

## THE CALEDONIAN MOUNTAINS, NORTHERN EUROPE, AND THEIR CHANGING ECOSYSTEMS

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*SUMMARY.- With the exception of solar conditions, the climate of the Caledonian Mountains, Northern Europe, is influenced more by the nearness to the Atlantic Ocean and the Gulf Stream than by altitude and latitude. The length of the photoperiod during the growing season increases with latitude, although the total solar influx decreases. Heaths composed of species with a boreal distribution are particularly characteristic at low altitudes and latitudes, whereas species with an arctic and arctic-alpine distribution dominate at high altitudes and latitudes. Periodic events in the population dynamics of certain plant and animal species distinguish the ecosystems at high latitudes from those at low latitude. The effects of global change are likely to become most pronounced in the north since the rate at which the ultraviolet-B (UV-B) absorbing ozone layer is being reduced and the increase in concentration of «greenhouse gases» in the atmosphere are both higher in the arctic than in regions further south. Changes in the ecosystems due to increased direct human impacts are also likely to occur in some areas.*

*RÉSUMÉ.- À l'exception des conditions solaires, le climat des montagnes dites «Caledonian», au Nord de l'Europe, est beaucoup plus influencé par la proximité de l'Océan Atlantique et le Gulf Stream que par l'altitude ou la latitude. La durée de la photopériode pendant la saison de végétation augmente avec la latitude, tandis que la radiation solaire total s'abaisse. À des altitudes et latitudes basses, les landes riches en espèces à distribution boréale deviennent caractéristiques, tandis que les espèces arctiques et arctico-alpines dominent dans les hautes altitudes ou latitudes. Des événements périodiques dans la dynamique de la population de certains animaux ou plantes peuvent distinguer les écosystèmes des hautes latitudes de ceux de basse latitude. Les effets du changement climatique global seraient bien sûr plus prononcés au nord, car d'une part le taux d'absorption de l'ultraviolet-B (UV-B) par la couche d'ozone devient plus bas et d'autre part la concentration de gaz à effet de serre est plus forte dans les régions arctiques que plus au sud. De plus, dans certaines régions, il y a de changements dans les écosystèmes dûs à un impact direct croissant des activités humaines.*

*RESUMEN.- Condiciones solares aparte, el clima de las montañas caledonianas, situadas en el N de Europa, viene condicionado por la cercanía del Océano Atlántico y la corriente del Golfo, más que por la latitud y la altitud. Es sabido que la duración del fotoperíodo en el período de crecimiento vegetativo se incrementa con la latitud, aunque el flujo total solar descienda. Los brezales en cuya composición entran especies de distribución boreal son muy característicos de las bajas altitudes y latitudes. Ahora bien, las perturbaciones periódicas que tienen lugar en la dinámica poblacional de ciertas plantas o animales distinguen los ecosistemas de latitudes elevadas de los que están situados a baja latitud. Sin duda, los efectos del cambio global serán más intensos en el Norte, por cuanto la tasa de absorción de rayos ultravioleta B (UV-B) por parte de la capa de ozono se aminora y el incremento de la concentración de los «gases-invernadero» es consecuentemente mayor en el Ártico que en las zonas más meridionales. Además, en los ecosistemas también se están notando cambios por causa de los crecientes impactos directos de las actividades humanas en ciertas áreas.*

**Keywords:** Changing ecosystems, climate and vegetation changes, human impact, Northern Europe.

## 1. Introduction

The characteristic mountains of northern Europe were formed in the Devonian Era during the Caledonian orogenesis. They are older and of a lower relief than those of central and southern Europe. The highest peak (2470 m) is, for instance, only half as high as the highest peak in the Alps (4810 m). The Caledonian Mountains of Northern Europe stretch from the eastern part of Greenland, across Scotland and the Svalbard Islands to Scandinavia, where they form the Scandinavian Mountain Range or the «Scandes» (Figure 1). Overall, they extend from latitudes 52° N to 80° N and from longitudes 30° W to 30° E. Their wide distribution and the heterogeneity in topography, bedrock composition and climate form the environmental basis for heterogeneous biota. Although there are still areas subject to little or no direct human influence, the indirect effects of man on the ecosystems have been increasing. The increased concentrations of «greenhouse gases» (Figure 2) and air pollutants have resulted, *inter alia*, in a decrease in the thickness of the stratospheric ozone column. Direct impacts such as overgrazing, human trampling and littering seem likely to increase even in the still relatively virgin areas owing to changed management practices in reindeer management and a booming European tourism.

This paper describes the principal characteristics of Northern European mountains, and explores the implications of global climate and environmental change on their ecosystems. Species names follow

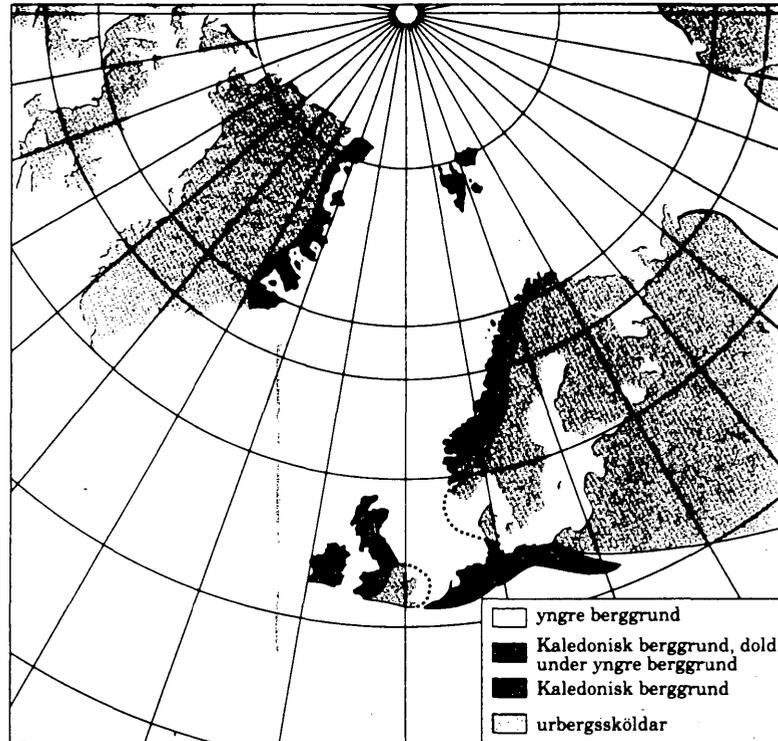


Figure 1. The Caledonian Mountains, Northern Europe (in black).  
From NATIONALENCYKLOPEDIN, 1993).

HYLANDER (1955) for vascular plants, MÅRTENSSON (1956) for bryophytes, and SANTESSON (1984) for lichens.

## 2. Climate

With the exception of eastern Greenland, the Atlantic Gulf Stream helps keep temperatures above the latitudinal norm and results in a relatively mild climate. The annual temperature amplitudes are small in comparison with areas at corresponding latitudes in Canada and Alaska. Terrestrial temperatures at these latitudes are related more to the distance from the sea and to altitude than to latitude (RATCLIFFE & THOMPSON, 1988; SONESSON & CALLAGHAN, 1991; WIELGOLASKI, 1997). There is a

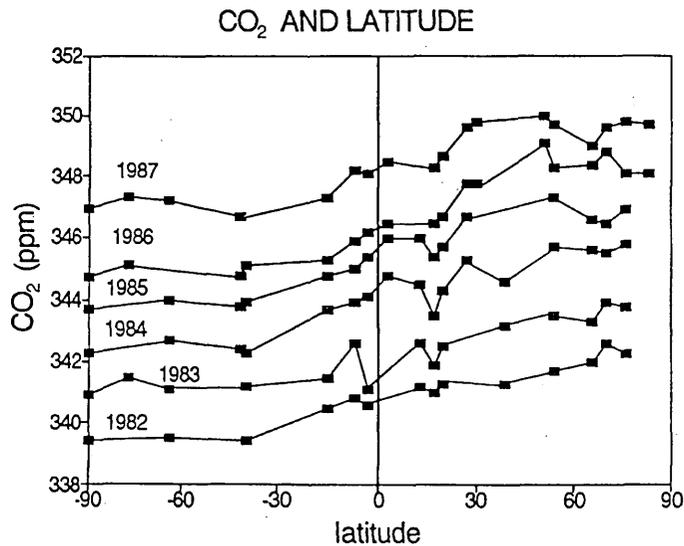


Figure 2. Latitudinal differences in the rate of increase in atmospheric CO<sub>2</sub> concentrations. From GOREAU (1990).

general east to west gradient in temperature and precipitation, which can be very sharp. For instance, within a distance of only 40 km in the northern part of the Scandes the annual precipitation increases from 300 mm to 1000 mm from east to west, whereas the annual temperature differences between the coldest and warmest month differ only by 2°C between the east and west (SONESSON, 1967).

Winter dominates the environment, its length increasing with latitude. However, north of the Arctic Circle there is continuous daylight in summer and the length of this period increases with latitude. The highly variable photoperiod can strongly affect both plant growth (HEIDE, 1980; HEIDE *et al.*, 1985) and the distributions of plants. Due to solar inclination light influx decreases towards the north. A photon flux density (PFD) of  $> 500 \mu\text{mol m}^{-2} \text{s}^{-1}$ , which is close to the optimum level for photosynthesis in many plants in the north, may occur less than 15% of the growing season at 68° N latitude (KARLSSON, 1989; SONESSON *et al.*, 1992 a, b; DIEMER, 1996). In contrast, a PFD of  $> 500 \mu\text{mol m}^{-2} \text{s}^{-1}$  occurs more than 50% of the growing season in the Alps at 47° N. In the latter, light saturation of photosynthesis is usually higher than in the northern Scandes (Figure 3; KÖRNER & DIEMER, 1987).

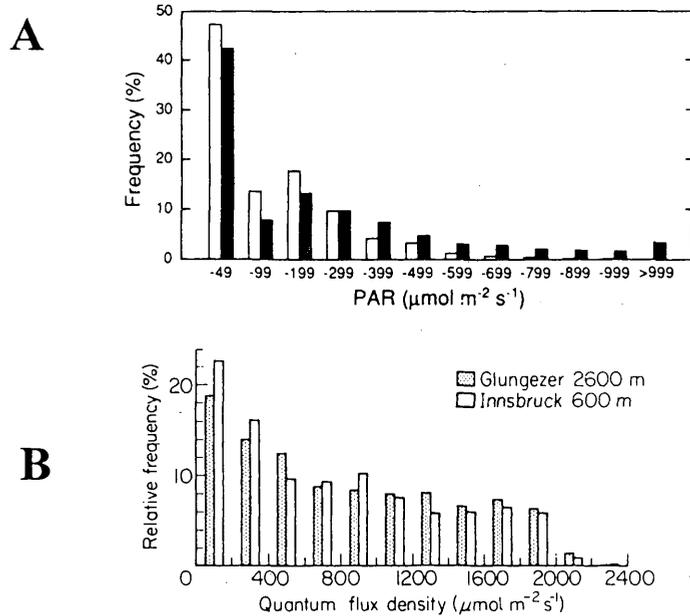


Figure 3. Frequency distributions of photon flux densities (PFD,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) of photosynthetic active radiation (PAR) in the alpine and subalpine belts at Abisko, northern Swedish Lapland (A: black bars=alpine site; open bars=subalpine site) and in the Alps (B: grey bars=subalpine site; open bars=alpine site), during the main growth period. From SONESSON *et al.* (1992a) and KÖRNER & DIEMER (1987).

In addition to daylength and light influx, spectral distribution is of great importance for plant life as the efficiency of many biological processes is highly dependent on wavelength (ROBBERECHT & CALDWELL, 1986). Well-known in this respect is UV-B radiation, its relation to the stratospheric ozone layer, and at least some of its biological effects (DNA damage and skin cancer).

### 3. Biotic zonation

Plant species diversity decreases gradually, but significantly, towards the north. In northernmost Fennoscandia there are only 150 vascular plant species, compared with 500 in more southern parts (Figure 4). On a local scale, vascular plant species distribution often reflects the oceanic-continental climatic gradients rather than the latitudinal differences. The

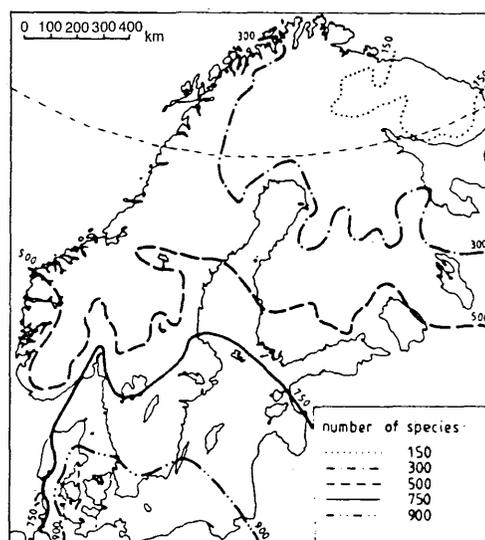


Figure 4. Number of vascular plant species in Fennoscandia.  
From ATLAS ÖVER SVERIGE (1966).

ecosystems are composed of species that can be divided into three principal types based on their origin and distribution, notably arctic, arctic-alpine, and boreal (Figure 5). The altitudinal treeline marks the major borderline between the alpine and sub-alpine zones, and the arctic treeline forms the border between the arctic and sub-arctic. In the lower parts of the alpine area boreal species dominate. They decrease in abundance upwards, while the arctic and arctic-alpine species become successively more important. Many more or less overlapping systems have been suggested for classifying European mountain vegetation (see HAAPASAARI, 1988 for a review). A Scandinavian system (DU RIETZ, 1925) defines three belts above the altitudinal treeline: low, middle, and high alpine. Several attempts have been made to match these with the low arctic, middle arctic, and high arctic zones in the arctic based on similarities in species composition and physiognomy, although the arctic zonation is principally horizontal (HAAPASAARI, 1988). In the northern parts of the Scandes the altitudinal distribution of most plants decreases both with closeness to the sea and with increased latitude. The altitudinal and latitudinal environmental gradients appear to «merge» towards the north, the ecological basis of which is complex. This results in difficulties in discerning the altitudinal belts and arctic zones at high latitudes.

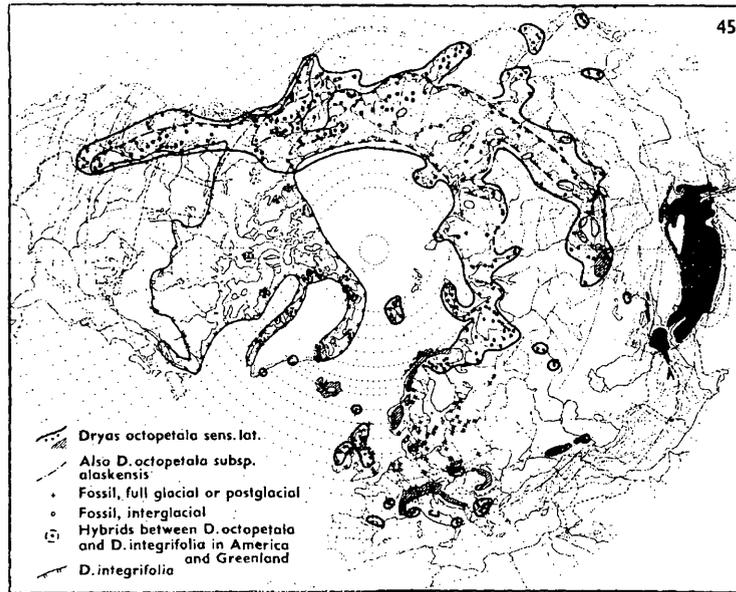


Figure 5a. Distribution of *Dryas octopetala* (45; arctic-alpine distribution).

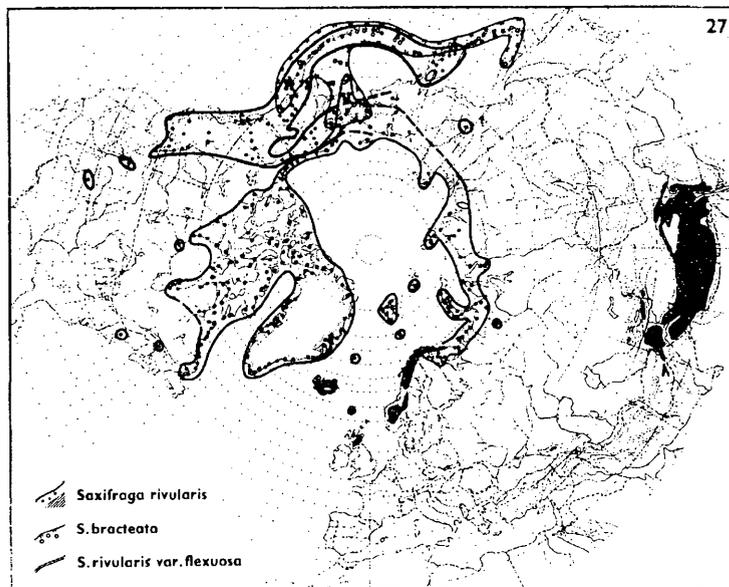


Figure 5b. Distribution of *Saxifraga rivularis* (27; arctic distribution).

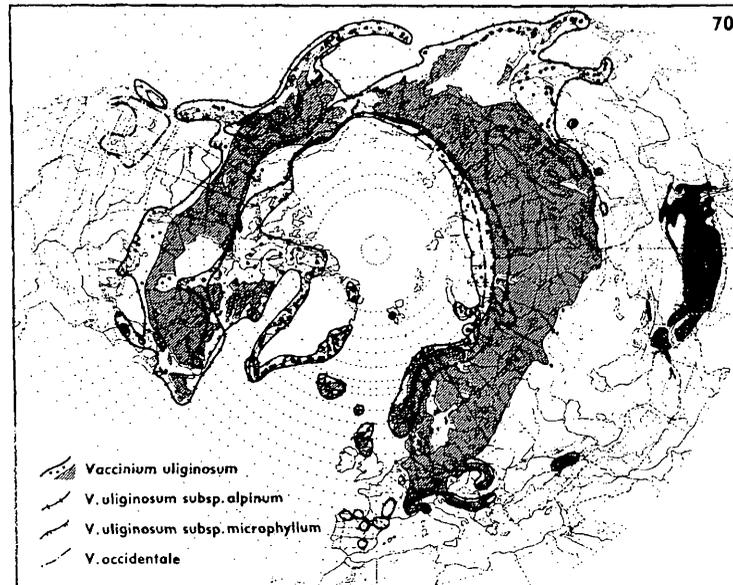


Figure 5c. Distribution of *Vaccinium uliginosum* (70; boreal distribution).  
The three maps from HULTÉN (1971).

#### 4. Human influence on the vegetation

Since the deglaciation period man has lived in the mountains, primarily at low altitudes. The human history of the Scottish Highlands started at 7000 BC (RATCLIFFE & THOMPSON, 1988; NATIONAL ENCYCLOPEDIA, 1993), though probably at least 1000 years before. The Scandes were probably colonised later, although evidence of human presence in northernmost Norway (Varanger Peninsula) dates back to before 8000 BC (VORREN, 1978; VORREN *et al.*, 1988). The Inuit in Greenland seem to be relatively recent immigrants from North America (2500-500 BC). The indigenous people of northern Fennoscandia, the Saamis, have not been mentioned in any historical documents until after about 1000 AD, but they probably existed in small settlements in the area long before then. Grazing by livestock, such as sheep (*Ovis aries* L.) and cattle (*Bos taurus* L.) has long been practised in the Scottish Highlands and in the southern Scandes, particularly on the Norwegian side and close to the sea (RATCLIFFE & THOMPSON, 1988; WIELGOLASKI, 1997). In the northern parts of the Scandes, however, there are large areas that have always been more or less unpopulated except for

sparse Lapp settlements. There, an extensive cattle grazing has never been practised. The reindeer (*Rangifer tarandus* L.), a native wild herbivore, was exclusively hunted by the Lapps until the 16th-17th century. Thereafter its domestication started, mainly in response to a taxation system that was imposed on the Lapps at that time (LUNDMARK, 1982). Nowadays, wild populations of reindeer exist only in the southern Scandes in Norway.

## 5. Ecosystems

Heath is the dominant type of ecosystem at all elevations. Heath is used here to describe ecosystems characterised by ericaceous dwarf shrubs, some narrow-leaved graminoids and only few herbs, but many mosses and lichens (SJÖRS, 1956). From low altitudes up to, and including the lower parts of the low alpine belt (i.e. approximately up to the upper limit of podsol formation (SJÖRS, 1956)) boreal vascular plants such as *Calluna vulgaris*, *Empetrum* spp., *Vaccinium* spp., *Deschampsia flexuosa*, *Trichophorum caespitosum* and *Nardus stricta* predominate together with the mosses *Hylocomium splendens*, *Pleurozium schreberi* and *Dicranum* spp. and some lichens such as *Cladina* spp. Their relative abundance in the ecosystems is mainly related to their location along the oceanic-continental gradient of the mountains. In the middle alpine belt some of these boreal plants still persist, but they are mixed with arctic and arctic-alpine plants such as *Cassiope tetragona*, *Phyllodoce coerulea*, *Carex bigelowii*, *Juncus trifidus*, and *Salix herbacea*. Due to frequent freezing and thawing of the soils plant cover is typically discontinuous, showing more or less narrow zones of bare soil that surround patches of vegetation. In the oceanic areas the moss *Racomitrium lanuginosum* is particularly prominent in this belt. No boreal species grows in the high-alpine belt. Stony, bare soil and soil covered with mosses and lichens dominate the ground together with few vascular plants of an arctic or arctic-alpine origin. They grow solitarily or in small aggregations of shoots. *Ranunculus glacialis*, *Salix herbacea*, *Luzula arcuata*, and *Huperzia selago* are species typical of this belt.

On sufficiently moist and well-drained calcareous soils grasslands dominate. Grasslands are characterised by the presence of herbs and broad-leaved graminoids, as well as moss and lichen species not found in the heaths, and by the absence of ericaceous plants. Common boreal plants in the sub-alpine and low alpine grasslands include *Cirsium heterophyllum*, *Ranunculus acris*, *Geranium sylvaticum*, *Trollius europaeus* and *Milium effusum*. In the middle alpine belt arctic-alpine species such as *Phleum alpinum*, *Saxifraga aizoides*, *Bartsia alpina*, *Polygonum viviparum* and *Dryas octopetala* become prominent.

Mires are common in areas with high precipitation and/or with a high and even stagnant water table. Oligotrophic mires (poor fens and bogs *sensu* SONESSON, 1970) and heaths have many vascular plant species in common, however mires are characterised by the presence of numerous peat-mosses in the ground-layer. Nutrient rich mires (rich fens of SONESSON, 1970) have many vascular plants in common with the grasslands, but it is the bryophytes other than peat mosses that give their special character.

## 6. Ecosystem Processes

### 6.1 *Evolution and Adaptation*

The last glaciation ended less than 10000 years ago in most of northern Fennoscandia (SONESSON, 1974), although some islands of northern Norway were deglaciated much earlier than that (VORREN, 1978; VORREN *et al.*, 1988). Following the deglaciation the biota of the present ecosystems either colonised new ice-free areas from pockets or refugia where they had survived the glaciation within the Arctic (DAHL, 1963, 1987; LÖVE & LÖVE, 1974) or immigrated from further south or east. There is evidence that genetic changes occurred at a high rate in certain plant species; some of which may even have evolved during post-glacial times (NORDAL, 1987; NORDAL *et al.*, 1988). However, the evolution of many traits fundamental to plant growth in arctic areas today may have occurred outside these areas. For instance, this may explain similarities between many arctic and temperate species in terms of their temperature optima for photosynthesis (TIESZEN, 1978), and the efficiency of the pre-winter hardening of their tissues (SAKAI & LARCHER, 1987). Some assumed adaptive traits recognised in arctic plants today may, therefore, reflect the results of selection pressures exerted on the biotypes during their migrations in the Pliocene and Pleistocene (SAVILE, 1972). Others, such as some forms of adaptation to continuous light in summer (an environmental factor with no parallel at lower latitudes) are likely to have been acquired at high latitudes. Furthermore, CO<sub>2</sub> exchange in the northern populations of the common boreal mosses *Pleurozium schreberi* and *Racomitrium lanuginosum* is adapted to the long continuous light in sub-arctic and arctic areas (KALLIO & VALANNE, 1975). The critical photoperiod for cessation of growth in the boreal willow (*Salix pentandra*) has been shown to have a clinal variation, and to increase with latitude. This species is also adapted to the latitudinal differences in irradiance and spectral energy distribution (JUNTTILA & 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, enabling them to replenish carbohydrates faster than temperate species (CRAWFORD & PALIN, 1981). This ability may also have evolved at high latitudes.

Adaptation to the arctic environment may occur in cases where genetic incompatibility 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 & VALANNE, 1973). The mountain birch (*Betula pubescens* ssp. *tortuosa*) of the sub-alpine and sub-arctic woodlands in Fennoscandia 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* and *B. verrucosa* as well as the dwarf birch (*B. nana*) contribute (KALLIO & LEHTONEN, 1975; KALLIO *et al.*, 1983). The curved trunks, polycormic growth form, tendency to propagate vegetatively, and vivid autumnal colours are all characteristics typical of the dwarf birch. One possible selection force that has contributed to the evolution of the mountain birch is herbivory by the caterpillars of the autumnal moths *Epirrita* (*Oporinia*) *autumnata* Bkh. and *Operophtera brumata* L. The caterpillars can defoliate and cause the death of birch trees over large areas. They tend to have the greatest impact on the monocormic form which in turn may result in a successive increase of the polycormic form in sub-arctic woodlands (KALLIO & LEHTONEN, 1975).

## 6.2 Periodicity

In northern ecosystems populations of both plants and animals often show a pronounced periodicity (TAST & KALELA, 1971; LAINE & HENTTONEN, 1983; HANSSON, 1984; HANSSON & HENTTONEN, 1985). For example, approximately every ten years there is a peak in the population of the moths, *E. autumnata* and *O. brumata* which feed on leaves of the mountain birch (TENOW, 1972, 1975, 1983; KALLIO & LEHTONEN, 1975; BYLUND, 1995; TENOW & HOLMGREN, 1987). As leaf biomass is reduced the chemical composition of the remaining and new leaves changes, apparently in response to the grazing (HAUKIOJA & 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. As a result, larvae feeding on such leaves grow more slowly (and are less fecund as adults) and are exposed for a longer period to natural enemies, populations of which will have also increased in response to high populations of their host or prey. The

decrease in food availability and quality and the increase of enemy pressure may explain why the outbreaks eventually decline.

Periodicity also occurs among some vertebrate herbivores. Every three to four years there is a peak in populations of microtine rodents, which are important herbivores on many plant species (HANSSON 1987). These cyclical changes have been the scope of comprehensive ecological research in Fennoscandia (OKSANEN *et al.*, 1981; 1987; TUOMI *et al.*, 1984; HAUKIOJA *et al.*, 1985; JONASSON *et al.*, 1986; ANDERSSON & JONASSON, 1986; LAINE & HENTTONEN, 1987), but their causes are still unknown.

Periodicity has also been reported in the flowering frequency of certain higher plants in the tundra. The most striking example is provided by the arctic cotton grass, *Eriophorum vaginatum* (G. SHAVER & U. MOLAU, pers. comm.), but periodic tendencies have also been observed in other arctic evergreens, such as *Cassiope tetragona* and *Ledum palustre* (G. SHAVER & D. WALKER, pers. comm.). In the case of *Eriophorum vaginatum* there is a basic main four-year period reflecting the time elapsed from tillering to flowering of new adventitious shoots, the tillering rate being correlated with summer temperatures. In addition, there is a secondary two-year periodicity, where mast years (during which more or less all available nutrients are used for flowering) are followed by a «hangover» that depresses flowering during the subsequent season. These two processes in concert generate an intricate pattern of drastic year-to-year fluctuations in the flowering frequency of *E. vaginatum*. Interestingly, these fluctuations seem to be synchronised over large areas and over decades. Global weather generators, such as the Mt. Pinatubo eruption in 1991, may be crucial in establishing this synchrony.

## 7. The Caledonian Mountain Ecosystems and Global Change

Global Circulation Models (GCM) predict that the temperature increases, particularly in response to increasing concentrations of atmospheric CO<sub>2</sub>, will be greatest at high latitudes (MITCHELL *et al.*, 1990). Species here are sensitive to changes owing to their slow growth, long generation times and infrequent reproduction. Each of these characteristics reduces their ability to adapt to environmental changes (CALLAGHAN *et al.*, 1992). Therefore, the earliest and most rapid changes are likely to occur in the northern mountains. In general, increases in atmospheric CO<sub>2</sub> concentration and temperature will enhance growth in many plant species, although the effects may be only transient since intrinsic physiological and environmental factors other than CO<sub>2</sub> and temperature may become limiting (LEMON, 1983).

Importantly, however, decreasing annual temperatures have been recorded in Svalbard (NORDLI, 1990) and in the oceanic parts of Fennoscandia (ERIKSSON, 1982). This is contrary to the trend in continental areas where temperatures have risen recently (JONES & BRIFFA, 1992; Figure 6). In the northern Scandes, the altitudinal treeline has ascended by about 50 m since the early 1930s (SONESSON & HOOGESTEGER, 1983). In the meantime, in the middle and southern parts of the Scandes, the treeline has been descending, possibly as a result of decreasing temperatures during the last few decades (KULLMAN, 1983, 1984). It seems likely that temperature changes and enhanced concentrations of greenhouse gases in the atmosphere

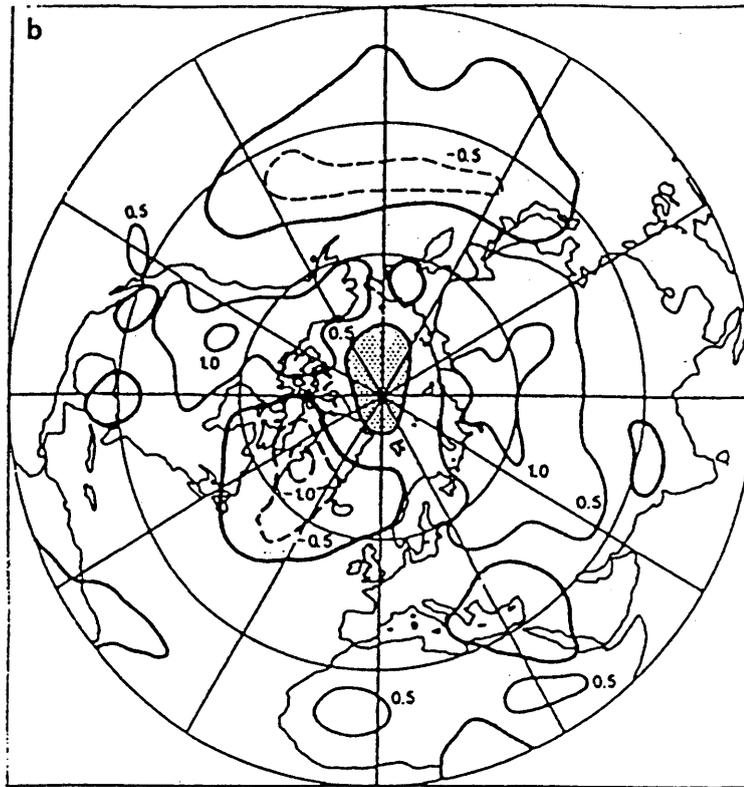


Figure 6. Anomalies in annual temperatures ( $^{\circ}\text{C}$ ) for the Arctic during 1981-90 in comparison with temperatures during 1950-79. The contour interval is  $0.5^{\circ}\text{C}$ . The shaded areas have inadequate coverage. From JONES & BRIFFA (1992).

will affect the northern ecosystems. However, changes in heat transport in the North Atlantic Sea could cause much larger and more drastic effects. Such changes could even have catastrophic consequences for today's ecosystems and most climate-related human activities in northern Europe.

The ozone layer at high latitudes in the Northern Hemisphere is still sufficient to keep the UV-B irradiation low relative to that at more southerly latitudes, but the ozone reduction rate is higher than that at lower latitudes (STOLARKSI *et al.*, 1992). Since plants at high latitudes have been exposed to lower levels of short wave radiation during their evolution than those at low latitudes (CALDWELL *et al.*, 1980; ROBBERECHT *et al.*, 1980) they are likely to be less adapted to UV-B and thus react more negatively to enhanced UV-B radiation. Indeed, effects on plants in the sub-arctic parts of the Scandes have been reported (JOHANSON *et al.*, 1995). A simulated enhancement of UV-B radiation in the field, corresponding to an ozone depletion of 15%, reduced leaf thickness significantly in *Vaccinium myrtillus* (a deciduous dwarf shrub), whereas the leaves of *Vaccinium vitis-idaea* (an evergreen dwarf shrub) became thicker over two growing seasons (JOHANSON *et al.*, 1995). Such changes in leaf thickness could have profound effects on photosynthesis and growth. Since these species grow together and are common in the mountain heaths, their competitive interactions and, thus, their relative abundances may change substantially.

Results from the International Tundra Experiment (ITEX) at Latnjajaure, a high alpine site near Abisko, Sweden (68°30' N), also show what may happen at high latitudes due to climate change. After five years of experiments with plants exposed to a temperature enhancement of about 3°C (the increase predicted to occur over the next 50 years according to the GCMs) some general trends could be discerned (HENRY & MOLAU, 1997; U. MOLAU, pers. comm.). Evergreen dwarf shrubs and graminoids tended to increase their turnover rate of leaves with little change in the standing crop of live tissue. Wintergreen graminoids, e.g., *Carex bigelowii*, increased not only their turnover rate (in terms of tillering), but also their standing crop and reproductive output. The leaf areas of deciduous dwarf shrubs and herbs increased significantly, apparently resulting in competitive stress on the evergreen dwarf shrubs of the tundra communities. Hence, if the warming continued a decrease in the relative abundance of the evergreen shrubs in the tundra could be expected (CHAPIN *et al.*, 1995) which may be accompanied by a decrease in species and community diversity. Such shifts have already been observed in long-term non-manipulated plots in tussock tundra in northern Alaska, where there has been a substantial warming since 1960 (CHAPMAN & WALSH, 1992; CHAPIN *et al.*, 1995) and in mid alpine experimental plots at Latnjajaure in northern Swedish Lapland (MOLAU & ALATALO, 1998).

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