas for the lawn-like vegetation near rock and talus has also been demonstrated by the enclosure experiments of Huntly (1987). When pikas were excluded from the lawn, all plants initially responded by strong population increases. After a couple of years, cushion plants started to suffer from the expansion of forbs and erect woody plants.

Pikas from our study are unprofitable herbivores for a predator to prey upon because of low densities: even at the edge between rocky and vegetated areas where pika densities were at their highest, the overall population density (including the non-vegetated parts of the territories) was only about four pikas per hectare (which corresponds to the densities reported by Southwick *et al.*, 1986). The density on the mountain face was much lower still. Besides the low density and consequent low attractiveness, pikas were indeed sheltered against some predators (especially raptors) by the physical nature of the habitat. However, the study area harbored predators well adapted to hunt in stony terrain (we observed a pine marten and a long-tailed weasel in the area). Thus, potential exploiters of a dense pika population were there. Moreover, one of the pikas (no. 7) actually disappeared after the observed visit of the long-tailed weasel. Thus, the intense grazing of alpine lawns

Table 3. *Species composition (dry weight percentages) of haypile samples for pikas utilizing Geum-meadows and lawns. Values for pikas with access to meadows are based on individuals 3, 4, 5 and 6 (piles of pikas 1 and 2 were not retrievable, piles of pikas 12 and 13 contained much material from wet meadows). Values for pikas confined to lawns are based on individuals 14, 15, 16 and 18 (pile of pika 8 not retrievable)*

Group/species	Access to meadow	Confined to lawn
<i>Tall and leafy herbs</i>		
<i>Erigeron peregrinus</i>	0.4 (± 0.2)	0.0 (± 0.0)
<i>Castilleja occidentalis</i>	12.3 (± 6.7)	0.3 (± 0.2)
<i>Pedicularis parryi</i> ¹	7.0 (± 6.0)	0.1 (± 0.1)
<i>Medium-sized herbs</i>		
<i>Artemisia scopulorum</i>	2.4 (± 1.2)	1.3 (± 0.4)
<i>Geum rossii</i>	29.0 (± 13.8)	32.8 (± 14.3)
<i>Polygonum bistortoides</i>	1.1 (± 0.7)	1.4 (± 0.4)
<i>Erigeron melanocephalus</i>	1.5 (± 0.5)	2.0 (± 0.9)
<i>Dwarf shrubs</i>		
<i>Vaccinium scoparium</i>	1.4 (± 0.9)	8.5 (± 4.2)
<i>Salix arctica</i>	4.3 (± 2.4)	14.5 (± 5.1)
<i>Salix reticulata</i> ²	0.0 (± 0.0)	5.0 (± 3.7)
<i>Dryas octopetala</i> ²	0.0 (± 0.0)	3.7 (± 3.4)
<i>Typical graminoids</i>		
<i>Poa epipis</i>	2.8 (± 2.8)	1.3 (± 1.3)
<i>Carex chalciolepis</i>	1.8 (± 0.9)	6.0 (± 1.1)
<i>Short graminoids</i>		
<i>Carex pyrenaica</i>	10.8 (± 8.8)	1.0 (± 0.4)
<i>Festuca brachyphylla</i> ³	3.3 (± 1.6)	5.4 (± 4.5)
<i>Cushion plants</i>		
<i>Trifolium dasyphyllum</i>	5.0 (± 1.8)	1.9 (± 1.0)
<i>Silene acaulis</i>	0.0 (± 0.0)	0.8 (± 0.4)
<i>Species of Deschampsia-meadow</i>		
<i>Deschampsia caespitosa</i>	10.0 (± 1.7)	4.3 (± 2.8)

¹Locally abundant in depressions.

²Abundant on *Dryas*-heaths.

³Locally abundant on loose gravel.

cannot be due to inaccessibility of pikas to predators but must rather be regarded as a consequence of the low density of pikas in the lawn-rock-talus complex.

Conclusions and Summary

The patterns of vegetational change from forests to arid steppes and arctic or alpine tundras show much better fit to Ellenberg's (1978) characterization of a grazing-dependent timberline than to his scheme for vegetational gradients of undisturbed environments. The model of Oksanen *et al.* (1981) predicts that lowering primary productivity should lead to a shift from predation-limitation to strict resource-limitation among grazing vertebrates, and to a consequent sharp increase in natural grazing pressure. A reanalysis of the argument with explicit analysis of evolutionary aspects (L. Oksanen, 1989a) suggests that, in spite of its initially purely population dynamical nature, the model of Oksanen *et*

Table 4. Species composition (dry weight percentages) of haypile samples for pikas utilizing *Deschampsia*-meadows and lawns. Based on individuals 7, 9 and 11 which had access to meadows (piles of individuals 10 not retrievable)

Group/species	
<i>Tall and leafy herbs</i>	
<i>Caitha leptosepala</i>	0.1 (± 0.1)
<i>Castilleja occidentalis</i>	0.1 (± 0.1)
<i>Medium-sized herbs</i>	
<i>Ranunculus adoneus</i>	0.1 (± 0.1)
<i>Artemisia scopulorum</i>	0.5 (± 0.5)
<i>Polygonum bistortoides</i>	0.6 (± 0.5)
<i>Erigeron melanocephalus</i>	3.4 (± 2.6)
<i>Senecio dimorphophyllus</i>	0.1 (± 0.1)
<i>Typical graminoids</i>	
<i>Deschampsia caespitosa</i>	41.5 (± 7.0)
<i>Juncus drummondii</i>	9.0 (± 4.9)
<i>Prostrate graminoids and herbs</i>	
<i>Carex pyrenaica</i>	16.3 (± 8.8)
<i>Sibbaldia procumbens</i>	3.7 (± 3.6)
<i>Species of Geum-meadow</i>	
<i>Geum rossii</i>	7.6 (± 4.0)
<i>Salix arctica</i>	2.9 (± 1.8)
<i>Poa epipis</i>	2.0 (± 2.0)
<i>Carex chalciolepis</i>	3.3 (± 3.2)

al. (1981) applies to coevolved grazing systems, provided that the soil is not extremely nutrient-poor. Under conditions of severe nutrient shortage, grazing can be expected to have smaller quantitative impacts than predicted by Oksanen *et al.* (1981). A reanalysis of the model including landscape heterogeneity (T. Oksanen, 1988) suggests that the arguments of Oksanen *et al.* (1981) apply to the prevailing habitat type of the landscape and to patches of more productive habitat but not to less productive habitat patches. In fine-grained patchiness, local productivity becomes irrelevant; dynamics will be determined by average productivity of the habitat patchwork.

A case study of a fine-grained habitat with decreasing sizes of vegetated patches showed that the vegetational changes in such a gradient can mimic the vegetational changes in a gradient from sub-alpine tall herb meadows to extreme high alpine snowbeds. In the studied gradient, population densities of a key herbivore, the pika (*Ochotona princeps*), could be estimated, and its impact upon the vegetation was quantified and found to be strong in habitats with lawn-like vegetation.

Thus, there are three pieces which fit: natural transitions from sub-alpine, sub-arctic and sub-arid woodlands, scrublands and meadows to arctic-alpine tundras and arid steppes look as if they were proximately caused by increasing grazing pressure. Such a change in natural grazing pressure is theoretically plausible. At least in one case, it can be regarded as empirically demonstrated, too.

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