Strategies of Survival in Plants of the Fennoscandian Tundra

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ABSTRACT. Many arctic species originated outside the Arctic and some of their physiological responses are similar to those in temperate latitudes. Unique adaptations to the Arctic have rarely been found. The recent influx of other species has, however, broken down reproductive barriers and gene flow has been stimulated.

In extreme arctic environments, selection forces driving evolution are mainly of the physical environment and plant interactions are positive. Elsewhere, biotic factors, such as herbivory, are important and plant interactions become negative through competition.

Physical selective forces operate in winter and summer. Low winter temperatures rarely affect arctic plants, but snow depth and duration influence species distributions. Deep and persistent snow deforms plants and limits the period of resource acquisition. Cryptogams are common in such snow beds. Little or no snow cover exposes plants to abrasion by wind-blown particles and desiccation. In such fell-field sites, deciduous species and xerophytes, such as evergreen cushion plants, are common.

Arctic summers are short and developmental processes are extended beyond one growing season, with perennials predominating. Cushion plants efficiently increase their temperatures above ambient, while evergreen and deciduous ericaceous dwarf shrubs coexist and have complementary strategies for intercepting radiation in a low canopy.

Tundra soils are generally infertile and may be disturbed by freeze/thaw cycles. Nutrients are conserved by recycling within shoots and between ramets within clones. Vegetative proliferation enhances the survival of young ramets, while physiological integration between ramets enables young ramets to forage across patchy environments.

Negative plant-animal relationships are particularly important in the Subarctic. Periodic infestations of moth caterpillars defoliate large areas of mountain birch and stimulate increases in populations of their predators. Periodic population peaks of small rodents graze or kill much vegetation and they may moderate the dynamic structure of plant communities, as the plant species have different abilities to regenerate.

Key words: arctic plants, tundra, winter, snow, frost

RÉSUMÉ. De nombreuses espèces arctiques ne sont pas originaires de l'Arctique, et certains de leurs comportements physiologiques sont semblables à ceux qu'on rencontre à des latitudes tempérées. On a rarement trouvé des adaptations qui soient uniques à l'Arctique; cependant, l'afflux récent d'autres espèces a détruit les barrières reproductrices, ce qui a stimulé le flux génétique.

Dans des environnements arctiques extrêmes, les forces de sélection qui guident l'évolution sont surtout celles de l'environnement physique, et les interactions des plantes sont positives. Ailleurs, ce sont des facteurs biotiques comme la présence d'herbivores qui sont importants, et les interactions des plantes deviennent négatives par le biais de la compétition.

Les forces physiques de sélection agissent en hiver et en été. Les basses températures hivernales affectent rarement les plantes de l'Arctique, mais l'épaisseur de la neige et la durée de sa présence sur le sol influencent la distribution des espèces. La neige profonde et persistante déforme les plantes et limite la période d'acquisition des ressources. Les cryptogames sont communes dans ces terrains enneigés. S'il y a peu ou pas du tout de neige, les plantes sont exposées à l'abrasion des particules soufflées par le vent, et à la dessication. Dans des terres nues de ce genre, on trouve des espèces caduques et des xérophytes comme les plantes coussinées à feuilles persistantes.

Les étés arctiques étant courts, les processus de développement prennent plus d'une saison de croissance, et les plantes vivaces prédominent. Les plantes coussinées accroissent leur température de façon efficace au-dessus de la température ambiante, tandis que les buissons nains d'éricacées persistantes et caduques coexistent et ont des stratégies complémentaires pour intercepter la radiation sous une voûte végétale basse.

Les sols de la toundra sont en général infertiles et peuvent être perturbés par des cycles de gel et de dégel. Les éléments nutritifs sont conservés grâce au recyclage interne dans les tiges et d'un ramet à l'autre à l'intérieur des clones. La prolifération de la végétation augmente les chances de survie des nouveaux ramets, tandis que leur intégration physiologique leur permet de se frayer un chemin dans un environnement inégal.

Les rapports négatifs entre plantes et animaux sont particulièrement importants dans la zone subarctique. Des invasions périodiques de chenilles de noctuelles défolient de grandes étendues de bouleaux des montagnes et stimulent une augmentation de population chez leurs prédateurs. La population périodiquement en explosion des petits rongeurs broute ou élimine une grande partie de la végétation et peut agir comme élément modérateur sur la structure dynamique des communautés végétales, vu que ces espèces ont des capacités différentes de régénération.

Mots clés: plantes arctiques, toundra, hiver, neige, gel

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INTRODUCTION

Arctic vegetation and wildlife have attracted substantial scientific interest during the past few decades. A major reason for this is that the Arctic's ecosystems are simple in structure and are relatively undisturbed. Fundamental biological processes experiencing environmental stress can, therefore, be studied *in situ* (Billings and Mooney, 1968; Billings, 1974, 1987). A comprehensive review of investigations on arctic plant species and vegetation was published by Savile (1972), who emphasized the North American studies up to the late 1960s in particular. In the 1970s and early 1980s a series of papers on tundra ecology was published based on the results of the International Biological Programme (IBP, 1968-74) (Wielgolaski and Rosswall, 1972; Bliss and Wielgolaski, 1973;

Wielgolaski, 1975a,b; Bliss, 1977; Tieszen, 1978; Brown *et al.*, 1980; Sonesson, 1980; Bliss *et al.*, 1981).

This paper aims to review the plant life of the tundra by taking examples from recent Fennoscandian literature. There are no general definition and delimitation of "arctic" and "tundra" and no agreement as to whether these are geographical-meteorological or biological-ecological concepts, or both (Hustich, 1979). This presentation, therefore, deals with the ecosystems at and beyond the latitudinal and altitudinal tree lines in northern Fennoscandia (Fig. 1). Thus, the transitional subarctic tundra or forest-tundra between the arctic and the boreal regions is also considered.

Northern Fennoscandia is characterized by arctic photo-period conditions due to the high latitude and higher tem-

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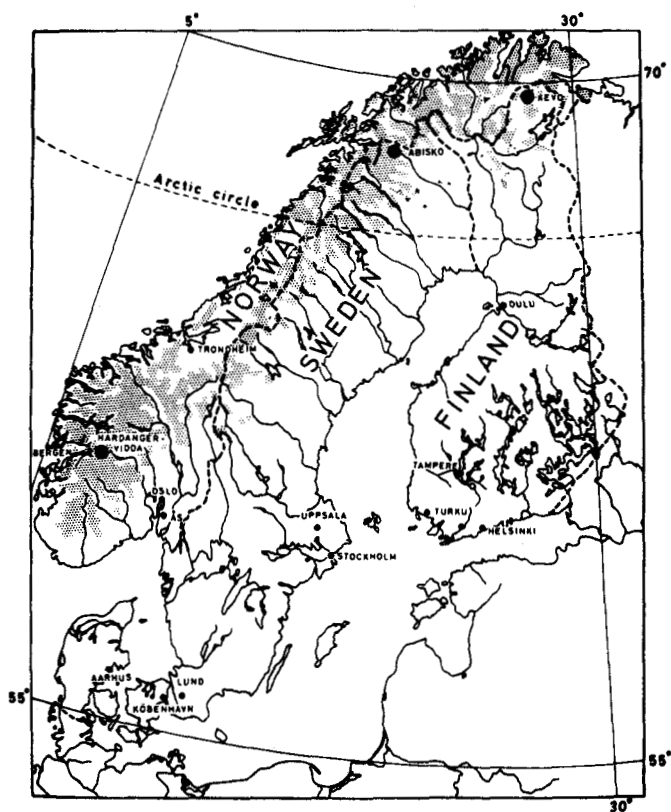
FIG. 1. Map of the Fennoscandian countries. Tundra areas are shaded. (Reproduced from Sonesson *et al.*, 1975, with permission of Springer-Verlag.)

peratures than would be expected there. Permafrost is only sporadic (Sonesson *et al.*, 1975) and agriculture is possible in places close to the sea at low altitudes. These temperature anomalies are primarily due to the influence of the Gulf Stream, and temperatures are more related to the distance from the sea and altitude than to latitude. For instance, at sea level at Vardö on the northernmost Norwegian coast (70°20'N. lat.) the mean temperatures of the coldest and warmest months are −4.8 and 8.9°C respectively, compared with −10.8 and 12.3°C at Abisko, Sweden, 68°20'N, 400 m a.s.l. and 50 km distant from the sea.

An understanding of the ecosystems of this area is now particularly urgent as predictions of climate change related to the greenhouse effect suggest that change will be greatest in the North and impacts will be identified here sooner than elsewhere.

ORIGINS OF THE SPECIES

Some arctic species are assumed to have originated in Tertiary times from temperate mountains, where selection over long periods resulted in the differentiation of biotypes capable of surviving in the environments of the higher latitudes. The plants migrated to arctic regions during Pliocene and Pleistocene times (Savile, 1972). Thus, the modern plant cover of the Arctic consists of old species, whereas the vegetation patterns and communities are young, particularly in areas exposed to the Quaternary glaciations.

The latest glaciation ended less than 10 000 years ago in most of northern Fennoscandia (Sonesson, 1974), although some islands of northern Norway were deglaciated much earlier (Vorren, 1978; Vorren *et al.*, 1988). After the

deglaciation the biota of the present ecosystems either colonized new ice-free areas from pockets or "refugia" where they had survived the glaciation within the Arctic (Dahl, 1963, 1987; Löve and Löve, 1963, 1974) or immigrated from farther south or east. The evolution of many fundamental processes determining the performance of plants in arctic areas of today may, therefore, have been completed outside these areas. This may explain, for instance, why the temperature optima of photosynthesis in arctic species are often similar to those of temperate species (Tieszen, 1978) and why the hardening of the tissue before the winter season tends to be equally efficient in species from arctic and temperate regions (Sakai and Larcher, 1987), although temperatures during summer may not differ very much between them. Some assumed adaptive traits recognized in arctic plants today may, therefore, reflect the results of the selection pressures exerted on the biotypes during their migrations.

Some traits must have been acquired at the high latitudes, however. This applies to some of the adaptations to continuous light in summer, which is an environmental factor with no parallel at lower latitudes. It has been shown that the CO_2 exchange of the northern populations of the common boreal mosses *Pleurozium schreberi* (Brid.) Mitt. and *Rhacomitrium lanuginosum* (Hedw.ex Hedw.) Brid. is adapted to the long, continuous light period in subarctic-arctic areas in contrast to southern populations (Kallio and Valanne, 1975). The critical photoperiod for growth cessation in the boreal willow, *Salix pentandra* L., shows a clinal variation increasing with increasing northern latitude (59°40'−69°39'N). This species is also adapted to the latitudinal differences in irradiance and spectral energy distribution (Junttila and Kaurin, 1985). Although temperature optima for photosynthesis are similar for many arctic and temperate plant species, ribulose biphosphate carboxylase levels are higher in arctic plants, and this enables them to replenish carbohydrates faster than temperate species (Crawford and Palin, 1981; Crawford, 1989). This ability may also have been acquired at high latitudes.

Adaptions to arctic environmental features may occur when genetic compatibility barriers operative in southern areas break down to some degree at higher latitudes. This applies, for instance, to the northern populations of the Fennoscandian *Betula* species (Hagman, 1971; Vaarama and Valanne, 1973). The mountain birch, *Betula pubescens* Ehrh. ssp. *tortuosa* (Led.) Nyman, of the subarctic woodlands in Fennoscandia (Sonesson and Hoogesteger, 1983), including Iceland and South Greenland, is assumed to have evolved from a gene pool in the North to which the tree birches *Betula pubescens* ssp. *pubescens* Ehrh. and *Betula verrucosa* Ehrh. (= *B. pendula*), as well as the dwarf birch, *Betula nana* L., contribute (Kallio and Lehtonen, 1975; Kallio *et al.*, 1983). The curved trunks, the polycormic growth form, which perpetuates the individual, and the vivid autumnal colours are all characteristics typical of the dwarf birch.

A possible selection force contributing to the evolution of the mountain birch is exerted by the caterpillars of the autumnal moth *Epirrita* (= *Oporinia*) *autumnata* Bkh. and *Operophthera brumata* L. These may defoliate and kill birch trees over large areas. They tend to have the greatest impact on the monocormic form, which may result in a successive increase of the polycormic form in the subarctic woodlands (Kallio and Lehtonen, 1975).

Many northern boreal bryophytes normally propagate vegetatively and do not form any sporophytes. Under extreme environmental conditions, however, they may develop sporophytes as a result of sexual crossings between populations of different genotypes (Sonesson, 1966). This produces new genetic combinations that may be able to meet changes in the environment and allow new habitats to be exploited. A rapid ecotypic differentiation in some northern lichens by vegetative intra- and interspecific recombination of the fungal and/or the algal components has also been suggested (Sonesson, 1986). There is evidence of a high rate of genetic changes in some vascular plants as well, indicating that some species may have evolved during postglacial times (Nordal, 1987; Nordal et al., 1988).

STRATEGIES OF GROWTH AND SURVIVAL

Winter Conditions

Little has been written about polar plant life in winter alone (Salisbury, 1984; Marchand, 1987). This is easy to understand because it is often difficult to make direct observations of the very slow metabolic activities that occur during the cold, dark season. Most of the winter's influence on plants occurs during the summer and is on the morphology, development, strategies of growth and reproduction and distribution patterns of individuals and species. The summer is the period when nutrients and energy necessary to support prolonged reproductive development and to buffer the winter losses have to be gained. Both seasons interact to determine the development of the tundra vegetation and both must be considered to understand polar plant life.

Winter is the longest season at high latitudes. The annual amount of precipitation falling as snow differs substantially both between and along the latitudes, whereas its relative distribution over the terrain is often remarkably similar (Vestergren, 1902; Sonesson, 1969). The snow provides shelter against the frequent high, desiccating winds and reduces temperature extremes. The relationship between frost drought and the snow surface was described long ago by Kihlman (1890) and Fries (1913). Fell-field plants tend to grow in small aggregations, allowing shelter from wind exposure, provision of moisture for germination and seed establishment (Callaghan, 1987). Bell and Bliss (1980) have shown that seedlings of High Arctic plants become established in mats of moss, algae and lichens.

A survey of the distribution of heath plant communities characterized by dwarf shrubs and graminoids in subarctic Scandinavia showed that the dwarf shrubs were most abundant in areas of moderate to poor snow cover, whereas the graminoids were dominant in terrain with deep snow (Sandberg, 1958). Sites with particularly deep and persistent snow are those where the snow bed communities exist. The vegetation of snow beds consists mainly of graminoids, dwarf willows and cryptogams. In the extreme snow beds, only cryptogams (i.e., plants that have no true flowers but propagate by spores, such as algae, fungi, lichens, mosses and ferns) are present (Gjaerevoll, 1949, 1965). The very short growing season here appears to select for plants that conserve sparse energy by investing only in tissues that can be used for both photosynthesis and the uptake of nutrients and water. Plants that need specialized tissue for these processes — i.e., those having roots — will be excluded. Also, short growing seasons limit the period required for flower development in higher plants (Callaghan, 1974).

Within the snow beds there is a gradient of varying snow depth characterized by different plant communities whose distributions result from complex factors. However, the low winter temperatures are practically never harmful to the plants, even if they grow under a thin or sporadic snow cover, since their aerial parts either die before winter or are hardened to withstand low temperatures. For example, Loiseleuria procumbens (L.) Desv. (Creeping Azalea), growing in exposed habitats, endures −60°C in winter and −7°C during summer, and leaves of Silene acaulis (L.) Jacq. (Moss Campion) can even survive liquid nitrogen (−198°C) after winter hardening (Sakai and Larcher, 1987). Diapensia lapponica L. (Lapland Diapensia) can stand −58°C in winter and −9°C in summer (Junnila, 1984; cf. Pihakaski and Junnila, 1988).

Plants of exposed sites are particularly vulnerable to abrasion by wind-blown snow crystals and mineral particles as well as drought. The risk of desiccation is particularly high during late winter, when shoots above the snow surface experience direct sunlight. The shoots are then heated to temperatures often substantially exceeding those of the air. The resulting evapotranspiration, while the rest of the plant under the snow is still frozen and therefore unable to replenish water, often kills the apical parts (Sakai and Larcher, 1987). Exposed sites are, therefore, characterized by xerophytic, often prostrate species, such as evergreen dwarf shrubs, with the ability to withstand abrasion and reduce water losses (Sörensen, 1941; Savile, 1972; Callaghan, 1987).

The vegetation of more protected sites with deeper snow consists of shrubs of deciduous willows (e.g., Salix phylicifolia L., S. myrsinifolia Salisb., S. lapponum L., S. glauca L. and S. lanata L.) and dwarf birch (B. nana L.). The deeper snow protects the shrubs from abrasion, while their deciduous character means that leaves are shed before being subjected to abrasion and desiccation. Upper twigs do, however, often show signs of "winter-desiccation." Their crowns are often smooth, as though they had been cut at a height that conforms with the surface of the snow layer. Winter grazing by the mountain hare, Lepus timidus L., the willow grouse, Lagopus lagopus L., and the moose, Alces alces L. (Berg et al., 1975; Myrberget, 1979; Spidsö, 1980) further contributes to this stunted morphology.

The pressure of deep, heavy snow was suggested long ago to be an important force behind the curved growth of the subarctic birch (Fries, 1913). It is also assumed to be a major factor behind the mortality of the birch at the altitudinal tree line in Fennoscandia (Kullman, 1983). Persistent snow, as in the snow beds, results in a short growing season, which limits the distribution of many plants while increasing the possibilities of others to exist (Fig. 2). Hence, deep or persistent snow cover in winter can be just as harmful as a thin snow cover or even the absence of snow at an exposed site.

Plants under deep snow may experience much higher temperatures than plants with a poor protection of snow (Eurola, 1968; Sonesson, 1969). Under deep snow, therefore, dark respiration may occur for extended periods, although at low rates. This will successively diminish the plant's energy resources (Havas and Mäenpää, 1972; Havas, 1984). The plants must then rebuild these stores during the short growing season. Starch and, for some cryptogams, the energy-rich lipids are particularly important storage compounds (Kallio, 1984), although Hetherington et al. (1984) showed that lipids
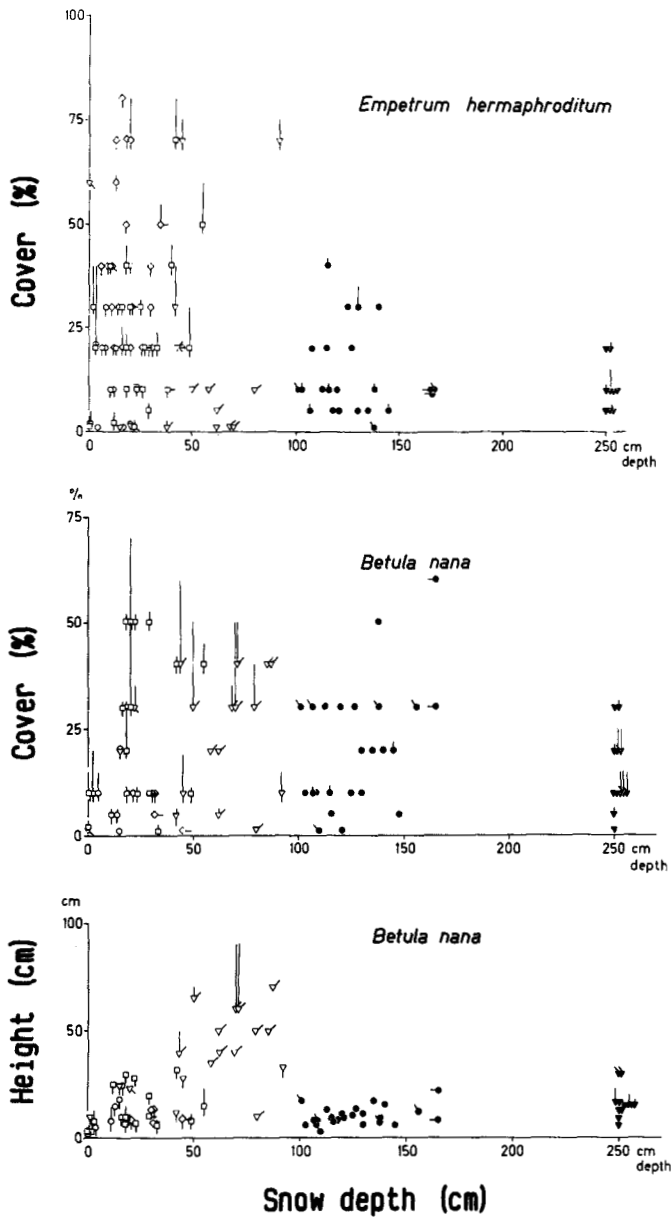
FIG. 2. Cover and height of shoots of *Betula nana* and *Empetrum hermaphroditum* in relation to snow depths in mid-winter. Different symbols indicate different localities. Vertical bars show dead parts of the shoots. (After Sonesson, 1969.)

were not important storage compounds for alpine populations of *Empetrum hermaphroditum* (Crowberry). In contrast, the lipid content of the epiphytic lichen *Parmeliopsis ambigua* (Wulf.) Nyl., which experiences at least six months of snow cover in northernmost Fennoscandia (Sonesson, 1989), was two to three times as high as that of *Parmelia olivacea* (L.) Ach., which grows above *Parmeliopsis* on the same trees and is practically never covered with snow (Sonesson, unpubl. data). Lipids are also known to be an energy-dense store when space is restricted, such as in the spores of *Lycopodium annotinum* L. (Interrupted Clubmoss) (Callaghan, 1980) and they are important for the hardening of plants (Sakai and Larcher, 1987). The content of carbohydrates is also closely related to the degree of frost hardiness of tissues (Kaurin et al., 1981, 1982).

Relating vegetation patterns to the depth and duration of the snow cover alone may be misleading. Many other factors are obviously important. For instance, the wind not only blows away the snow from exposed places, it also removes litter and prevents the formation of a humus layer. The thin, discontinuous humus on exposed ridges can be as important for the exclusion of some plants as the thin, discontinuous snow in winter (Jonasson, 1986). Furthermore, Wijk (1986a,b) found that the highest productivity and fastest turnover of shoots of *Salix herbacea* occurred in a part of the snow gradient where *Vaccinium myrtillus* L. (Bilberry) becomes particularly abundant and the snow depth is moderate (Fig. 3). The highest shoot density and cover were observed under deep and persistent snow, however. He concluded that competition with *V. myrtillus* as well as the periodic impact of herbivores will increase the mortality of the dwarf willow where the snow is moderate because it is a weak competitor. Its dominance of habitats under deeper snow is because competitors are lacking there.

The depth of the snow together with the water conditions of the soil result in the development of different types of patterned ground, which are common phenomena in tundras (Lundqvist, 1962). For instance, the frost-heaving of the ground due to freeze-thaw cycles (Rydén and Kostov, 1980) is related to a large extent to thin snow cover over fine-grained soils with high water content. Jonasson (1986) suggested that the vegetation on frost-heaved soils in Scandinavia is controlled by two main factors: 1) disruptive effects on the below-ground parts when the soil heaves; 2) an increase of nutrient availability, pH and base saturation. The plant cover is characterized by fibrous-rooted perennials — e.g., *Lycopodium selago* L. (Fir Clubmoss), *Pinguicula alpina* L. (Alpine Butterwort) and other small forbs — on the most disturbed soils, whereas dwarf shrubs having non-fibrous roots or below-ground stems, such as *Empetrum hermaphroditum* Hagerup, *Betula nana* and *Vaccinium myrtillus*, are abundant on the stable soils (Jonasson, 1983, 1986). The fibrous-rooted plants are not severely damaged even by intensive frost, since most of their below-ground system dies before the onset of freeze-thaw cycles. As the soils heave, unweathered soils of higher nutrient content than in the top soil are brought to the ground surface, allowing plant species adapted to high nutrient conditions to persist in otherwise very nutrient-poor areas (Jonasson, 1986).

Winter Herbivory

Winter activity by herbivores can have a great influence on the structure and composition of the vegetation cover (Emanuelsson, 1984; Hansson, 1984; Andersson and Jonasson, 1986). Voles, such as *Microtus agrests* L. and *Clethrionomus rufocanus* Sundevall, have population peaks every three to four years in northern Fennoscandia (Kalela, 1962; Myrberget, 1973; Christiansen, 1983; Hansson and Henttonen, 1985; Andersson and Jonasson, 1986) and are active under snow of moderate depths. The optimum snow depth for the voles appears to be a compromise between the need for protection from predation from above and the risk of flooding of their tunnels during the thaw or the lethal levels of carbon dioxide under deep snow. Concentrations of carbon dioxide and methane can be high under snow when the soil is unfrozen because of aerobic and anaerobic soil respiration (Svensson et al., 1975; Svensson, 1980; Aaltonen et al., 1984).

The activity of the rodents can affect extensive areas, particularly when the snow is loosely packed and there is a
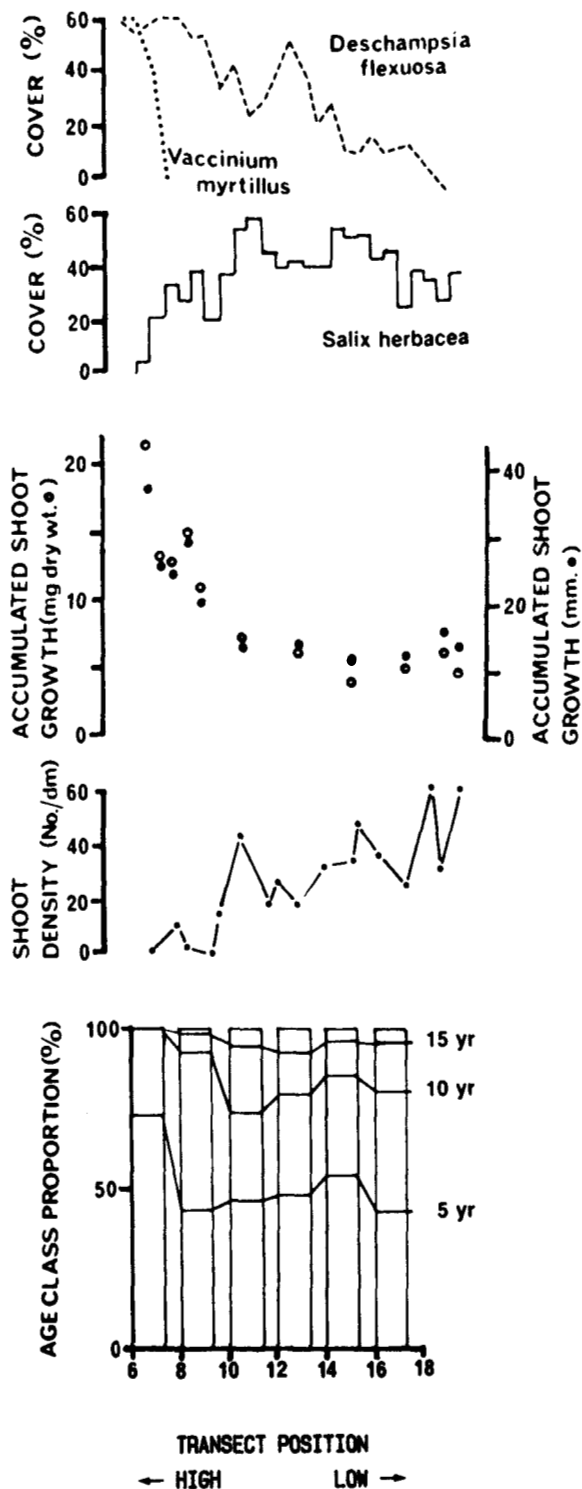
by these rodents (Fig. 4). Some shoots are consumed, *Vaccinium myrtillus* being particularly preferred (Table 1), but many are left as litter, which is visible on the surface of the ground after the snow has melted (Fig. 4).

Plants such as *Empetrum hermaphroditum* have no dormant buds on the older branches to form new shoots when the apical dominance has been broken and will, therefore, be disadvantaged by this grazing (Emanuelsson, 1984). In contrast, dwarf shrubs such as *Vaccinium myrtillus* and *V. vitis-idaea* L. (Cowberry) develop tillers from a subterranean rhizome, and they will show particularly efficient recovery (Emanuelsson, 1984). Emanuelsson concludes that the micromosaic pattern of dwarf shrubs in the subarctic tundra is due to a large extent to the voles and that *Empetrum hermaphroditum* would be much more dominant over tundra heaths without periodic herbivory.

Rodent grazing may also stimulate plant growth. The litter and the faeces left after grazing may speed up the slow decomposition rates of the tundra and be important for plant nutrition. North American studies (Pitelka, 1964; Schulz, 1964) even indicated that the recovery of normal tissue concentrations of nutrients in the food plants after decomposition could explain the rodent cycles on tundras. But Scandinavian data (Andersson and Jonasson, 1986) do not support this hypothesis.

Summer Conditions

The low plant production on tundras is primarily caused by the short growing season rather than slow growth. Indeed,

FIG. 3. The response of *Salix herbacea* to a snow bed environment where competition (mainly with *Vaccinium myrtillus*) is associated with that part of the gradient experiencing the longest snow-free period and decreased shoot growth is associated with the shortest growing seasons. Large individual shoots, low shoot density, low cover abundance and a high proportion of young individuals of *S. herbacea* (signifying fast turnover) are associated with the competitive situation, and the reverse applies to areas experiencing the longest duration of snow cover. X-axis shows distance in m. (After Wijk, 1986.)

subnival space more or less free of snow (Coulianos and Edström, 1971; Emanuelsson, 1984). The bases of the perennial shoots of the plants are cut along the tracks formed

TABLE 1. Food preferences of the vole *Clethrionomus rufocanus* Sundevall from an experiment with 23 caged animals at Abisko in July 1978

	I[1]		II[2]	
	Mean	SD	Mean	SD
Plant combination 1 (N = 10)				
Vaccinium myrtillus	63	51	100	81
Polytrichum spp.	38	20	60	32
Deschampsia flexuosa	9	3	14	5
Plant combination 2 (N = 10)				
Vaccinium myrtillus	39	12	100	31
Vaccinium uliginosum	21	16	54	41
Empetrum hermaphroditum	7	6	18	15
Vaccinium vitis-idaea	2	4	5	10
Plant combination 3 (N = 8)				
Vaccinium vitis-idaea	73	50	100	68
Linnaea borealis	51	25	70	34
Plant combination 4 (N = 7)				
Empetrum hermaphroditum	28	23	100	82
Linnaea borealis	17	23	61	82
Plant combination 5 (N = 6)				
Polytrichum spp.	48	35	100	73
Pleurozium schreberi	48	35	75	42
Hylocomium splendens	1	1	2	2
Sphagnum spp.	0	0	0	0
Plant combination 6 (N = 8)				
Deschampsia flexuosa	71	11	100	100
Calamagrostis lapponica	28	21	39	30
Festuca ovina	4	4	6	6

[1]The mean percentage and standard deviations of each plant species in six combinations.
[2]The mean percentage and standard deviations expressed in relation to the most preferred species in the combination (from Emanuelsson, 1984).
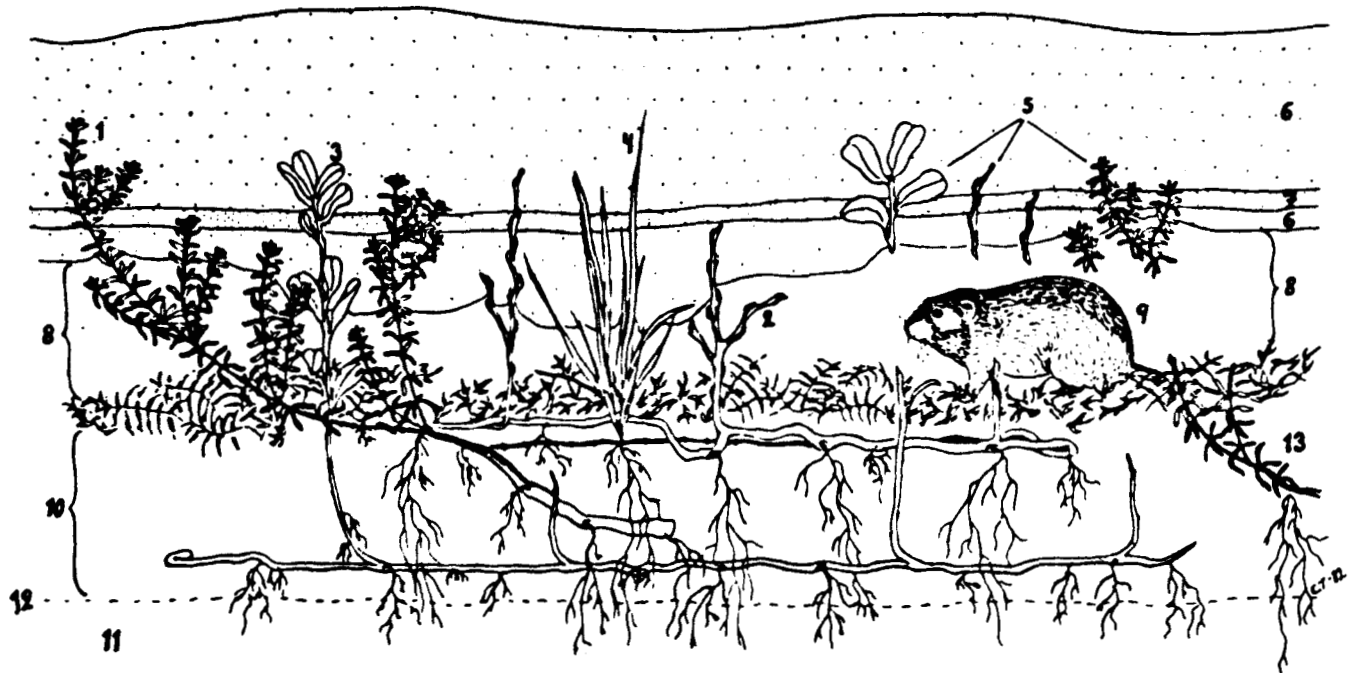
FIG. 4. Grazing of tundra heath plants by a vole during winter. 1) *Empetrum hermaphroditum*; 2) *Vaccinium myrtillus*; 3) *Vaccinium vitis-idaea*; 4) *Calamagrostis lapponica*; 5) top shoots frozen into the compact snow layer; 6) snow; 7) ice layer; 8) sub-nival space; 9) grazing vole; 10) peaty soil; 11) mineral soil; 12) surface of mineral soil; 13) damaged shoots of *Empetrum hermaphroditum*. (After Emanuelsson, 1984.)

the growth rates of tundra plants during the summer can be at least as high as those of temperate plants (Chapin, 1987).

The short growing season results in the prolongation of plant life cycles and developmental processes, such as flower and leaf development. Most tundra plants are, therefore, perennial (Callaghan and Emanuelsson, 1985) and only few can complete the whole life cycle during one year, e.g., *Koenigia islandica* L. (Iceland Koenigia) and some hemiparasites. These species play only a minor role in the plant cover, however.

The short, cold growing season is met by a number of adaptations allowing the plants to maximize their production. The growth cycles of tundra plants are either periodic or aperiodic or are a combination of both strategies (Sörensen, 1941). Periodic plants grow until a particular stage of development has been reached, when the growth ceases until the next season. Aperiodic plants grow at any time of the year if environmental conditions permit. Periodic growth is the safe strategy in less harsh environments with predictable weather conditions, but it will not allow fitness to be increased by the opportunistic use of temporary periods of favourable weather. In contrast, the aperiodic strategy is opportunistic but always involves a risk of mortality during severe conditions. This strategy is common in habitats with the most severe and unpredictable conditions and it is found increasingly among plants of northern latitudes, particularly in snow beds (cf. Sörensen, 1941). These melt during late spring to summer but the length of the growing season may vary greatly from year to year.

Plants in exposed habitats may absorb radiant energy very efficiently, due to deep pigmentation, etc., whereas the compact cushion form in plants such as *Silene acaulis* and *Diapensia lapponica* reduces air mixing (Gauslaa, 1984). Species such as these may have temperatures much higher than those of the ambient air (Stoutjesdijk, 1970; Mölgaard,

1982; Gauslaa, 1984). Narrow, elongated leaves or leaves equipped with hairs at the margins also result in these plants having a poor capacity for heat exchange with the surrounding air (Gauslaa, 1984). This is an advantage when the ambient temperature is low but it may be harmful in areas of high summer temperatures due to overheating. This may be one mechanism that restricts many tundra plants to high latitudes and altitudes rather than temperate lowland areas at the present time (Dahl, 1951; Conolly and Dahl, 1970; Skre, 1979; Gauslaa, 1984), although some grow in temperate gardens if competition is removed. It has also been shown that northern plants have a poorer capacity to save stored carbohydrates during high winter temperatures than do southern plants, which could explain their southern distribution limits (Crawford and Palin, 1981).

A different adaptation for increasing plant tissue temperature is found in plants with heliotropic movements (i.e., movement towards the source of light) of the flowers. Such movements, occurring in, for example, *Dryas octopetala* L. (Mountain Avens), have been shown to increase the temperature of the gynoecium and the weight of the seeds (Kjellberg *et al.*, 1982).

Plant water balance is a serious problem mainly for species growing in exposed, dry habitats, although plants in cold, wet soils may experience water stress. For the so-called chionophobous plants — i.e., plants showing a preference for sites without snow (Dahl, 1956) — desiccation is avoided by the high cuticular diffusion resistances of the leaves and by stomata that close even at low wind speeds (Gauslaa, 1984). Junnila (1984) found a seasonal acclimation in *Diapensia lapponica*, which has a higher tolerance of water deficiency stress during late autumn to late spring than during summer.

However, the xerophytes are not the typical life form of the tundra. There are also mesophytes with low diffusion resistances and high capacities of heat exchange. They have

thin, wide leaves — e.g., *Oxyria digyna* (L.) Hill. (Mountain Sorrel), *Viola biflora* L. (Yellow Wood Violet) and several *Salix* species — and they are often chionophilous plants (Gauslaa, 1984) — i.e., plants typical of sites with good snow protection in winter (Dahl, 1956; Gjaerevoll, 1965).

The high latitudes have a relatively low annual influx of solar energy, although irradiance to unshaded plants during the bright summer days and nights is often above compensation level throughout the diurnal cycle. The growth of the solitary or small aggregations of plants of the fell-fields is probably less light-limited than in the closed tundra vegetation, where competition and efficient light-intercepting canopies are important. Karlsson (1987a) showed that the deciduous *Vaccinium uliginosum* L. (Arctic Blueberry) avoids competition for light in closed subarctic heath communities by overtopping its neighbours and having an efficient orientation of its leaves (Figs. 5 and 6). Its top leaves are both steeply inclined and large, so that the interception of direct light from a low solar angle is efficient. The lower leaves of the shoots are more horizontal, however, optimizing the interception of the diffuse light through a dense canopy. The evergreens *Vaccinium vitis-idaea* and *Empetrum her-maphroditum*, usually associated with *V. uliginosum*, experience reduced competition for light during spring and autumn, when *V. uliginosum* and other deciduous species are leafless. These evergreen leaves permit photosynthesis to start early in the season and decrease the annual losses of carbon and nutrients to litter. The evergreen species also have a lower saturation level of light, so that maximum photosynthetic rate is reached at lower irradiance. Since a large fraction of their biomass is in the leaves, this results in a large amount of CO_2 assimilated per unit biomass (Karlsson, 1987b).

In other species, e.g., *Vaccinium myrtillus*, the shoot axes are green and they undergo photosynthesis in early spring and late autumn, at the same time as the leaves of the evergreen species (Karlsson, unpubl.). The steeply inclined leaves of *V. myrtillus* and the distribution of leaves along its shoot axes would render this species an inferior competitor for light in a closed canopy (Karlsson, 1987a). Despite this, the periodic grazing of the rodents increases the light influx through the canopy of the tundra heath sufficiently for *V. myrtillus* to survive (Emanuelsson, 1984).

Many higher plants of the tundra save and conserve nutrients by recycling. This process is important within the shoots of individual plants (Jonasson, 1983) and particularly within clonal plants, which are particularly abundant in the closed vegetation of the tundra. Movement of water, carbon and nutrients between tiller generations of graminoids (Callaghan, 1984; Jonsdottir and Callaghan, 1988, 1990) allows the subsidized growth of stressed young tiller generations (Jonsdottir and Callaghan, 1989). The integration of ramets within clones seems far more advanced in tundra habitats than elsewhere (Callaghan, 1988). Connections between ramets may persist for at least 11 years, thereby enabling the survival of old, leafless tillers, which supply nutrients and water to young tillers (Jonsdottir and Callaghan, 1990).

Although nutrients are limiting in the tundra, they often have a patchy distribution with, for example, stoney areas where roots cannot be produced (Svensson and Callaghan, 1988a). Clonal plants with long rhizomes or stolons, such as *Lycopodium annotinum* L. (Interrupted Clubmoss), can forage for such nutrient patches (Svensson and Callaghan,
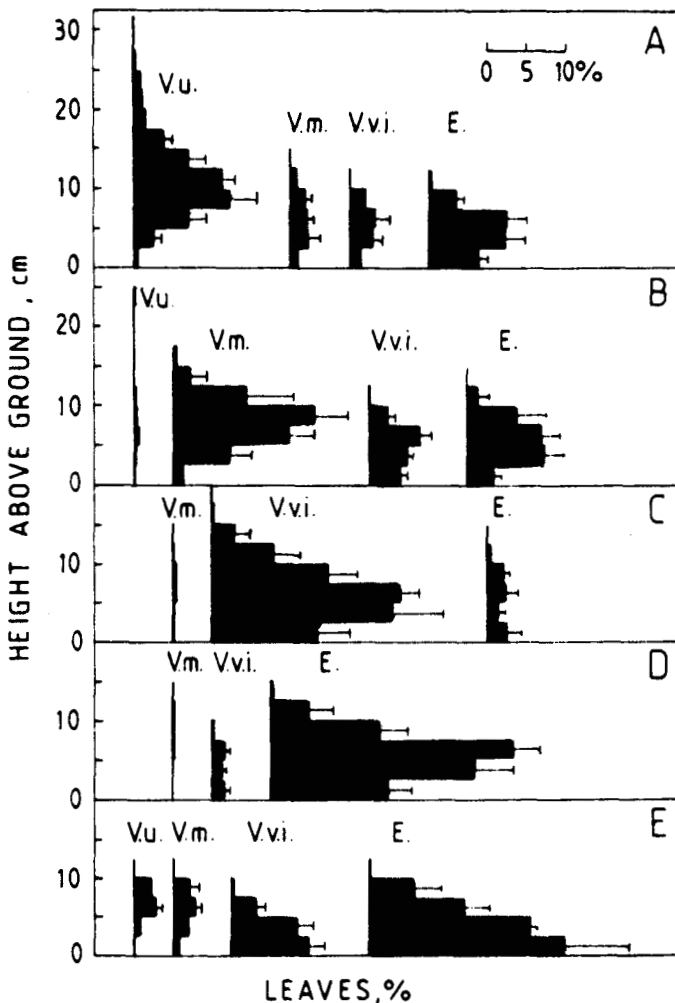
FIG. 5. Leaf mass distribution of four dwarf shrubs in a tundra heath community at Abisko. Vu=*V. uliginosum*, Vm=*V. myrtillus*, Vvi=*V. vitis-idaea*, E=*Empetrum hermaphroditum*. A) sites domitated by *V. uliginosum*; B) sites dominated by *V. myrtillus*; C) sites dominated by *V. vitis-idaea*; D) sites dominated by *Empetrum hermaphroditum*; E) sites with a mixed species composition. (Reproduced from Karlsson, 1987a, with permission of Springer-Verlag.)
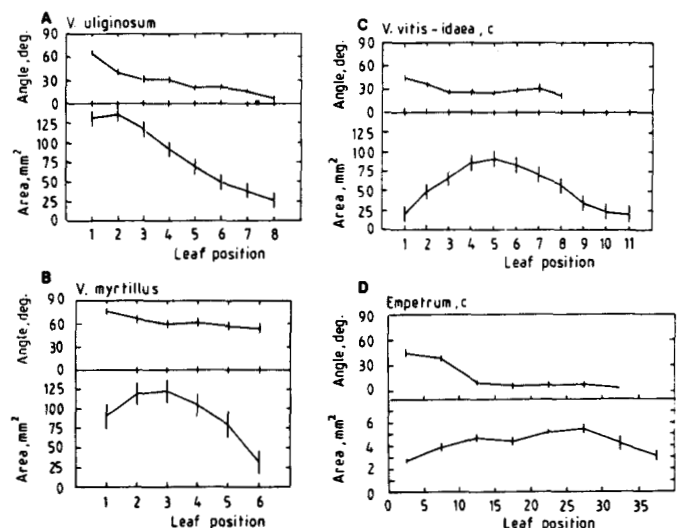
FIG. 6. Leaf area and leaf angle deviations from the horizontal along the shoot axis of four dwarf shrubs. Leaf number 1 is the top leaf. Vertical lines indicate two SE. (Reproduced from Karlsson, 1987a, with permission of Springer-Verlag.)

1988b) because the growing points preferentially receive water and nutrients from areas where roots have been established (Headley *et al.*, 1988a,b). The clonal growth form is, therefore, a successful buffer against stress due to grazing and climate, as well as patchy resource availability.

Although tundra plants save and conserve many of their nutrients by recycling, their growth is often limited by soil nutrient availability, particularly by the deficiency of nitrogen and phosphorus (Malmer and Nihlgård, 1980; Aldenius *et al.*, 1983; Jonasson, 1983; Karlsson and Carlsson, 1984; Jonasson and Chapin, 1985; Karlsson, 1987b; Karlsson and Nordell, 1987, 1988). Callaghan (1971) showed that the growth of *Phleum alpinum* (Alpine Timothy) was limited far more when grown in the soils from an altitudinal gradient than when grown in a standard soil under the different microclimates along the gradient.

In polar environments, the input of nitrogen to the ecosystems through microbial fixation is strongly limited by environmental conditions. The nitrogen fixation mediated mainly by cyanobacteria can be high locally (Granhall and Lid-Torsvik, 1975; Crittenden and Kershaw, 1978). Jonasson (1986) found high fixation from free-living cyanobacteria on circumneutral soils of frost-heaved ground. The abundance of lichens with cyanobacteria as symbionts, such as *Stereocaulon* spp., *Peltigera* spp. and *Nephroma arcticum* (L.) Forss., is high in arctic nutrient-poor, acidic soils. Even if their fixation rates are slow, they still probably contribute substantially to maintain the nitrogen status of the soil, particularly as other inputs of nitrogen are very small (Kallio and Kallio, 1975; Malmer and Nihlgård, 1980; Rosswall and Granhall, 1980).

Reindeer often graze lichens extensively during winter, but with a preference for genera and species without cyanobacteria, such as *Cladonia* spp. and *Cetraria* spp. (Gaare and Skogland, 1975; Eriksson *et al.*, 1981; Table 2). The reindeer may therefore exert a substantial indirect effect on the nutrition of tundra plants in addition to their direct, mechanical and fertilizing impacts.

Vegetative reproduction predominates in the closed vegetation and conserves the genotype. However, sexual reproduction occurs and appears to be related to changes in the environment in either space or time (Heide, 1988). Reproduction by seeds in a particular species is less efficient at the highest latitudes in Fennoscandia, particularly on stable soils (Eurola, 1972), and this seems to apply to higher altitudes as well. Thus germinability of seeds of the mountain birch decreases with altitude and may be very low at the tree line (Kullman, 1984). In the High Arctic, however, the importance of vegetative reproduction and clonal plants diminishes as seed production and vivipary predominate (Callaghan and Emanuelsson, 1985). Seeds of most species in the North

TABLE 2. Plant categories as percentage of dry weight in the rumen content of five reindeer from northern Swedish Lapland (from Eriksson *et al.*, 1981)

	Mean	SE
Dwarf shrubs	20.7	2.5
Pine needles	18.3	1.6
Grasses	1.0	0.3
Mosses	5.0	0.8
Cladonia spp.	40.7	3.5
Stereocaulon spp.	14.3	1.8

American tundra germinate at optimal temperatures of 15-20°C, higher than those experienced in the field and characteristic of cool, temperate species (McGraw, 1980).

Summer Herbivory

In the most extreme habitats, such as the late snow beds, fell-fields and strongly frost-heaved soils, physical factors in the environment, such as wind, temperature and light, as well as positive interactions among individuals probably exert a greater influence on the life processes of plants than competition and negative biotic influences (Callaghan, 1987). In contrast, in habitats with closed vegetation negative interactions through competition and herbivory are probably more important (Grime, 1979; Oksanen *et al.*, 1981; Callaghan and Emanuelsson, 1985).

In northern ecosystems a periodicity of dynamic changes is typical in the populations of both plants and animals (Tast and Kalela, 1971; Laine and Henttonen, 1983; Hansson and Henttonen, 1985). For example, approximately every ten years there is a peak in the population of the autumnal moths, *Epirrita autumnata* and *Operophthera brumata*, which feed on the leaves of the mountain birch (Tenow, 1972, 1975, 1983; Kallio and Lehtonen, 1975). The leaf biomass is reduced but the chemical composition of the remaining and new leaves changes, apparently as a response induced by grazing (Haukioja and Koponen, 1975; Niemelä *et al.*, 1979; Tuomi *et al.*, 1984; Haukioja *et al.*, 1985). Unpalatable phenolic compounds with adverse effects on the herbivores increase, whereas the nitrogen content decreases. When the populations of the insects are high, they also stimulate an increase in the populations of their predators.

The size of the population of *Epirrita* caterpillars and the topographical distribution of their effects on the birch trees are related to winter temperature (Tenow, 1975). The eggs hibernate on the branches of the birch and hatch during budbreak in spring. They may be killed by low temperature in late winter when exposed to the cold air collected in depressions of the landscape, e.g., along water courses and in valley bottoms. The topoclimate is thus of great importance for the local distribution of an outbreak (Tenow, 1972, 1975, 1983; Niemelä, 1979; Tenow and Holmgren, 1987).

Cyclicity also occurs among some vertebrate herbivores. Every three to four years there is a peak in the populations of microtine rodents, which are important herbivores of many plant species (Table 1; Hansson, 1987). Investigations by Andersson and Jonasson (1986) showed no relationship between the microtine cycles and the quality of the food. Laine and Henttonen (1987) and Oksanen *et al.* (1987) were also unable to find any evidence of phenol-based defence of woody plants that can explain the periodicity of the populations of small rodents in the North. These cyclical changes are the scope of comprehensive ecological research today in Fennoscandia (Oksanen *et al.*, 1981, 1987; Tuomi *et al.*, 1984; Haukioja *et al.*, 1985; Jonasson *et al.*, 1986; Andersson and Jonasson, 1986; Laine and Henttonen, 1987). Their causes are still virtually unknown, although winter snow cover and spring melt appear to be critical in arctic areas.

Predictions that the climate changes in the Arctic will be greater than elsewhere open a new challenge to arctic ecologists, who must now address the problems of how tundra ecosystems will change and how they contribute to climate change through biological feedbacks such as gas exchange.

CONCLUSIONS

1. Many species of the Fennoscandian Arctic have characteristics evolved long ago outside their present distribution. Thus care must be taken when interpreting their autecology in their present location. In contrast, the plant associations are young and increased gene flow has resulted in the formation of species complexes where a particularly dynamic period of evolution may be in progress.

2. In the closed vegetation of the Subarctic, vegetative reproduction predominates and conserves the genotype. However, sexual reproduction occurs and appears to be related to changes in the environment in either space or time.

3. In the extreme habitats, physical factors in the environment as well as positive interactions among individuals exert a greater influence on the life processes of the plants than competition and negative biotic influences. In less extreme habitats with a closed plant cover, negative interactions through competition and herbivory are more important than the physical factors.

4. Physical factors are important selective forces in both winter and summer. Snow depth and duration are important in determining species distributions but their effects may only be interpreted indirectly in summer. During summer, growth rates are high and arctic plants have circumvented the limitations of short growing seasons by living and developing over long periods of time. They have adapted to their infertile soils by conserving and recycling nutrients, and clonal plants with interdependent ramets seem well fitted to exploit patchy tundra environments.

5. Plant-animal relationships are important in the Fennoscandian Arctic. The cyclical nature of infestations of defoliating caterpillars and grazing rodents is poorly understood, yet exerts a considerable influence on the dynamics of the plant communities and relationships among plant species.

6. The magnitude of predicted changes in the climate of the Arctic suggests that gaining an understanding of how Fennoscandian arctic ecosystems will change and how they feed back to climate change is now a major challenge for ecologists in the North.

REFERENCES

AALTONEN, K., PASAREN, S., and AALTONEN, H. 1984. Measuring system for analysing of the CO_2 concentration under snow. Aquilo Series Botanica 23:65-68.

ALDENIUS, J., CARLSSON, B., and KARLSSON, S. 1983. Effects of insect trapping on growth and nutrient content of *Pinguicula vulgaris* L. in relation to the nutrient content of the substrate. New Phytologist 93:53-59.

ANDERSSON, M., and JONASSON, S. 1986. Rodent cycles in relation to food resources on an alpine heath. Oikos 46:93-106.

BELL, K.L., and BLISS, L.C. 1980. Plant reproduction in a high arctic environment. Arctic and Alpine Research 12:1-10.

BERG, A., KJELVIK, S., and WIELGOLASKI, F.E. 1975. Distribution of ^{14}C photosynthates in Norwegian alpine plants. In: Wielgolaski, F.E., ed. Fennoscandian tundra ecosystems. Part 1: Plants and microorganisms. Berlin: Springer. Ecological Studies 16:121-128.

BILLINGS, W.D. 1974. Arctic and alpine vegetation: Plant adaptations to cold summer climates. In: Ives, J.D., and Barry, R.G., eds. Arctic and alpine environments. London: Methuen and Co. Ltd. 403-443.
_____. 1987. Constraints to plant growth, reproduction, and establishment in arctic environments. Arctic and Alpine Research 19(4):357-365.

BILLINGS, W.D., and MOONEY, H.A. 1968. The ecology of arctic and alpine plants. Biological Review 43:481-529.

BLISS, L.C., ed. 1977. Truelove Lowland, Devon Island, Canada. A High Arctic Ecosystem. Edmonton: The University of Alberta Press 1977. 714 p.

BLISS, L.C., and WIELGOLASKI, F.E. 1973. Primary production and production processes, tundra biome. International Biological Programme Tundra Biome. Proceedings of the conference in Dublin, Ireland, April 1973. Swedish IBP Committee, Stockholm 1973:3-256.

BLISS, L.C., HEAL, O.W., and MOORE, J.J., eds. 1981. Tundra ecosystems: A comparative analysis. International Biological Programme (IBP) 25. London: Cambridge University Press. 813 p.

BROWN, J., MILLER, P.C., TIESZEN, L.L., and BUNNELL, F.L., eds. 1980. An arctic ecosystem. The coastal tundra at Barrow, Alaska. US-IBP Series 12. Stroudsburg, Pennsylvania: Dowden, Hutchenson & Ross, Inc. 571 p.

CALLAGHAN, T.V. 1971. The growth of *Phleum alpinum* L. in contrasting habitats at a sub-Antarctic station. New Phytologist 70:1143-1154.
_____. 1974. Intraspecific variation in *Phleum alpinum* L. with special reference to polar populations. Arctic and Alpine Research 6:361-401.
_____. 1980. Age related patterns of nutrient allocation in *Lycopodium annotinum* from Swedish Lapland. Oikos 35:373-386.
_____. 1984. Growth and translocation in a clonal southern hemisphere sedge *Uncinia meridensis*. Journal of Ecology 72:529-546.
_____. 1987. Plant population processes in arctic and boreal regions. Ecological Bulletins 38:58-68.
_____. 1988. Physiological and demographic implications of modular construction in cold environments. In: Davy, A.J., Hutchings, M.J., and Watkinson, A.R., eds. Plant population ecology. Oxford: Blackwell. 111-135.

CALLAGHAN, T.V., and EMANUELSSON, U. 1985. Population structure and processes of tundra plants and vegetation. In: White, J., ed. The population structure of vegetation. Dordrecht: Dr. W. Junk Publishers. 399-439.

CHAPIN, F.S., III. 1987. Environmental control over growth of tundra plants. In: Sonesson, M., ed. Research in arctic life and earth sciences: Present knowledge and future perspectives. Ecological Bulletins 38:69-76.

CHRISTIANSEN, E. 1983. Fluctuations in some small rodent populations in Norway 1971-1979. Holarctic Ecology 6:24-31.

CONOLLY, A.P., and DAHL, E. 1970. Maximum summer temperature in relation to modern and quaternary distribution of certain arctic-montane species in the British Isles. In: Walker, D., and West, R.G., eds. Studies in the vegetational history of the British Isles. Cambridge: Cambridge University Press. 159-223.

COULIANOS, C.C., and EDSTRÖM, R. 1971. Djuren, växterna och vintern [Animals, plants and winter]. Stockholm: Svenska Naturskyddsföreningen. 1-76. In Swedish.

CRAWFORD, R.M.M. 1989. Studies in plant survival: Ecological case histories of plant adaptation and adversity. Oxford: Blackwell Scientific Publications. 296 p.

CRAWFORD, R.M.M., and PALIN, M.A. 1981. Root respiration and temperature limits to the North-South distribution of four perennial maritime plants. Flora 171:338-354.

CRITTENDEN, P.D., and KERSHAW, K.A. 1978. Discovering the role of lichens in the nitrogen cycle in boreal arctic ecosystems. Bryologist 81:258-267.

DAHL, E. 1951. On the relation between summer temperature and the distribution of alpine vascular plants in the lowlands of Fennoscandia. Oikos 14:22-52.
_____. 1956. Rondane. Mountain vegetation in South Norway and its relation to the environment. Skrifter Norske Videnskaps Akademien. I. Matematisk naturvidenskapelige klasse 1956(3). 374 p.
_____. 1963. Plant migrations across the North Atlantic Ocean and their importance for the palaeogeography of the region. In: Löve, A., and Löve, D., eds. North Atlantic biota and their history. New York: Pergamon Press. 173-188.
_____. 1987. The nunatak theory reconsidered. In: Sonesson, M., ed. Research in arctic life and earth sciences: Present knowledge and future perspectives. Ecological Bulletins 38:77-94.

EMANUELSSON, U. 1984. Ecological effects of grazing and trampling on mountain vegetation in northern Sweden. Dissertation, Department of Plant Ecology, University of Lund.

ERIKSSON, O., PALO, T., and SÖDERSTRÖM, L. 1981. Renbetningen vintertid [Reindeer grazing in winter]. Växtekologiska Studier (Svenska Växtgeografiska Sällskapet, Uppsala) 13:25-59. In Swedish.

EUROLA, S. 1968. Über die Ökologie der nordfinnischen Moorvegetation im Herbst, Winter und Frühling. Annales Botanici Fennici 5:83-97.

_____. 1972. Germination of seeds collected in Spitsbergen. Annales Botanici Fennici 9:149-159.

FRIES, T.C. 1913. Botanische Untersuchungen im nördlichsten Schweden. Vetenskapliga och praktiska undersökningar i Lappland, Flora och Fauna 2. 361 p.

GAARE, E., and SKOGLAND, T. 1975. Wild reindeer food habits and range use at Hardangervidda. In: Wielgolaski, F.E., ed. Fennoscandian tundra ecosystems. Part 2: Animals and systems analysis. Berlin: Springer. Ecological Studies 17:195-205.

GAUSLAA, Y. 1984. Heat resistance and energy budget in different Scandinavian plants. Holarctic Ecology 7:1-78.

GJAEREVOLL, O. 1949. Snöleievegetasjon i Oviksfjellene. Acta Phytogeographica Suecica 25:1-105.

_____. 1965. Chionophilous plant communities. Acta Phytogeographica Suecica 50:262-268.

GRANHALL, U., and LID-TORSVIK, V. 1975. Nitrogen fixation by bacteria and free-living blue-green algae in tundra areas. In: Wielgolaski, F.E., ed. Fennoscandian tundra ecosystems. Part 1: Plants and microorganisms. Berlin: Springer. Ecological Studies 16:305-315.

GRIME, J.P. 1979. Plant strategies and vegetation processes. New York: John Wiley and Sons. 222 p.

HAGMAN, M. 1971. On self- and cross-incompatibility shown by Betula verrucosa Ehrh. and Betula pubescens Ehrh. Communicationes Forestalia Fennici 73(6):1-125.

HANSSON, M. 1984. Composition of cyclic and non-cyclic vole population: On the causes of variation in individual quality among Clethrionomys glareosus in Sweden. Oecologia (Berlin) 63:199-206.

_____. 1987. An interpretation of rodent dynamics as due to trophic interactions. Oikos 50:308-318.

HANSSON, M., and HENTTONEN, H. 1985. Gradients in density variations of small rodents: The importance of latitude and snow cover. Oecologia (Berlin) 67:394-402.

HAUKIOJA, E., and KOPONEN, S. 1975. Birch herbivores and herbivory at Kevo. In: Wielgolaski, F.E., ed. Fennoscandian tundra ecosystems. Part 2: Animals and systems analysis. Berlin: Springer. Ecological Studies 17:181-188.

HAUKIOJA, E., NIEMELÄ, P., and SIRÉN, S. 1985. Foliage phenols and nitrogen in relation to growth, insect damage, and ability to recover after defoliation, in the mountain birch Betula pubescens ssp. tortuosa. Oecologia (Berlin) 65:214-222.

HAVAS, P. 1984. Winter and the boreal forests. Aquilo Series Botanica 23:9-16.

HAVAS, P., and MÄENPÄÄ, E. 1972. Evolution of carbon dioxide at the floor of a Hylocomium Myrtillus type spruce forest. Aquilo Series Botanica 11:4-22.

HEADLEY, A.D., CALLAGHAN, T.V., and LEE, J.A. 1988a. Phosphate and nitrate movement in the evergreen clonal plants Lycopodium annotinum L. and Diphasiastrum complanatum (L.) Holmb. New Phytologist 110:487-495.

HEADLEY, A.D., CALLAGHAN, T.V., and LEE, J.A. 1988b. Water uptake and movement in the evergreen clonal plants Lycopodium annotinum L. and Diphasiastrum complanatum (L.) Holmb. New Phytologist 110:497-502.

HEIDE, O. 1988. Environmental modifications of flowering and viviparous proliferation in Festuca vivipara and F. ovina. Oikos 51:171-178.

HETHERINGTON, A.M., HUNTER, M.J.S., and CRAWFORD, R.M.M. 1984. Evidence contrary to existence of storage lipid in leaves of plants inhabiting cold climates. Plant, Cell and Environment 7:223-227.

HUSTICH, I. 1979. Ecological concepts and biographical zonation in the North: The need for a generally accepted terminology. In: Sonesson, M., and Kallio, P., eds. Fennoscandian Tree-Line Conference at Kevo-Abisko, 6-14 September 1977. Holarctic Ecology 2:208-217.

JONASSON, S. 1983. Nutrient content and dynamics in north Swedish shrub tundra. Holarctic Ecology 6:295-304.

_____. 1986. Influence of frost heaving on soil chemistry and on distribution of plant growth form. Geografiska Annaler 68A(1986)3:185-195.

JONASSON, S., and CHAPIN, F.S., III. 1985. Significance of sequential leaf development for nutrient balance of the cotton sedge, Eriophorum vaginatum L. Oecologia (Berlin) 67:511-518.

JONASSON, S., BRYANT, J.P., CHAPIN, F.S., III, and ANDERSSON, M. 1986. Plant phenols and nutrients in relation to variations in climate and rodent grazing. American Naturalist 128:394-408.

JONSDOTTIR, I.S., and CALLAGHAN, T.V. 1988. The interrelationships between different generations of interconnected tillers of Carex bigelowii. Oikos 52:120-128.

JONSDOTTIR, I.S., and CALLAGHAN, T.V. 1989. Localised defoliation stress and the movement of ^{14}C photoassimilates between tillers of Carex bigelowii. Oikos 54:211-219.

JONSDOTTIR, I.S., and CALLAGHAN, T.V. 1990. Intraclonal translocation of ammonium and nitrate nitrogen in Carex bigelowii using ^{15}N and nitrate reductase assays. New Phytologist 114:419-428.

JUNNILA, S. 1984. Seasonal changes in cold hardiness of Diapensia lapponica. Aquilo Series Botanica 23:81-85.

JUNTTILA, O., and KAURIN, Å. 1985. Climatic control of apical growth cessation in latitudinal ecotypes of Salix pentandra L. In: Kaurin, Å., Junttila, O., and Nilsen, J., eds. Plant production in the North. Proceedings Workshop Plant Adaptation, Tromsö, 4-10 September 1983. Oslo: Universitetsforlaget. 83-91.

KALELA, O. 1962. On the fluctuations in the numbers of arctic and boreal small rodents as a problem of production biology. Annales Academiae Scientiarum Fennicae, Series A(IV) 66:1-38.

KALLIO, P. 1984. Adaptation and evolution at the northern limits of life. Acta Universitatis Oulensis F1. 1984. Scripta Academica. Oulu: Printing Centre of the University of Oulu. 131-150.

KALLIO, P., and LEHTONEN, J. 1975. On the ecocatastrophy of birch forests caused by Oporinia autumnata (Bkh) and the problems of reforestation. Report from the Kevo Subarctic Research Station 10:70-84.

KALLIO, P., and VALANNE, N. 1975. On the effect of continuous light on photosynthesis in mosses. In: Wielgolaski, F.E., ed. Fennoscandian tundra ecosystems. Part 1: Plants and microorganisms. Berlin: Springer. Ecological Studies 16:121-128.

KALLIO, P., NIEMI, S., SULKINOJA, M., and VALANNE, T. 1983. The Fennoscandian birch and its evolution in the marginal forest zone. Nordicana 47:101-109.

KALLIO, S., and KALLIO, P. 1975. Nitrogen fixation in lichens at Kevo, North-Finland. In: Wielgolaski, F.E., ed. Fennoscandian tundra ecosystems. Part 1: Plants and microorganisms. Berlin: Springer. Ecological Studies 16:292-304.

KARLSSON, P.S. 1987a. Niche differentiations with respect to light utilization among coexisting dwarf shrubs in a subarctic woodland. Polar Biology (1987)8:35-39.

_____. 1987b. Micro-site performance of evergreen and deciduous dwarf shrubs in a subarctic heath in relation to nitrogen status. Holarctic Ecology 10:114-119.

KARLSSON, P.S., and CARLSSON, B. 1984. Why does Pinguicula vulgaris L. trap insects? New Phytologist 97:25-30.

KARLSSON, P.S., and NORDELL, O. 1987. Growth of Betula pubescens and Pinus sylvestris seedlings in a subarctic environment. Functional Ecology 1:37-44.

KARLSSON, P.S., and NORDELL, O. 1988. Intraspecific variation in nitrogen status and photosynthetic capacity within mountain birch populations. Holarctic Ecology 11:293-297.

KAURIN, Å., JUNTTILA, O., and HANSEN, J. 1981. Seasonal changes in frost hardiness in cloudberry (Rubus chamaemorus) in relation to carbohydrate content with special reference to sucrose. Physiologia Plantarum 52:310-314.

KAURIN, Å., STUSHNOFF, C., and JUTTILA, O. 1982. Vegetative growth and frost hardiness of cloudberry (Rubus chamaemorus) as affected by temperature and photoperiod. Physiologia Plantarum 55:76-81.

KIHLMAN, O. 1890. Pflanzenbiologische Studien aus Russisch Lappland. Ein Beitrag zur Kenntnis der regionalen Gliederung und der polaren Waldgrenze. Acta Societatis pro Fauna et Flora Fennica 6(3). 256 p.

KJELLBERG, B., KARLSSON, S., and KERSTENSSON, I. 1982. Effects of heliotropic movements of flowers of Dryas octopetala L and gynoecium temperature and seed development. Oecologia (Berlin) 54:10-13.

KULLMAN, L. 1983. Past and present tree-lines of different species in the Handölan valley, Central Sweden. Nordicana 47:25-47.

_____. 1984. Germinability of mountain birch (Betula pubescens ssp. tortuosa) along two altitudinal transects downslope from the tree-limit, in Sweden. Report from the Kevo Subarctic Research Station 19:11-18.

LAINE, K., and HENTTONEN, H. 1983. The role of plant production in microtine cycles in northern Fennoscandia. Oikos 44:407-414.

LAINE, K., and HENTTONEN, H. 1987. Phenolics/nitrogen ratios in the blue berry Vaccinium myrtillus in relation to temperature and microtine density in Finnish Lapland. Oikos 50:389-395.

LÖVE, A., and LÖVE, D., ed. 1963. North Atlantic biota and their history. London: Pergamon Press. 430 p.

LÖVE, A., and LÖVE, D. 1974. Origin and evolution of the arctic and alpine floras. In: Ives, J.D., and Barry, R.G., eds. Arctic and Alpine Environments. London: Methuen and Co. Ltd. 571-603.

LUNDQVIST, J. 1962. Patterned ground and related phenomena in Sweden. Sveriges Geologiska Undersökning Stockholm Serie C No. 583:1-101.

McGRAW, J.B. 1980. Seed bank size and distribution of seeds in cotton grass tussock tundra, Eagle Creek, Alaska. Canadian Journal of Botany 58:1607-1611.

MALMER, N., and NIHLGÅRD, B. 1980. Supply and transport of mineral nutrients in a subarctic mire. Ecological Bulletins 30:63-95.

MARCHAND, P.S. 1987. Life in the cold: An introduction to winter ecology. Hanover: University Press of New England. 176 p.

MÖLGAARD, P. 1982. Temperature observations in high arctic plants in relation to microclimate in the vegetation of Peary Land, North Greenland. Arctic and Alpine Research 14:105-115.

MYRBERGET, S. 1973. Geographical synchronism of cycles of small rodents in Norway. Oikos 24:220-224.

———. 1979. Winter food of willow grouse in two Norwegian areas. Meddelelser Fra Norsk Viltforskning (Trondheim) 3(7):1-32.

NIEMELÄ, P. 1979. Topographic delimitation of Oporinia damages: Experimental evidence of the effect of winter temperature. Report from the Kevo Subarctic Research Station 15:33-36.

NIEMELÄ, P., ARO, E.-M., and HAUKIOJA, E. 1979. Birch leaves as a resource for herbivores. Damage-induced increase in leaf phenols with trypsin-inhibiting effects. Report from the Kevo Subarctic Research Station 15:37-40.

NORDAL, I. 1987. Tabula rasa after all? Botanical evidence for ice-free refugia in Scandinavia reviewed. Journal of Biogeography 14:377-388.

NORDAL, I., WESENBERG, J., and ÖDEGAARD, M. 1988. "Overvintrings-teorien" belyst ved populasjonsgenetiske analyser — presentation av et prosjekt. Blyttia 46:85-96. With an English summary.

OKSANEN, L., FRETWELL, S.A., ARRUDA, J., and NIEMELÄ, P. 1981. Exploitation ecosystems in gradients of primary productivity. American Naturalist 118:240-261.

OKSANEN, L., OKSANEN, T., LUKKARI, A., and SIRÉN, S. 1987. The role of phenol-based inducible defence in the interaction between tundra populations of the vole Clethrionomys rufocanus and the dwarf shrub Vaccinium myrtillus. Oikos 50:371-380.

PIHAKASKI, K., and JUNNILA, S. 1988. Cold acclimation of subarctic Diapensia lapponica L. Functional Ecology 2(2):221-228.

PITELKA, F.A. 1964. The nutrient recovery hypothesis for arctic microtine cycles. Introduction. In: Crisp, D.J., ed. Grazing in terrestrial and marine environments: A symposium of the British Ecological Society, Bangor, 11-14 April 1963. Oxford: Blackwell. 55-56.

ROSSWALL, T., and GRANHALL, U. 1980. Nitrogen cycling in a subarctic mire at Stordalen. In: Sonesson, M., ed. Ecology of a subarctic mire. Ecological Bulletins 30:209-234.

RYDÉN, B.E., and KOSTOV, L. 1980. Thawing and freezing in tundra soils. In: Sonesson, M., ed. Ecology of a subarctic mire. Ecological Bulletins 30:251-281.

SAKAI, A., and LARCHER, W. 1987. Frost survival of plants. New York: Springer. Ecological Studies 62:1-321.

SALISBURY, F.B. 1984. Plant growth under snow. Aquilo Series Botanica 23:1-7.

SANDBERG, G. 1958. Fjällens vegetationsregioner, vegetationsserier och viktigaste växtekologiska faktorer. In: Skunke, F., ed. Renbeten och deras gradering. Lappväsendet-Renforskningen: Meddelande 4(1958):36-60. In Swedish.

SAVILE, D.B.O. 1972. Arctic adaptation in plants. Canadian Department of Agriculture Monograph 6:1-81.

SCHULZ, A.M. 1964. The nutrient recovery hypothesis for arctic microtine cycles. II. Ecosystem variables in relation to the arctic microtine cycles. In: Crisp, D.J., ed. Grazing in Terrestrial and Marine Environments: A Symposium of the British Ecological Society, Bangor, 11-14 April 1963. Oxford: Blackwell. 57-68.

SKRE, O. 1979. The regional distribution of vascular plants in Scandinavia with requirements for high summer temperatures. Norwegian Journal of Botany 26:295-318.

SONESSON, M. 1966. On Drepanocladus trichophyllus in the Torneträsk area. Botaniska Notiser 119(3):379-400.

———. 1969. Studies on mire vegetation in the Torneträsk area, northern Sweden. II. Winter condition of the poor mires. Botaniska Notiser 122:481-511.

———. 1974. Late Quaternary forest development of the Torneträsk area, North Sweden. 2. Pollen analytical evidence. Oikos 25:288-307.

———, ed. 1980. Ecology of a subarctic mire. Ecological Bulletins 30. 313 p.

———. 1986. Photosynthesis in lichen populations from different altitudes in Swedish Lapland. Polar Biology 5:113-124.

———. 1989. Water, light and temperature relations of the epiphytic lichens Parmelia olivacea and Parmeliopsis ambigua in northern Swedish Lapland. Oikos 56:402-415.

SONESSON, M., and HOOGESTEGER, J. 1983. Recent tree-line dynamics (Betula pubescens Ehrh. ssp. tortuosa (Ledeb.) Nyman in northern Sweden. Nordicana 47:47-54.

SONESSON, M., WIELGOLASKI, F.E., and KALLIO, P. 1975. Description of Fennoscandian tundra ecosystems. In: Wielgolaski, F.E., ed. Fennoscandian tundra ecosystems. Part 1: Plants and microorganisms. Berlin: Springer. Ecological Studies 16:3-28.

SÖRENSEN, T. 1941. Temperature relations and phenology of the northeast Greenland flowering plants. Meddelelser om Gronland Kobenhavn 125(9):1-305.

SPIDSÖ, K. 1980. Food selection by Willow Grouse Lagopus lagopus chicks in northern Norway. Ornis Scandinavica 11:99-105.

STOUTJESDIJK, P. 1970. A note on vegetation temperatures above the timberline in southern Norway. Acta Botanica Neerlandica 19:918-925.

SVENSSON, B.H. 1980. Carbon dioxide and methane fluxes from the ombrotrophic parts of a subarctic mire. In: Sonesson, M., ed. Ecology of a subarctic mire. Ecological Bulletins 30:235-250.

SVENSSON, B.H., VEUM, A.H., and KJELVIK, S. 1975. Carbon losses from tundra soils. In: Wielgolaski, F.E., ed. Fennoscandian tundra ecosystems. Part 1: Plants and microorganisms. Berlin: Springer. Ecological Studies 16:279-286.

SVENSSON, B.M., and CALLAGHAN, T.V. 1988a. Small-scale vegetation pattern related to the growth of Lycopodium annotinum and variations in its micro-environment. Vegetatio 76:167-177.

SVENSSON, B.M., and CALLAGHAN, T.V. 1988b. Apical dominance and the simulation of metapopulation dynamics in Lycopodium annotinum Oikos 51:331-342.

TAST, J., and KALELA, O. 1971. Comparison between rodent cycles and plant production in Finnish Lapland. Annales Academiae Scientarum Fennicae, Series A(IV)186:1-14.

TENOW, O. 1972. The outbreaks of Oporinia autumnata Bkh. and Operophthera ssp. (Lep. Geometridae) in the Scandinavian mountain chain and northern Finland 1862-1968. Zoologiska Bidrag Uppsala Supplement 2. 107 p.

———. 1975. Topographical dependence on an outbreak of Oporinia autumnata Bkh. (Lep. Geometridae) in a mountain birch forest in northern Sweden. Zoon 3:85-110.

———. 1983. Topoclimatic limitations to the outbreaks of Epirrita (= Oporinia) autumnata (Bkh.) (Lepidoptera: Geometridae) near the forest limit of the mountain birch in Fennoscandia. Nordicana 47:159-164.

TENOW, O., and HOLMGREN, B. 1987. Low winter temperatures and an outbreak of Epirrita autumnata along a valley of Finnmarksvidda, the "cold-pole" of northern Fennoscandia. In: Axelsson, H., and Holmgren, B., eds. Climatological extremes in the mountain, physical background, geomorphological and ecological consequences. Department of Physical Geography of the University of Uppsala, UNGI Rapport 15:203-216.

TIESZEN, L.L. 1978. Photosynthesis in principal Barrow, Alaska, species: A summary of field and laboratory responses. In: Tieszen, L.L., ed. Vegetation and production ecology of an Alaskan arctic tundra. New York: Springer. Ecological Studies 29:241-268.

TUOMI, J., NIEMELÄ, P., HAUKIOJA, E., SIRÉN, S., and NEUVONEN, S. 1984. Nutrient stress: An explanation for plant herbivore responses to defoliation. Oecologia (Berlin) 61:208-210.

VAARAMA, A., and VALANNE, T. 1973. On the taxonomy, biology and origin of Betula tortuosa Ledeb. Report from the Kevo Subarctic Research Station 10:70-84.

VESTERGREN, T. 1902. Om den olikformiga snötäckningens inflytande på vegetationen i Sarekfjällen. Botaniska Notiser 1902:241-268. With a German summary.

VORREN, K.-D. 1978. Late and Middle Weichselian stratigraphy of Andöya, North Norway. Boreas 7:19-38.

VORREN, T., VORREN, K.-D., ALM, T., GULLIKSEN, S., and LÖVLIE, R. 1988. The last deglaciation (20,000 to 11,000 B.P.) on Andöya, northern Norway. Boreas 17:41-77.

WIELGOLASKI, F.E., ed. 1975a. Fennoscandian tundra ecosystems. Part 1: Plants and microorganisms. Berlin: Springer. Ecological Studies 16. 366 p.

———, ed. 1975b. Fennoscandian tundra ecosystems. Part 2: Animals and systems analysis. Berlin: Springer. Ecological Studies 17. 337 p.

WIELGOLASKI, F.E., and ROSSWALL, T. 1972. Proceedings IV. International Meeting on the Biological Productivity of Tundra, Leningrad U.S.S.R., October 1971. Stockholm: Swedish IBP Committee. 3-320.

WIJK, S. 1986a. Influence of climate and age on annual shoot increment in Salix herbacea. Journal of Ecology 74(3):685-692.

———. 1986b. Performance of Salix herbacea in an alpine snow-bed gradient. Journal of Ecology 74(3):675-684.