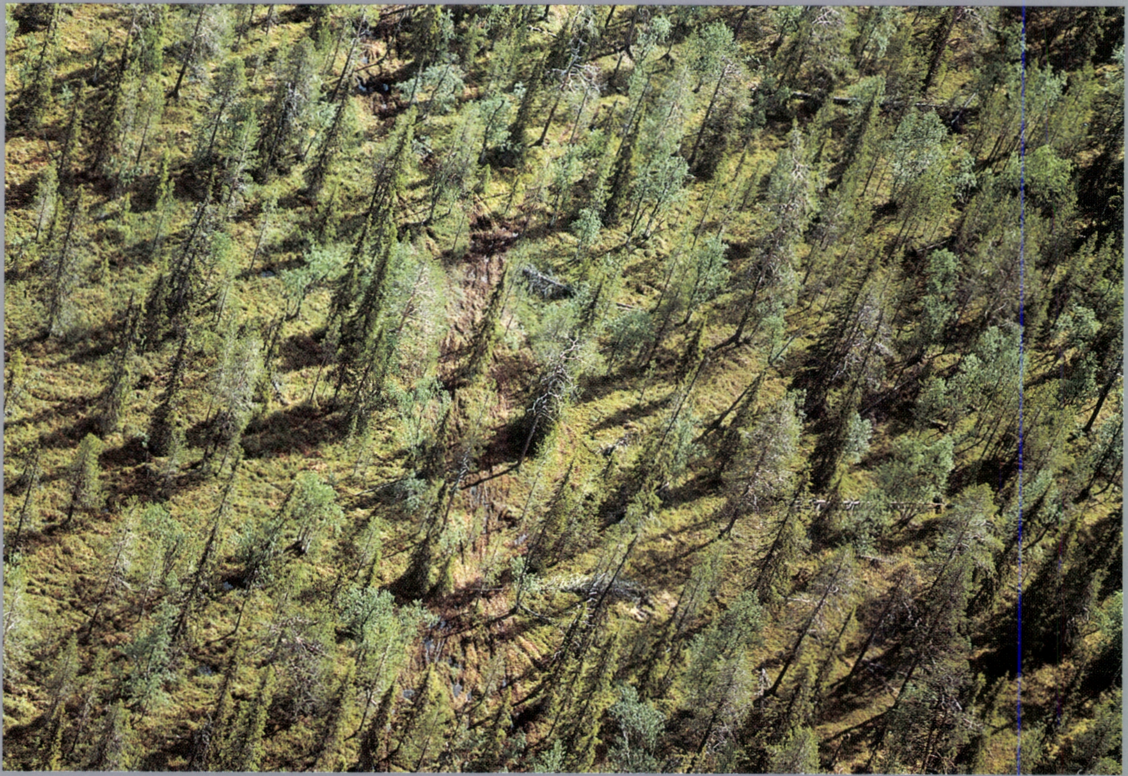

The northern timberline and timberline forests in Fennoscandia

Pertti Veijola

The Finnish Forest Research Institute
Kolari Research Station

Metsäntutkimuslaitoksen tiedonantoja 672
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Cover photo:
Spruce dominated open forest in the southern part
of Inari. Photo: Ariel Ilmakuva Oy 1994.

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A qualitative research approach and multidisciplinary perspective are employed to examine the ecology of the northern timberline in Fennoscandia and its position relative to the world's other timberlines.

The ecotone principle is found to be highly suitable for considering timberlines in Fennoscandia, and a new interpretation of the northern limit of coniferous forests in Finland is put forward in which the timberline is hemiarctic between Karesuvanto and Skietsim, altitudinal around the Muotkatunturit area and hemiarctic again between Kaamasmukka and Näätämö. The pine forests of the northern valleys are regarded as extrazonal.

The limit of the coniferous forests in Finland cannot be regarded as a "starvation boundary" as allowed for in the general carbon balance theory, i.e. a boundary that can be explained in terms of the effective temperature sum. The altitudinal pine forest limit is usually climatically determined, but the hemiarctic limit is regulated by reproductive factors, the species dynamics between pine and mountain birch, which is itself dependent on disturbance factors, and human influence. The best general explanation for the position of the timberline is the theory of relative and absolute treelessness.

The dynamics of the timberline ecotone cause it to stand out distinctly from the boreal forest, as the incomplete canopy cover means that the impact of competition is less marked. Two possible states of equilibrium exist at the northern coniferous timberline in Finland: pine-dominated forest or birch-dominated forest. The outcome is determined by disturbances and climatic fluctuations. The vegetatively reproducing mountain birch forest is a permanent feature relative to the pubescent birch stands of the boreal forests.

Fluctuations in climate do not influence the pine treeline directly. Instead there are a wide variety of factors that mediate the reaction to warming, for instance. A clear difference exists between a reaction in terms of generative reproduction and one in terms of growth. The warmer climatic period in the first half of the present century led to the generation of young pines at the treeline, although it is still not possible to make reliable predictions regarding their future. The main effect of the climatic warming has undoubtedly been the increase in the density of the forests in the area south of the timberline to produce stands of uneven-aged structure.

Open forests form an integral part of the subarctic region, where many ecological parameters differ from those in the true boreal forests.

Timberline forests also constitute distinct entities on geographical grounds, regions in which the needs for nature conservation and the preservation of indigenous cultures exceed timber production in importance.

Keywords: timberline, treeline, ecotone, open forest, succession, climatic change

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Contents

Foreword

The aim of the present study is to give an overall picture of the geology of the northern timberline in Fennoscandia and the the definition of timberline forests. This publication is a result of the further studies of the author in the University of Helsinki at the Department of Forest Ecology. The licenciate study, compiled under guidance of professor Matti Leikola and approved in the year 1994, has been worked further.

The author has been in these years an external reseacher of the Kolari Research Station of the Finnish Forest Research Institute. The services of the libarary of the Forest Research Institute had an important role for this work. The cooperation with Director of the Kolari Research Station, Lic. For. Tapani Tasanen, has been very close. He has read the manuscript and given many valuable comments. The Director of Pazvik Nature Reserve Mr Anatoly Khokhlov, and the Deputy Director, Mrs Olga Makarova, as well as the Director of the Dendrological Laboratory of the Polar-Alpine Botanical Garden in Kirovsk, Mr Leriy Kazakov, have helped the author to find Russian publications and organize excursions to the Murmansk area.

The Department of the Environmental and Nature Resource Research of the Finnish Academy and the Foundation of Foresters (Metsämiesten Säätiö) have financed this work.

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Ivalo, December 1997

Pertti Veijola

The northern timberline and timberline forests in Fennoscandia

1 Introduction

1.1 Aims and methods

The timberline as an object of study is a complex entity involving many fields of science. Thus it may not be treated in detail as one single problem, but as consisting of a great number of separate problems. The timberline may be approached scientifically in two ways: either from the angle of the timberline as a whole, analyzing the separate problems within the appropriate disciplines, or from the angle of the general aims of these disciplines, in so far as such problems occur visibly at the timberline.

The aim of the present study is to give an overall picture of the ecology of the northern timberline in Fennoscandia and of the definition of timberline forests.

The tasks of the research may be specified as follows:

1. To create an overall picture of the ecology of the northern timberline of Fennoscandia and of the character of this timberline in relation to others. To describe the properties and features that distinguish the northern timberline of Finland from the other timberlines of the world.
2. To present a broad outline of the history of the mapping of the northern timberline in Fennoscandia.
3. To clarify the principles and alternative solutions for the delineation of timberline forests.

No ready-made method exists for creating a synthesis of the timberline problem, which consists of elements from many disciplines. The methods of experimental ecological research are not suited to this problem, but the findings of ecological and other research concerning the timberline form the basic material for this work and are treated by the methods of qualitative research. The aim is to proceed via interpretation of the basic material to an eventual synthesis.

Publications concerning the timberline and timberline forests in the northern part of Fennoscandia were analyzed as comprehensively as possible, and additional literature concerning the timberline in general and its causes was treated on a broader basis. A database was created in order to facilitate the management of the great volume of reference material. Since the Russian literature in this field is very poorly known in Finland, it is treated here particularly thoroughly. In addition to published works, archive references and other documents are used to some extent. The author has been working in the timberline region for a long time and his knowledge of local conditions has served as a starting point for interpreting and criticizing the sources.

1.2 Fennoscandia as an object of study

The area of Fennoscandia is separated from the rest of Europe by the Baltic Sea, the Gulf of Finland, Lake Ladoga, Lake Onega, the White Sea, and the isthmuses between these. In addition to Finland, Sweden and Norway, Fennoscandia also includes the Kola Peninsula and Russian Karelia. One of the factors that distinguishes this region from its surroundings is the crystalline Archaean bedrock which constitutes the basement of the Fennoscandian Shield (Isachsen 1962). This crystalline bedrock and covered by thin surficial deposits eroded from it form approximately 90% of the area of Finland, 75% of that of Sweden and 30% of that of Norway. The Scandes, the Caledonian mountain range running to the west of the basement area, is entirely different in its rock types and topography (Gjaerevoll 1992).

The climate is characterized by the low solar radiation levels typical of northern latitudes and by its location on the western edge of the Eurasian continent, within the range of influence of the North Atlantic and the Baltic (Wallén 1962). Due to these factors, most of Fennoscandia has an oceanic climate with milder winters than is usual for these latitudes. The varied topography nevertheless means that internal variations are great, and a markedly oceanic climate exists west of the Scandes in particular (Gjaerevoll 1992).

The concept of Fennoscandia and the definition of its eastern boundary have been of interest to Finnish scientists for a long time. The parts belonging to Russia are generally referred to as Eastern Fennoscandia (Hiitonen 1962). Leikola (1986) has studied the significance of its eastern border as a border for Finland in terms of natural history, a concept which earlier carried political connotations in terms of national identity (Auer 1942). The eastern border of Fennoscandia has been considered by some to be the most distinct phytogeographical border in Eurasia, but Ahti et al. (1968) find this opinion an exaggeration, stating that the eastern border of the Scandes, lying within Fennoscandia, is still more distinct.

In the system of geographical regions of Russia, Fennoscandia, consisting of Karelia and the Kola Peninsula and bounded in the east by the Russian plains, is defined as one region on the basis of its bedrock, landforms, climate and vegetation (Pavlova 1979). The major part of Fennoscandia belongs to the boreal vegetation zone, which is divided into the southern, middle and northern boreal zones (Ahti et al. 1968), but opinions on its phytogeographical division vary, especially concerning the northern part.

The timberlines in Fennoscandia are mostly alpine. The Scandes of southern Norway, at a latitude of 59°, already possess timberline regions, and this mountain range extends to latitude 70° in the north (Sonesson et al. 1975). In their extensive phytogeographical study, Walter and Breckle (1986) regarded only the Scandes and the Khibiny Mountains as distinct orobiomes in Fennoscandia. The timberline regions become arctic-alpine in character in the north (Holtmeier 1974), and a maritime timberline also enters the picture on the shores of the Arctic Ocean (Hämet-Ahti 1963). These timberlines comprising several elements have been explained and classified in many ways, and still no firm principles have been established. The Kola area already displays some eastern features, although from a Russian viewpoint it is an oceanic area, clearly differing from the continental timberline regions dominating in Eurasia.

2 General features of timberlines

2.1 The concept of timberline

In order to define a timberline, it is essential to determine the minimum level of crown density and the minimum size of a tree. The basic questions are: What is a tree? What is a forest? In order to assess crown closure, the minimum area for a stand must be stated. Kullman (1983), for instance, considers ten trees at least two metres in height to be the minimum size of a stand, while Sirois (1992) considers the limit to be the smallest stand distinguishable on an air photograph to the scale of 1:50 000. Tsvetkov and Chibisov (1993) suggest that for extensive surveys of forest and tundra areas using satellite images to a scale of 1:1 000 000, areas consisting of 30% forest or more can be denoted as forest.

Mork (1970) defines the timberline in a fell forest as the point where the distance between trees of more than three metres in height exceeds 30 metres, while at the tree line the largest trees are less than two metres high. Mork's definition is used in the guidelines for the management of protected forests issued by the Norwegian Ministry of Agriculture, in addition to which a definition formulated by the Norwegian Land Survey is given, i.e. a minimum of six trees at least five metres high per 0.1 ha (Landbruksdepartementet 1992).

The definition of a tree has generally been based on the criteria of an arborescent growth form and a height of two or three metres (Tuhkanen 1984), or sometimes as much as five metres (Hermes 1955, Payette 1983). The interpretation of arborescent growth form has been variable, especially concerning the mountain birch (Tuhkanen 1993). Ellenberg (1966) proposed the two metre limit, stating that it takes a tree of this size to cause distinct shading and root competition effects in the field and ground layers. On the other hand, he went on to state that a plant may be considered a tree if its height exceeds the thickness of the normal maximum snow depth.

The concepts related to the forest limit may be based on floristic, climatological or physiognomic-structural principles (Sirois 1992). The system of concepts for the northern timberline presented by Hustich (1966), which emphasizes physiognomic properties (Figure 1), is one of the best known and most widely used, having been developed as a result of a long-term study of timberlines in North America and Fennoscandia from the 1930's onwards. Hustich (1939) began with a comparison of timberlines and related terms in North America and Eurasia, distinguishing the following limits on a gradient from forest growing under normal conditions to treeless tundra:

Economic timberline. South of and below this line the regeneration of trees is regular and normal forestry is possible. This limit cannot generally be observed by eye but its determination requires separate investigations, since the ecological prerequisites for forest regeneration, for example, vary greatly. The location of this line may also vary according to changes in economic criteria. The terms 'economic forestline' and 'productive forestline' are used as synonyms in the literature published in English.

Payette (1983) proposed the term 'limit of continuous forest' as equivalent to Hustich's economic timberline in Labrador, referring in effect to the limit between boreal forest and forest tundra. The general term timberline in North America denotes the northern limit of forests that can be profitably exploited (Hustich 1966). Hall (1995) maintained that this limit in the boreal forests of Canada in the 1980's was located where the volume of merchantable wood to be harvested was 90 m^3/ha. Viereck (1979) defined the economic timberline in Alaska as the region where annual increment was at least 1.5 m^3/ha and regeneration regular.

During the 1980's, when timber prices in Finland were high, even the most distant coniferous forests were within the range of profitability if the volume of merchantable wood to be harvested was at least 30-40 m^3/ha. Felling was undertaken in places as remote as Sevettijärvi and Vätsäri east of Lake Inari, but once prices had fallen in the early 1990's the most distant timberline forests were left outside the area of profitable exploitation.

The term economic timberline is at least partly equivalent to 'generative timberline' as used by Kihlman (1890) and the 'rational timberline' of Heikinheimo (1921). For Kalliola (1973), the rational timberline was the line formed by the last trees producing germinating seeds.

Physiognomic or actual timberline. The area between the economic timberline and the physiognomic timberline is occupied by continuous forest, but its regeneration is slow and uncertain. This limit is also called the 'empirical timberline' (Kihlman 1890, Kalliola 1973) or 'vegetative timberline' (Kihlman 1890), as the trees that have advanced to it have grown either from seeds that were transported to the area or vegetatively. The physiognomic timberline is the timberline proper, and when only the word 'timberline' is used, it is generally this limit that is referred to. The terms 'forest limit' and 'timberline' are synonyms in English and correspond to 'Waldgrenze' in German and 'skogsgräns' in Swedish. Payette (1983) uses 'forest limit' to refer to the limit formed by isolated tree stands within the forest tundra. In Russia the names of the vegetation zones are more frequently used than the term 'timberline' as such.

Treeline. Although the continuous forest ends at the physiognomic timberline, isolated trees and clumps of trees generally occur at favourable sites up to the treeline, which is formed by the extreme individuals meeting the definition of 'tree'. For the sake of clarity the tree species must also be stated in connection with each treeline mentioned. Treter (1984) points out that from an ecological viewpoint there is little sense in basing the concept of treeline on any minimum size; it is more important to pay attention to the ecosystem as a whole. In his study of the advance of the treeline, Sirén (1993a) defined the pine treeline as being located at a point where there is still at least one seed tree per square kilometre, while Atkinson (1981) defined the treeline in Canada as the limit where the trees disappear from the ridges, so that the last arborescent individuals occurring in sheltered valleys mark the 'tree-form line'. The treeline, at which tree-like forms disappear, is the most distinct area of change in the height of plants (Grace 1989).

Hustich (1949, 1957) used the concept of 'main tree-line' in many connections. This is in no way related to the concept of treeline, however, but refers to a zone in Canada resembling the 'limes norrlandicus' in Sweden, where the southern limits of the distribution of boreal tree species are concentrated.

Tree species line. The same the tree species may occur beyond the treeline in the form of bushes or seedlings. In the mountains of Central Europe these forms, mostly *Pinus mugo*, are called 'Krummholz' and the area between the treeline and the tree species line the 'Krummholz zone'. This term has also been adopted elsewhere (e.g. Arno 1984). In Labrador, Hustich (1949) named the corresponding horizontal zone formed by coniferous trees a 'brushwood formation' and the still lower vegetation formed by coniferous trees in windy places near the coast 'coniferous bush tundra'.

The tree species line has also been termed in English the 'scrub line' (Heikkinen 1984). Leibundgut (1986) defined the 'Krüppelgrenze' as marked by the occurrence of 0.5 m high shrub-formed individuals of tree species that do not require especially sheltered sites. The shrub form may be caused by environmental or genetic factors (Grace 1989). The term used to denote stunted forms of coniferous trees in Russian is 'stlanik'. In addition to the common stunted forms of spruce, Kozubov (1961) describes 'stlanik' forms of *Pinus sylvestris* growing above the treeline in the Khibiny Mountains. These forms are also common at timberlines in Finland. When describing the plant communities of the tree species line, Cajander (1933) used the terms 'brushwood' and 'dwarf-shrub trees'. Krylov (1964) stressed the view that the occurrence of shrub-like stunted forms of trees at the limits of the vegetation zones is a universal phenomenon, encountered at all vegetation limits caused by climatic factors in both the south and the north. Rundel (1991) defined the 'Krummholz' forms of conifers as found at cold timberlines as one main group of shrub life-forms occurring under multiple environmental stresses.

Historical timberline. Dead trees or parts of trees can be found beyond the tree species line in many places, bearing witness to growth of the tree species in question in that area during more favourable climatic periods. The extreme limit of these fossils may then be termed the historical timberline. There are many problems related to the definition and dating of the historical timberline, since it may be influenced by highly varied phenomena. The most difficult problem is how to distinguish between climatic changes and the effects of human action. Random observations suggest that no far-reaching conclusions can be made on this. In a broad sense, the historical timberlines and tree lines may be considered to be related to climatic changes since the last glaciation (Payette 1983).

Present and potential or climatic timberlines and treelines. All the limits described above except the historical timberline are present, actual limits. The historical timberline may, of course, give indications of a potential limit, i.e. one that is climatically possible today. Leibundgut (1986) defined the climatic timberline in mountain areas as running via those uppermost stands whose upper limit is unaffected by the rock or soil type or by anthropogenic factors. The potential limit differs markedly from the present one in places where the effect of man on the formation of the present timberline and treeline has been great.

The potential, climatic timberline has been studied in Scotland (Pears 1968), Norway (Aas 1969), Canada (Mitchell 1973) and the Alps (Leibundgut 1968), for example. Mayer and Ott (1991) claim that the present timberline in the Alps is located as much as 400 m below the potential timberline. On the basis of reforestation experiments, Ødum (1990) arrives at the conclusion that areas exist in southwestern Greenland that are below the potential coniferous treeline, while Blöndal (1993) maintains that the areas below 400 m a.s.l. in Iceland are potential locations for boreal coniferous forests. The main research work on the potential timberline for pine in Finland has been carried out by Sirén (1958, 1961, 1993a, b).

Tuhkanen (1993b) was of the opinion that it is impossible to develop timberline and treeline definitions to cover all circumstamces, since the diversity of environmental conditions and species is so great. Thus descriptions of timberlines and treelines even in a single area may contain significant differences attributable to the definitions used. Likewise, it is not always clear whether the timberline or the treeline is being described, or according to what definition. Daubenmire (1954) noted this problem and stated that where alpine timberlines were concerned he would use the mid-point of the area between the timberline and the treeline. Elliott and Short (1979) use the east coast of Labrador as an example of the difficulty of determining the treeline, as thickets of bush-like *Alnus crispa, Salix sp.* and *Betula glandulosa* of a height up to two metres were still interpreted as forest in mapping based on aerial photographs in the 1960's. Since a tree is defined in that same area as having a distinct main stem and a minimum height of two metres, the treeline, formed by *Picea glauca*, lies more than 50 km farther south.

Additional concepts and terms are necessary for the examination of causes and altitudes of timberlines over extensive areas and under varying conditions. Holtmeier (1974) defined the following concepts:

- Climatic, orographic and anthropogenic timberlines may be distinguished on the grounds of the most significant limiting factor.

- An upper and lower timberline may be distinguished on the grounds of altitude.
- Northern and alpine timberlines may be distinguished on the grounds of geographical location and altitude.
- The lower timberlines can be maritime, continental or latitudinal (northern) in characater. In Scandinavia the northern timberline has certain points in common with the alpine timberline (Figures 2,3,4 Appendix 1).

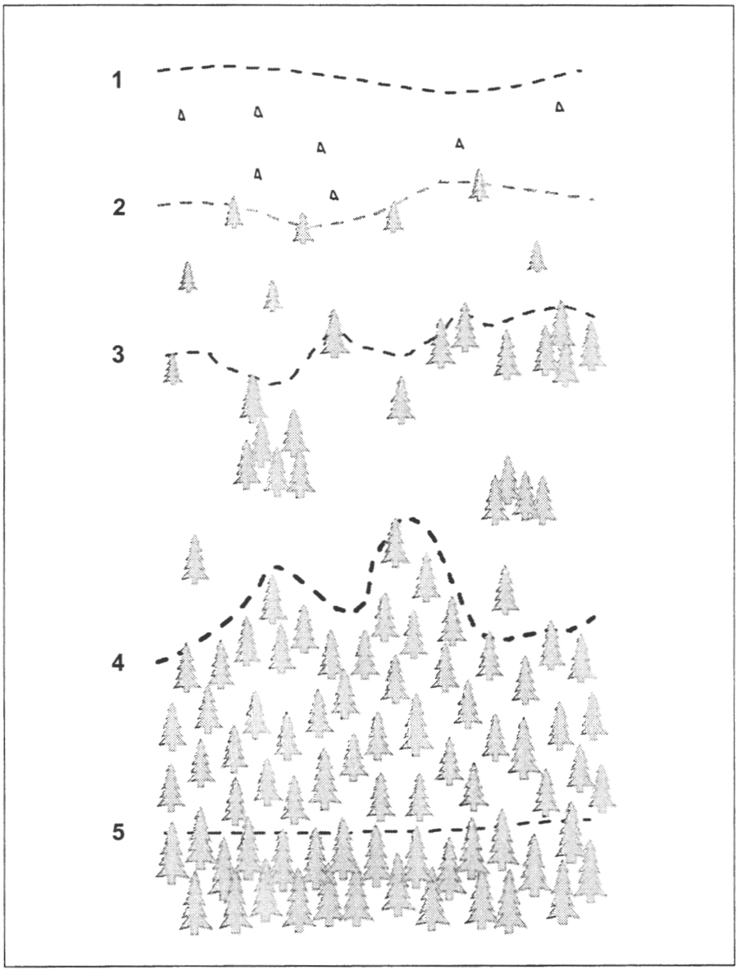

Figure 1. Various timberlines and tree lines (Tasanen and Veijola 1994). Based on Hustich (1966), Tuhkanen (1982, 1993 a) and Heikkinen (1984). 1. Historical timberline; the line connecting extreme arboreal occurrences of a tree species during favourable climatic periods. 2. Tree species line; line connecting extreme occurrences of a species regardless of size or form. 3. Treeline connecting extreme arboreal occurrences of a tree species. 4. Physiognomic timberline; boundary of continuous forest. 5. Economic timberline; line within forest regeneration is regular and forestry is possible.

2.2 The timberline ecotone

2.2.1 General

The approach in ecology over the last few decades has generally changed from a paradigm of systems in equilibrium to a paradigm of non-equilibrium systems controlled by random factors (e.g. Saarinen 1982, Haila and Levins 1992), and developments in landscape ecology have taken much the same course. From the viewpoint of patch dynamics, a landscape represents in its properties and development a combination of patches influenced by complex interactions of climate, disturbances and biotic processes. The structure and function of the landscape are determined by the outcome of the collective behaviour of this mosaic. The ecotone, one of the central concepts of landscape ecology, is defined by Di Castri (1992) as a zone of transition between adjacent ecological systems, having a set of characteristics uniquely defined in space and time and by the strength of the interactions between ecological systems. According to Di Castri the concept of ecotone thus defined may be applied at all levels of a hierarchy from population to biosphere, and the spatial scale may be from centimetres to thousands of kilometres. As Gosz (1991) remarks, the distinction between an ecotone and a mosaic is a matter of scale, since what appears to be an ecotone on one spatial scale may be seen as a mosaic at a finer scale.

Delcourt and Delcourt (1992) specify the concept of ecotone by stating that these may constitute buffer zones between adjacent communities by acting as semi-permeable barriers through which energy, nutrients and propagules may pass. On the other hand, they may be boundaries in the landscape that safeguard the stability of neighbouring communities. Having studied ecotones and edge effects, Wiens (1995) presents the general conclusion that an ecotone as a boundary grows steeper as the number of ecological processes passing through it decreases. Thus a steep ecotone prevents movement, whereas ecological corridors promotes it.

The ecotone-based viewpoint is especially suited to the examination of timberlines, since the changes occurring in the tree layer and finally the disappearance of the arborescent life form altogether give the timberline ecotone a concrete and clear physiognomic structure. The ecological significance of a steep timberline may be different from that of an extensive, gradually changing ecotone. Forests in river valleys that extend across the timberline, and treeless highlands extending into a forest zone may serve as distinct ecological corridors. In addition to being ecological limits, timberlines may at the same time act as either boundaries or uniting factors between cultures and ways of life. The timberline areas of Fennoscandia, for instance, are the core areas of Sàmi culture and the associated traditional means of livelihood. The traditional annual cycle of reindeer husbandry includes migration between summer pastures on the tundra or fells and the winter pastures in the forest zone.

The timberlines and treelines shown on maps and defined on various criteria are always interpretations of reality. A timberline may occasionally be present in the field in the form of a distinct limit, but even in this case there is a transition zone. Especially at the northern timberline in continental areas the transition zone may be hundreds of kilometres wide. According to Arno (1984), this is possibly the most extensive vegetational ecotone on a global scale. Slatyer and Noble (1992) considered the alpine treeline between the subalpine forest and the alpine tundra to be the most extensive and most clearly distinguishable ecotone among plant communities.

It is more important from an ecological point of view to understand this entire transition zone and the factors influencing it than to identify the line formed by the last trees or forest stands (Holtmeier 1974). Treter (1984) defined the timberline ecotone as a transition zone between more or less closed forest and treeless tundra or the alpine altitude zone.

In the timberline ecotone, the conditions and vegetation of sites change markedly with the gradual shift from forest to open land. This change has been studied extensively and from various perspectives in connection with investigations into the causes of timberlines. Many radiation parameters change markedly within the timberline ecotone, and Hare and Ritchie (1972) state that the main reason for the difference in net radiation is the significantly greater albedo during spring in the tundra than in the forest. At the same time total phytomass has been observed to vary in Canada from less than 5 tn/ha in the tundra to 25 tn/ha at the treeline, rising rapidly in the closed forest to 300-400 tn/ha. In a worldwide survey, Basilevich and Rodin (1971) presented the following average phytomass values: tundra 2.5-5.0 tn/ha, forest tundra 25-50 tn/ha and northern taiga 50-150 tn/ha. Kjelvik and Kärenlampi (1975) obtained the following phytomass values at Kevo in Finland: timberline pine stand 35.2 tn/ha, mountain birch stand 19.3 tn/ha and subalpine heath 5.9 tn/ha.

Andreyev (1966), having studied the variation in phytomass in detail in the timberline region west of the Ural Mountains, presents findings concerning variations in the ratios between plant species groups as well as total changes (Figure 5). This is still considered to be one of the most thorough biomass investigations to be carried out in the tundra (Tikhomirov et al. 1981).

Nikonov (1985) studied phytomass and production in the vegetation zones of the Kola area and observed that the values are also affected by the geomorphological location of the site. Total phytomass in the tundra was 4-8 tn/ha, increasing to as much as double this figure on the slopes. That in the birch stands of the forest tundra was 8-10 tn/ha and that on the slopes 20-70 tn/ha. The values for the northern taiga varied, ranging from 12 to 188 tn/ha. Although the changes within the timberline ecotone are great, the relative change is still greater between the southern edge of the tundra zone and its northern parts (Chernov 1985).

In many parts of the world, tundra is related to open forest, where the climate is more favourable than in the tundra. In the northern hemisphere the ecotone between forest and tundra is a mosaic formed by trees, groups of trees and forest stands against a background of low shrubs and dwarf shrubs along with grasses and sedges (Bliss 1981). The main exceptions are the treeless maritime areas of the North Atlantic, including the northern coast of Fennoscandia and the corresponding coasts of the northern Pacific Ocean, which are considered parts of the boreal zone on floristic grounds whereas an absence of trees causes problems in the interpretation of the transition zone between tundra and taiga (Yurtsev et al. 1978).

When examining the timberline ecotone, it is possible to distinguish on the one hand various geographical viewpoints, i.e. the North American, Russian, Alpine and Scandinavian perspectives, and on the other hand between the viewpoints of the various sciences, i.e. those of phytogeography, geography and forestry.

The timberline ecotone is approached in the present work on two levels. First the character of the timberline proper is examined along with that of the ecotone directly related to it, extending from the tree species line to the physiognomic timberline. The second level is the examination of the timberline forests, where the object of study is the southern or lower part of the timberline ecotone in the broad sense, from the physiognomic timberline to the economic timberline.

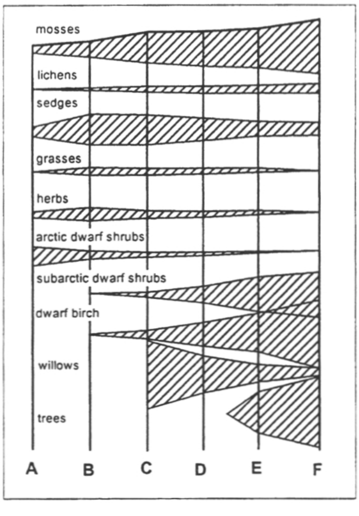

Figure 5. Relative above-ground phytomass of some plant species groups in the various vegetation zones of the timberline region in the eastern part of Europe (Andreyev 1966).
A = arctic semidesert, B = arctic tundra, C = northern tundra, D = southern tundra, E = forest tundra and F = northern edge of northern taiga.

2.2.2 North America

In the area between the boreal forest and tundra is marked by a gradual weakening of the growth and development of trees by the cold climate, which leads to changes on the population and plant community levels observable in the form of a transition zone between these two biomes (Sirois 1992). The area between the boreal forest and tundra is generally referred to as the northern forest tundra ecotone, which is a direct translation of the Russian term 'lesotundra' (Hare 1950). The concept was brought to North America by Marr (1948), who defined the forest tundra as a combination of subarctic forest and arctic tundra vegetation communities.

Larsen (1989) defined this ecotone as the area where, measured from large-scale aerial photographs, the proportion of closed-crown forest is less than 75% and the proportion of open tundra less than 75%. Thus 25 % or more of the area is a mixture of tundra and forest. The tundra is generally located in the high land and the forests in the depressions, where the trees are partly protected by snow. The peatlands may be ignored for the present purpose. In Larsen's opinion, 'open lichen woodland' should be regarded as forest for this purpose. This definition is considered suitable for the needs of both biogeography and forestry.

The dominant tree species in the forest tundra are *Picea mariana, Picea glauca* and *Larix laricina*. The field layer is characterized by an impoverished plant community dominated by *Vaccinium vitis-idea, V. uliginosum, Betula glandulosa, Empetrum nigrum, Rubus chamaemorus* and the arctic species *Arctostaphylos alpina, Ledum decumbens, Dryas integrifolia, Cassiope tetragona, Diapensia lapponica, Salix arctica, Oxytropis arctica* and *Polygonum viviparum*. The same species are also found in the southern tundra.

The forest tundra extends across Canada in the form of a zone of variable width where the vegetation remains quite constant in spite of variations in geological conditions and terrain. Larsen (1980) was of the opinion that past variations in climate are a possible cause of the mosaic-like structure of the forest tundra vegetation, while Elliott-Fisk (1983) considered the present width of the forest tundra zone to be a possible consequence of a former, extensive fluctuation in the location of the timberline.

The form of the crown as well as the density and height of the forest has been used to formulate a definition of the timberline ecotone in North America (Scott et al. 1987). One typical feature of the forest tundra in the vicinity of Churchill, Manitoba, was the presence of individuals of *Picea glauca* in which the crown consisted of a living basal rosette followed upwards by a stem without branches and a living growing tip. Timoney et al. (1993), studying the structure of the forest tundra in northwestern Canada, arrived at the conclusion that the spatial vegetation gradient between forest and tundra is best represented by a sigmoid curve with the mean treeline situated in an area of abrupt change in the middle of it. At the same time the patches of tundra and forest increase in size on either side of the timberline.

2.2.3 Russia

Walter and Breckle (1986) define the forest tundra as the ecotone between the Eurosiberian boreal coniferous forest zone and the arctic tundra, the 'Zono-Ökoton' which extends all the way to the treeline. They consider the forest tundra analogous to the forest steppe, because both are made up of a vegetation mosaic.

Tikhomirov (1970) explains that the concept of 'lesotundra' entered the Russian literature during the latter half of the 19th century and that the matter has been studied very extensively and from various viewpoints. Russian phyto-geographers have put forward various opinions on the character of the forest tundra. According to Tikhomirov (1967), the following parts are considered to be as included: the 'redkostoynye lesa' or open forest part of the northern taiga, the 'redkolesya' or stunted forest, isolated patches of forest and areas with single trees representing various life-forms.

Norin (1961) identified the position of the forest tundra by stating that it had earlier been considered either a part of the northernmost taiga or a southerly part of the tundra. The first scholar to give it the position of an independent vegetation zone was Tsinzerling (1932) in his studies of the vegetation of the Kola Peninsula. Referring to the work of Fries (1913), he regarded the forest tundra as extending into Sweden. The same types of podzol soils predominate in the forest tundra as in the northern taiga, and this is taken as one of the arguments for including it in the taiga (Manakov 1967). Many Russian scientists, however, consider the forest tundra a separate zone (Tikhomirov 1970). Nowadays, however, the forest tundra is generally considered part of the taiga, both in North America and in Eurasia. Bliss and Matveyeva (1992) state that other than in river valleys, the climatic treeline is generally regarded as the southern border of the arctic zone. In the southern tundra trees may occur in river valleys and other sheltered places.

An important concept in the definition of the northern vegetation zones and the timberline in Russian phytogeography is 'placor' (Russian 'plakor'), which denotes normal soils and conditions occurring outside river valleys in the vegetation zone concerned. Under 'placor' conditions, the limits of a vegetational district, 'oblast', or zone, 'zona', are determined according to the dominant vegetation type, e.g. the tundra vegetation type or boreal coniferous forest. The Russian concept 'vegetation type' is equivalent to the western notion of 'formation' (Yurtsev 1988).

It is characteristic of a zonal vegetation of the forest tundra type that the influence of trees and shrubs as 'edificators' of the ground vegetation is only partial (Norin 1966). In connection with topographic factors the tundra-type vegetation may make extrazonal excursions into the taiga and the taiga into the tundra (Aleksandrova 1971, 1980). Other vegetation types as well as these zonal types also occur, controlled mainly by soil factors, topography and vegetation history, e.g. the northernmost isolated forest patches and various peatlands.

The geomorphological location of the site must also be taken into consideration when analysizing the vegetation of the timberline regions. As far as nutrient regimes are concerned, the 'placor' areas are autonomous sites. Transition areas are represented by the transelluvial sites on the upper slopes and the transaccumulative sites on the lower slopes. Accumulative sites are located in depressions, where organic deposits are common. The greatest phytomass and production are generally found on transaccumulative sites (Manakov and Nikonov 1979). The Russian system of concepts related to the northern vegetation zones and the timberline are analyzed by Chernov (1985) (Figure 6).

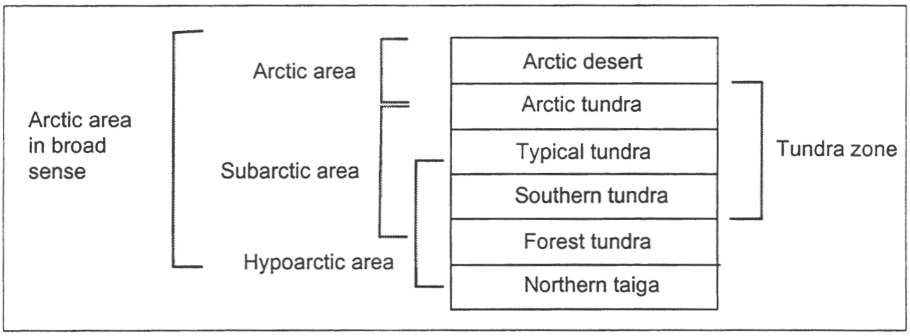

Figure 6. Russian concepts and terms related northern vegetation zones and the timberline (Chernov 1985).

Tikhomirov (1962) described the tree species of the northern timberline of Russia as follows. The main tree species in the western parts of the forest tundra are *Betula pubescens* Ehrh., *Pinus sylvestris* and *Picea obovata*. East of the White Sea these are joined by *Larix sukaczewii* Dylis, which is replaced by *Larix sibirica* east of the River Ob. The main timberline species in eastern Siberia is *Larix gmelini*, which grows in the permafrost region. Among the deciduous trees of the eastern timberline, species particularly worth mentioning are *Populus suaveolens* and *Chosenia macrolepis*, which occur in valleys up to the timberline, and *Betula Ermanii*, which forms the timberline on the

Kamchatka Peninsula. The shrub-formed *Pinus pumila* dominates in vast areas north of the timberline proper, and another common shrub-formed species in the eastern forest tundra is *Alnaster fruticosus*.

The birch-dominated forests of the timberline ecotone in Russia are classified into subarctic forests and subalpine mountain forests (Isachenko and Lukicheva 1956). The subarctic birch forests comprise the atlantic birch forests located near the tundra in Fennoscandia, and the corresponding forests on the Pacific coast. The subalpine birch forests of mountain areas form groups of their own.

The genus *Larix* predominates at the northern timberline in Russia, but there are conflicting views as to the relations between the various species of this genus. According to Iroshnikov (1995), the following species occur, from west to east, with increasing continentality: *Larix Sukaczewi Dylis, Larix sibirica Ldb., Larix gmelini* Rupr. and *Larix Kajanderi* Mayr., although many researchers do not consider *Larix Kajanderi* an independent species but a continental, eastern race of *Larix gmelini.*

Norin (1961) maintained that the southern limit of the forest tundra occurs at the point where the forest tundra type of vegetation is still dominant in the highlands and at similar sites, and summarizes the characteristics of the forest tundra type of vegetation as follows:

Structure of stand. Open forest with simultaneous high density of the root system, which together with the crown coverage serves to shape the ground vegetation. A mosaic-structured plant cover is formed. For practical purposes the stands with a crown coverage of less than 0.3 on a scale of 0-1 are classified as included in the forest tundra. Norin (1993) later made a thorough analysis of the relations between trees and ground vegetation in a mosaic vegetation.

Presence of special life forms of trees; stunted forest, 'krivoles`ye'.

The flora includes a hypoarctic element or certain species which are common to the northern part of the boreal zone and the southern part of the tundra. Parmuzin (1979) presents the following examples of the most typical species: *Betula nana, B. exilis* and *B. middendorfii, Salix sp., Ledum palustre* and *decumbens, Empetrum sp., Arctostaphylos uva-ursi* and *alpina, Rubus chamaemorus, Vaccinium vitis-idea* and *uliginosum, Dryas octopetala, Eriophorum sp., Draba nemorosa, Potentilla sp., Astrogalus sp.* and *Silene acaulis*.

On the basis of the work of Govorukhin on the Yamal Peninsula, Tikhomirov (1962) concluded that there are differences between the northern taiga, forest tundra and tundra in certain environmental factors and properties, namely average July temperature, average wind velocity, snow depth, thickness of the moss layer, peat thickness and the location of tree root systems in this, ground temperature during the growth season, and the thickness of the unfrozen mineral soil layer during the growth season. Tolchelnikov (1970) stressed the significance of soil factors as regulators of the vegetation in the forest tundra. The scarcity of available nutrients, which is caused by the cold, leads to a situation similar to that in arid areas, where the plants strive to adapt themselves to the conditions by developing an extensive root system.

2.2.4 Scandinavia

In the vast timberline regions of North America and Russia the mountains are clearly distinguishable from the plains, e.g. the Rocky Mountains and the Ural Mountains, while south of the northern boreal zone there are no timberlines other than clearly alpine one. In northern Scandinavia, however, the northern and alpine elements of the vegetation are so closely related that it is difficult to define the character of the timberline ecotone, and numerous interpretations have been put forward.

The principal tree species of the timberline ecotone in Scandinavia is the mountain birch, known today by the name *Betula pubescens* subsp. *czrepanovii* (Orlova) Hämet-Ahti (Hämet-Ahti et al. 1992). *Pinus sylvestris* and *Picea abies*, which occur mainly as admixtures within the mountain birch forests, may in some places also form the timberline. Clones of *Populus tremula* may occur even further north than the mountain birch.

Subalpine birch zone. According to the traditional view (Wahlenberg 1812), the birch-dominated timberline ecotone has generally been defined as a more or less independent subalpine or subalpine-arctic birch zone (Kalliola 1973, Du Rietz 1964). Dahl (1986) states that the term subalpine has been used to mean different things in different parts of the world. In Scandinavia it is frequently used as an approximately equivalent of the northern boreal zone in the mountains, while the timberline ecotone is of a distinctly alpine character in the southern and central parts of the Scandes. Eurola (1974) considered the areas above the timberline throughout the length of the Scandes as alpine, although with certain arctic features.

Subarctic area - forest tundra. Hustich (1952, 1960, 1966) used the term subarctic area to denote the timberline ecotone from the economic timberline to the tree species line forest tundra, whereas Sjörs (1967) used forest tundra to denote the northernmost and uppermost subzone of the boreal zone. Sirén (1991) and Gjaerevoll (1992) also used the term forest tundra. Kallio et al. (1969) considered the pine timberline in Inari, Finnish Lapland, as the northern limit of the northern boreal vegetation zone. On the basis of their floristic research they regarded the mountain birch forests with pine stands as a separate subarctic zone, and the fell tops rising above this as an alpine zone.

Kallio et al. (1969) analyzed the factors influencing the formation of this transition zone, considering the following the most important: 'northern character', including decreasing temperature, a short, light growth season and special soil features, and also topography, oceanity, vegetation history and anthropogenic influence. Ahti and Oksanen (1990) considered the term forest tundra, as a synonym for the hemiarctic zone and the treeless areas above the timberline, to belong to the hemiarctic zone, the best indicators of which are lichens and mosses.

The northern boreal, orohemiarctic and hemiarctic zones. Ahti et al. (1968) included the mountain birch forests largely in the northern boreal zone, and to some extent in the orohemiarctic zone. The report of the Nordic Council of Ministers (1984) and Moen (1987) both consider that the northern boreal zone, which includes the mountain birch forests, borders directly on the arctic-alpine or alpine zone. Dahl (1986) recognizes the upper limit of the northern boreal zone is the climatic timberline.

Hämet-Ahti and Ahti (1969) stressed that the mountain birch forests of Scandinavia should not be considered an extension of the forest tundra, and that they are neither typical subarctic or arctic vegetation types as a whole, but belong to the maritime sector of the boreal coniferous forest zone. Hämet-Ahti (1987) was later of the opinion that the open, brush-formed mountain birch forests may be considered part of the southernmost arctic or hemiarctic subzone.

Within the timberline ecotone, Haapasaari (1988) distinguishes the northern boreal/oroboreal zone, which also includes treeless heaths, and the mainly treeless hemiarctic/orohemiarctic zone, which includes isolated forest stands and trees. Using evidence from Ahti et al. (1968) and Haapasaari (1988), Eurola and Virtanen (1991) define the position of the mountain birch forests, mainly using findings from the Kilpisjärvi area. They consider the continental mountain birch forests south and southeast of the Scandes to be northern boreal and those located on the Atlantic side of the Scandes to be northern boreal up to an altitude of 200 m a.s.l. and northern oroboreal above this level. They further divide the region they called Maritime Lapland (Kalela 1961) into an hemiarctic part with scattered birch forests and a treeless southern arctic part, following Haapasaari (1988). Eurola and Virtanen (1991) called the northern oroboreal birch forests subalpine, and in their view the northern mountain birch forests may as a whole be called subarctic.

The latest interpretation of the vegetation zones in northern Fennoscandia is that presented by Oksanen and Virtanen (1995), who defined a hemiarctic zone on both climatic and vegetational criteria which extends from north of Lake Torne in Sweden to the Varanger Peninsula in Norway and consists mainly of barren areas with some mountain birch forest. They stress that the prefix oro-should be used only when the altitudinal component is strong enough to cause ecological conditions differing from those of the latitudinal zone in the area (Figure 7). Thus the forests in the Utsjoki river valley and on the shores of the fjords in eastern Finnmark are northern boreal, extrazonal occurrences within the hemiarctic zone. The forests of the Alta and Reisa valleys are northern boreal and the forests of the Troms area middle boreal. This view also fits in well with the criteria used for forestry purposes and our knowledge of the properties of northern pine stands.

Arctic, alpine and oceanic timberline. The timberline in Lapland clearly displays a complex double character with arctic and altitudinal features (Holtmeier 1974). In the opinion of Heikinheimo (1921), Finland has an arctic timberline only in the northeastern part of Utsjoki and in Petsamo. Piirola (1972) interpreted a line extending west-east from the River Inarijoki via the Neiden valley to the Norwegian border as the arctic timberline for pine, while he regarded the timberlines on the fells further south as alpine ones. In the opinion of Ahti et al. (1968) there is no real northern timberline in Fennoscandia. By the time the Arctic Ocean coast of Norway is reached the oceanic element becomes the third factor to enter the picture. Special details related to this area have been studied by Eurola and Vorren (1980), for example. According to Hämet-Ahti (1963), the continental, subalpine mountain birch forests in the interior of Fennoscandia form an alpine timberline, while in more maritime areas this line is formed by the oceanic, subalpine birch forests. The maritime timberline is formed lower down by the submaritime birch forests.

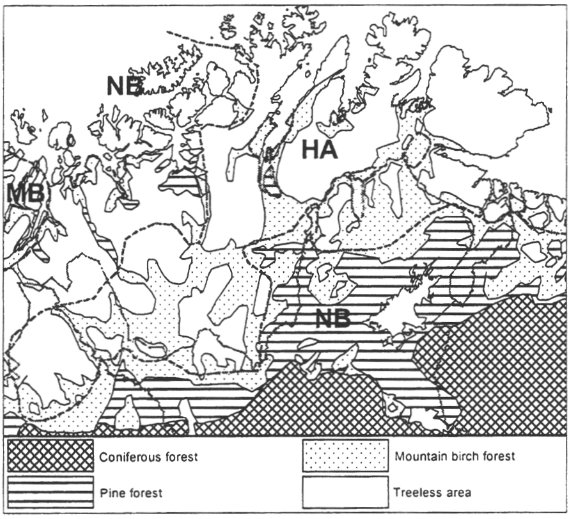

Figure 7. The vegetation zones of northern Fennoscandia (Oksanen and Virtanen 1995). HA = hemiarctic zone, NB = northern boreal zone and MB = middle boreal zone.

Finland's northern hemiarctic and vertical coniferous timberline. On the basis of the arguments put forward by Oksanen and Virtanen (1995), the northern coniferous timberline in Finland may be considered hemiarctic between Karesuvando and Skietsim (Figure 8), after which this line curves away into Norwegian territory and returns to Finland only at Karigasniemi. The pine forests of the Inari and Utsjoki river valleys may be considered extrazonal valley occurrences. The coniferous timberline is clearly altitudinal around the Muotkatunturi fells, and hemiarctic again from Kaamasmukka to Neiden. All the timberlines further south in Finland are altitudinal. There is no distinct altitudinal zonation in the hemiarctic section, but the pine forest grades into birch forest as the ground slowly rises towards the north (in Enontekiö) or remains fairly level (northern Inari). This interpretation is also supported by the map compiled by Lavrenko and Isachenko (1979), in which the barren areas and mountain birch forests of the western Kola Peninsula are interpreted as zones of the plains except for the higher mountains, where distinct altitudinal zones occur (Figures 9, 10, 11, Appendix 1).

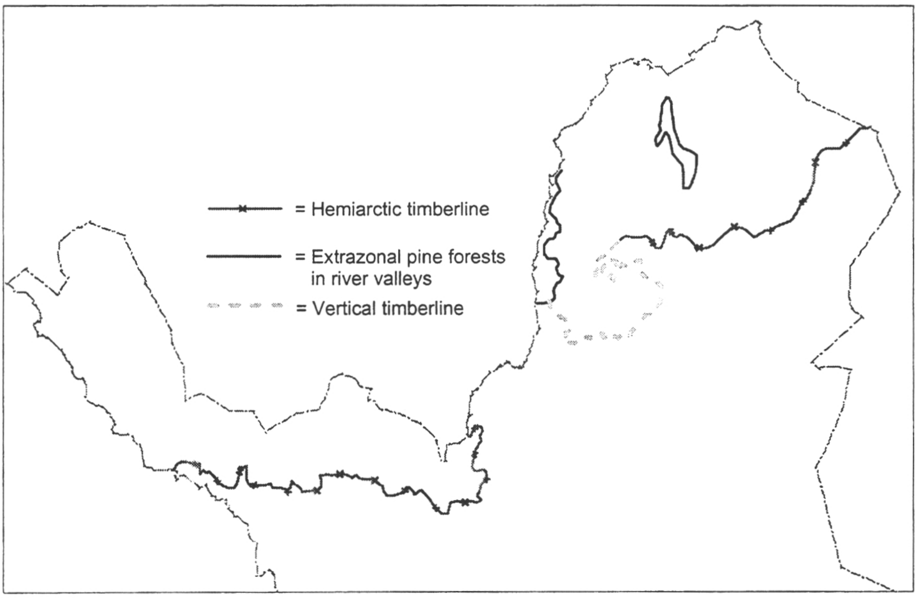

Figure 8. The northern hemiarctic and vertical coniferous timberline and extrazonal pine occurrences in river valleys in Finland

2.2.5 Alpine timberline ecotone

Mayer and Ott (1991) define the following altitude zones in the European Alps:

Snow zone: 2700/3000-4800 m. The area above the climatic snowline.

Alpine zone: 1600/2400-2700/3000 m. The area above the climatic timberline and the continuous layer of shrubs and dwarf shrubs.

Subalpine zone: 1200/1400-2400 m. The uppermost conifer-dominated forest zone, related to the 'Kampfzone' of the forest. May be divided into the upper subalpine zone, where the dominant tree species are *Larix europea* and *Pinus cembra* and the lower subalpine zone, where they are *Pinus sylvestris* and *Picea abies*.

Montane zone: 600/800-1200/1400 m. The central zone of mixed forest, which may be divided into upper, middle and lower montane zones.

Submontane zone: 300/500-600/800 m. The lower zone of mountain forest, with forests dominated by mainly deciduous trees.

Lowest montane zone: 200/400-300/500 m. (In German Kollinzone). The lowermost border zone of the mountains, bordering on the plains and containing mixed forests dominated by deciduous trees.

Ozenda (1988) points out that the mountain zones are not schematic altitudinal zones but are caused by the location of the vegetation on the basis of ecological factors, the most critical of which is temperature. Other factors with a major influence are humidity and soil. Significant variation in the zones may be caused by exposure, geomorphology and the local climate.

The subalpine zone, a transition between the uppermost forest zone and the treeless alpine zone, is characterized by an area of open forest and the 'Krummholz' area above it (Walter and Breckle 1986). According to Ozenda (1988), the subalpine zone may include a pseudoalpine part which is treeless for reasons connected with the soil, geomorphology or anthropogenic influence. Malyshev (1977) distinguished a forest zone and an alpine zone as altitudinal zones proper in the northern mountains of Asia, and the subalpine zone as a transitional zone between them. Holtmeier (1974) stressed that the use of the term alpine timberline should be limited to mountain areas proper where the winters are cold and snowy. Grabherr (1995) states that derivates of the term alpine like subalpine should be avoided for mountains others than nemoral or warm temperate ones.

Opinions differ among botanists as to how the altitudinal zones of the mountains and the latitudinal zones may be compared (e.g. Kildyushevski 1959, Ahti et al. 1968). Holdridge (1967) presents a general global 'life zone' classification in which the latitudinal zones and altitudinal zones are connected with the same system, and the circumpolar classification system presented by Tuhkanen (1984) is similar. For the Ural Mountains, Gorchakovski (1967) presented an analysis of the relations between latitudinal zones and altitudinal ones from the tundra to the steppes. The degree of divergence between the vegetation of the western and eastern slopes increases from north to south. The principles followed in the vegetational mapping of the Urals are described in detail by Gorchakovski et al. (1975). Nearly all studies of the vegetation zones of northern Fennoscandia take some sort of stand regarding the relations between altitudinal and latitudinal zones (e.g. Ahti et al. 1968, Haapasaari 1988, Oksanen and Virtanen 1995).

In estimating the similarities and differences between environmental factors in alpine and arctic regions, Gjaerevoll (1992) states that the daily temperature variation is greater and solar radiation stronger in alpine regions, permafrost is of minor significance and precipitation generally higher than in arctic areas. The southern alpine areas differ more from the arctic ones than do northern mountain regions. Bliss (1981) considered the alpine plant communities of Scandinavia, the Yukon and Alaska to be closer to an arctic vegetation than to the alpine vegetation of more southerly regions.

2.3 Alpine timberlines

Although the timberline may vary greatly in location and structure and it may be difficult to find a common explanation for all instances of it, timberlines around the world do have certain features in common. It is true of all natural timberlines, for example, that either the minimum level of some factor essential for tree growth or reproduction fails to be reached or that the limit of maximum tolerance in some respect is exceeded. Thus limits of this kind are absolute. Wardle (1981) estimates that among land ecosystems, timberlines mark the absolute limits to the growth of trees. The tree species of the area studied here are living within the limits of their prevailing physiological amplitude, whereas the distribution limits of most other plants are influenced significantly by competing species (Ellenberg 1966). As Hermes (1955) puts it, the timberline is a manifestation of a labile equilibrium in tree growth between possible and impossible conditions, which are mainly controlled by climatic factors.

The description by Arno (1984) of the timberlines of North America may be mentioned as an example of an extensive piece of research into variable timberlines. He describes how timberlines are formed by many tree species in areas of oceanic, continental, continental-oceanic, semi-desert, polar and tropical climate. The altitudes of treelines range from more than 3000 m to near sea level, and the factors affecting them under differing climatic conditions are highly diverse. In the driest parts of the Rocky Mountains there is a double timberline, where the species that can tolerate dryness form an upper, alpine timberline and a lower timberline with the semi-desert. The upper timberline in the tropical zone of Mexico and the northern timberline in Canada are the furthest apart on the American continent with respect to distance, structure and causes. No actual arctic timberline is formed in Alaska or the Yukon as it is elsewhere in Canada, but an alpine timberline does exist on the slopes of Brooks Range, formed by *Picea glauca* at an altitude of 600-900 metres.

The tree species growing at the highest altitude on a global scale is *Polylepis tomentella*, the treeline of which lies at 4800-5000 metres in the Cordilleras on the border between Chile and Bolivia (Troll 1973a). The altitude of the timberline rises towards the south in North America (Fig. 12), as on other continents, reflecting the effect of temperature on the formation of alpine timberlines. Malyshev (1933) concluded that the altitude of the alpine timberline in the Urals changes in a linear manner, by 71 metres per degree of latitude, while the correlation along longer transects in Asia is a curvilinear one. He also observed that the altitude of the timberline is related to humidity, which varies with longitude. This explains the higher altitude of the timberlines in Siberia and Central Asia than in Europe and the Far East, where the climate is more temperate and humid.

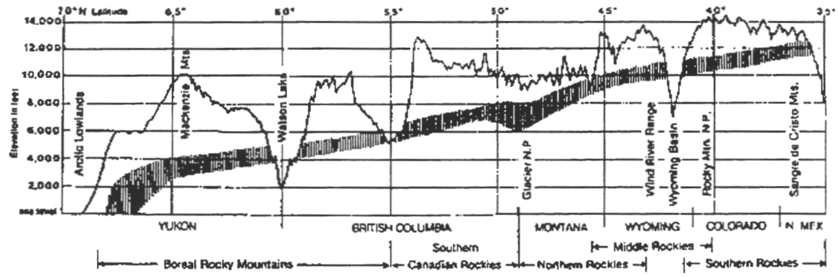

Figure 12. Longitudinal section of the Rocky Mountains from north to south showing that the alpine timberline rises towards the south (Arno 1984).

According to Cogbill and White (1991), studies in the Appalachians show that the altitude of the timberline changes curvilinearly by 83 metres per degree of latitude. They also conclude that the timberline in Quebec-Ungava, further north, differs markedly from that in the Appalachians, because the altitudinal limit merges into the northern one, the level of which is controlled more by the local topography and soil factors than by altitude.

The timberline lies at a lower level in areas where the maritime factor plays a role than in corresponding latitudes further inland. Parker (1994) observed that the elevational displacement of the occurrence of typically subalpine tree species along a latitudinal gradient in the mountains of California is markedly greater than that of tree species growing lower down in the mountains. This is caused by the different biogeographical affinities of the tree species.

Walter and Breckle (1986) distinguished a group of orobiomes in the boreal coniferous zone of Eurosiberia where the forest zone forming the actual timberline consists of coniferous forests, these being followed by a subalpine ecotone and then by the alpine zone and snow zone (Fig. 13).

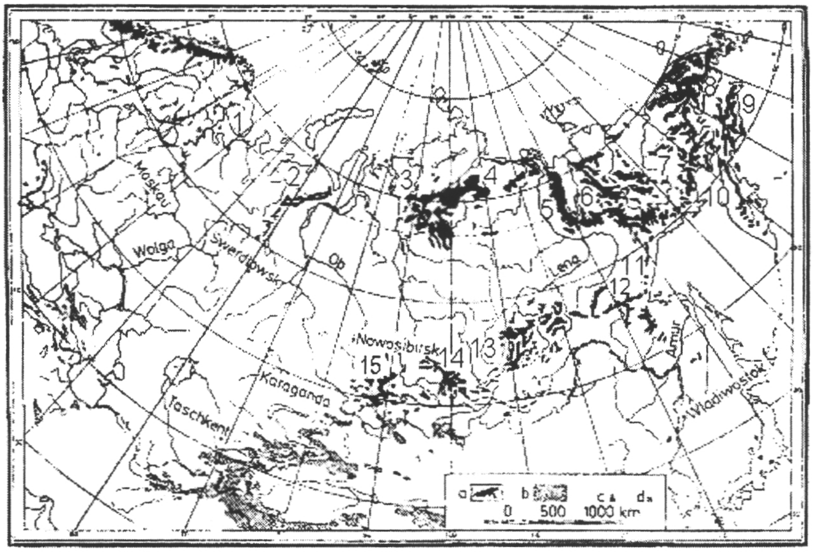

Figure 13. Distribution of the mountain tundra (a and c) and alpine vegetation (b and d) (Walter and Breckle 1986). Individual mountain ranges: 1. Khibiny, 2. Ural, 3. Putorana, 4. Anabar, 5. Verkhoyansk, 6. Cherski, 7. Kolyma, 8. Anadyr and Chukchen, 9. Koryaken, 10. Kamchatka, 11. Coast Range, 12. Stanovoy, 13. surroundings of Lake Baikal, 14. Sayan, 15. Altai.

2.4 Northern timberline

Compared with the diversity of structures and species at alpine timberlines, the northern timberline and treeline are formed by a fairly small number of tree species. More specific knowledge concerning the location of the northern circumpolar timberline began to accumulate during the latter half of the 19th century. Middendorf (1864) was of the opinion that the picture of the northern timberline on maps published in the mid-19th century was generally somewhat incorrect, and that the first scheme that was in principle correct was a small-scale map published by A. Petermann based on the publication 'Polar Chart, illustrating Dr. Sutherlands Account of Capt. Penny's Expedition, 1850, 1851, and showing the chief physical features of the Arctic Regions'.

More exact information on the location of the timberline gradually began to emerge, and by 1919 Brockmann-Jerosch was able to describe the northern timberline in considerable detail in his comprehensive study of the timberlines of the world. Hustich (1966) presented a preliminary synthesis of the northern timberline, stating that some generalization and simplification is inevitably necessary when describing the 20 000 km of the timberline in Eurasia, and additional research is also required in many areas. General descriptions of the circumpolar timberline have also been presented by Tikhomirov (1962) and on the same basis by Walter and Breckle (1986) and Tuhkanen (1993 a, b) (Figure 14). The phytogeographical division of the arctic and antarctic regions by Aleksandrova (1980) also provides a general picture of the timberlines, since she considers the timberline as marking the southern limit of the arctic .

Figure 14. Tree species forming the northern timberline (Tasanen and Veijola 1994). The figure was compiled on the basis of Walter and Breckle (1986), see also Tikhomirov (1962), Hustich (1966) and Tuhkanen (1933 a, b). Tree species: 1. *Picea mariana* and *Picea glauca*, 2. *Betula pubescens ssp. czrepanovii*, 3. *Picea abies ssp. obovata*, 4. *Larix sibirica*, 5. *Larix gmelini*, 6. *Betula Ermani.*

The northernmost point on the northern timberline has generally been considered to be the forested island of Ary-Mas containing *Larix gmelini* in the River Novoj on the Taimyr Peninsula in Russia. This island extends approximately 17 km along the river to latitude 72°37', with the last individual trees occurring at 72°40'. The second northernmost forest exists on an island named Tit-Ary in the delta of the River Lena, at latitude 72°. This occurrence was described as early as 1901 by A. K. Cajander (Cajander and Poppius 1903, Tikhomirov 1957, Walter and Breckle 1986). Kryuchkov (1978) provides more exact information on the northernmost occurrence of *Larix gmelini*, reporting the correct location of Ary-Mas as being 72°27'-28' and that of the northernmost continuous larch forest, beside the River Lugunskaja, as 72°34' (Figure. 15).

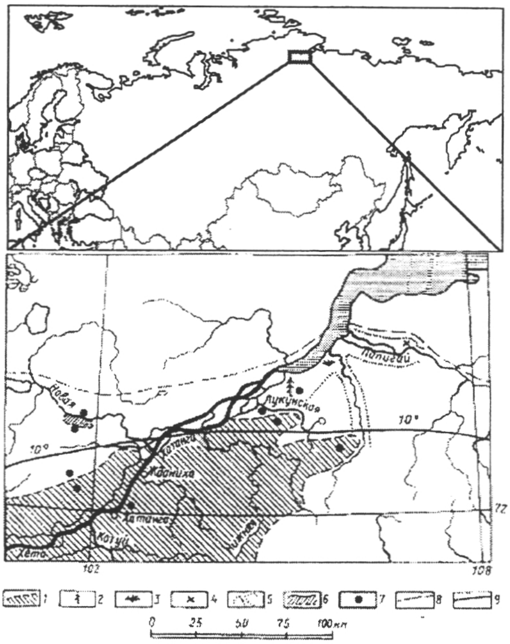

Figure 15. Structure of the northern timberline in the Khatanga valley on the Taimyr Peninsula (Kryuchkov 1978). 1 = continuos larch forest, 2 = northernmost larch groups, 3 = northernmost brush-formed growths of Alnaster fruticosus, 4 = northernmost brush-formed larches, 5 = area where brush-formed larches may occur, 6 = Ary-Mas, 7 = Kryuchkov´s observation points, 8 = northern limit of relative treelessness, 9 = 10°C isotherm fo July

The location of the northern timberline varies greatly. Malyshev (1993) has studied the location of the northern timberline in Russia (Table 1). In Canada the timberline is located south of the arctic circle in extensive areas and its northernmost point, at the Mackenzie delta, lies somewhat north of 69° latitude (Larsen 1980). The *Picea mariana, Picea glauca* and *Larix laricina* treelines are practically identical, but the the proportions of these species vary greatly (Hare 1950).

The southernmost point of the northern timberline is more a question of interpretation than the northernmost point. A narrow belt of the Newfoundland coast is treeless to 48° latitude and the treeless Aleutian Islands extend as far south as 52° (Tuhkanen 1993 a). The structure of the timberline in Alaska is complex due to permafrost, maritimity, variable topography and river valleys, so that no distinct vegetation zones such as forest tundra can be distinguished (Viereck 1979).

Table 1. Location of the arctic timberline and values of the most important climatic parameters (Malyshev 1993). The temperature sum was calculated without subtracting the threshold value. The climatic information is from the publication Climatic Atlas of USSR 1960.

Longitude	Latitude	Mean temp. of July °C	Growth period >5°C, days	Temperature sum, >5°C, d.d
35 Lovozero	69.2	10	110	800
40 Kanevka	67.3	11	105	1000
45 Mezen′	66.4	12	108	1150
50	67.5	11.2	98	1000
55	67.1	13.2	105	1050
60	67.4	12.5	92	900
65	67.4	10	90	750
70 Ob	67.4	11.8	85	800
75	67.4	12.5	85	750
80	67.4	13.2	90	850
85 Jenisei	69.7	11.5	80	1000
90	70.5	12	75	800
95	71	11	75	800
100	72	11	75	600
105 Hatanga	72.5	9	70	600
110	72.5	10	75	650
115	71.9	11	75	650
120	71.8	11	75	600
125	71.7	10.5	80	600
130 Lena	70.9	8	70	450
135	70.9	10.2	73	500
140	70.7	10.8	71	450
145	70	12	75	800
150	69.9	11	50	550
155	69.6	11.8	70	600
160 Kolyma	68.8	12.1	102	600
Keskiarvo	69.6	11.2	83	742

Krylov (1961) gives a good picture of the distribution of tree species in relation to the arctic timberline in the fairly even terrain of Western Siberia. The influence of the river valleys on the northern treeline is easily distinguished (Table 2).

Table 2. Norhern limits of tree species in West Siberia (Krylov 1961).

	Northern limit		
Tree species	Highland (plakor)	Valley of Ob	Valley of Yenisei
Larix sibirica	65°	67°50′	69°40′ (72°)
Picea obovata	65°	66°20′	69°25′
Pinus cembra	64°	66°	68°30′
Pinus sylvestris	63°50′	64°30′	66°
Abies sibirica	60°	62°30′	67°40′

The timberline in Eastern Siberia, which mainly lies north of 69° latitude in the plains as far as the delta of the River Kolyma, turns southwards to 65° latitude on the Chukotsky Peninsula, assuming clearly alpine features in the mountain areas, at the same time as the species *Populus, Chosenia, Alnus* and *Pinus pumila* appear at the timberline. The altitude of the timberline and proportions of the tree species may vary under conditions of variable topography (Chertovskoi et al. 1987).

North-eastern Siberia provides a good example of how different results may be arrived at even when describing the arctic timberline and treeline. Tuhkanen (1982) mentions that the arctic timberline in the easternmost parts of Eurasia is formed by *Chosenia arbutifolia* (syn. *C. macrolepis*) and *Populus suaveolens*, which occurs almost as far north, and the same author (Tuhkanen 1993a) states on the basis of the map published by Hustich (1966) that in the approximately 1000 km wide area between the River Kolyma and the Bay of Anadyr certain species of *Chosenia, Betula* and *Populus* occur hundreds of kilometres further north than does *Larix gmelini*. Hustich's view (1966) of the occurrence of *Chosenia macrolepis* was based on the map of Norin (1958a). Tikhomirov (1962), on the other hand, states that *Chosenia macrolepis* occurs at the arctic timberline only in the valleys, and his map of the northern limits of the tree species indicates *Larix gmelini* as forming the timberline markedly further south than the boundary of the deciduous trees proposed by Tuhkanen, stating that *Larix gmelini* forms the 'frontier line', of the forests. In the same publication, Tikhomirov (1962) presents a separate distribution map for the tree species belonging to the Bering group, suggesting their potential for afforestation in the tundra (Fig. 16). The arctic timberline as presented by Walter and Breckle (1986) follows the interpretation of Tikhomirov (1962) (Fig. 14).

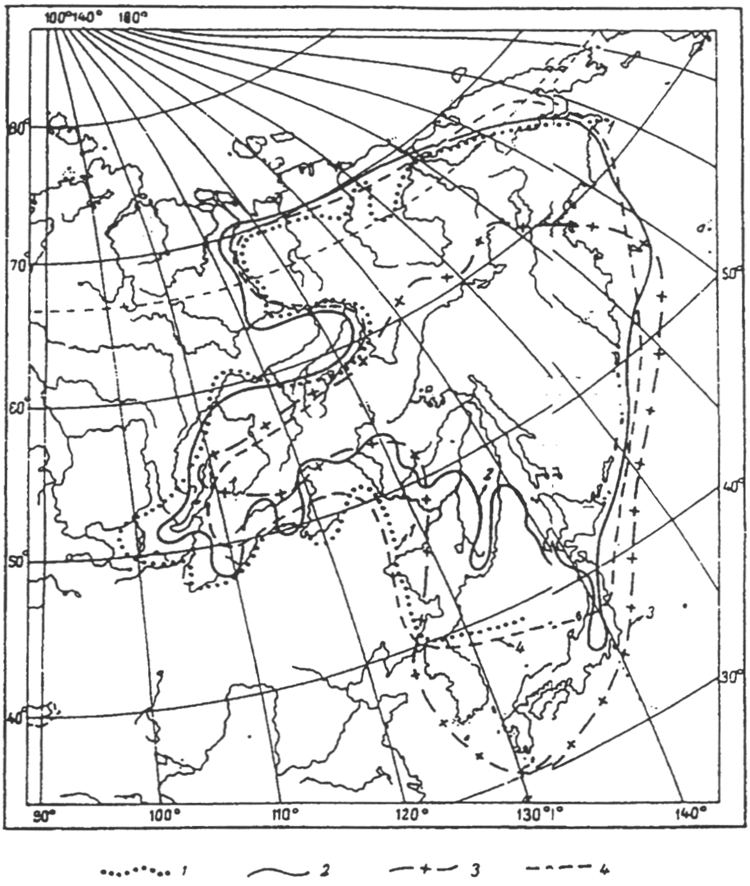

Figure 16. Distribution of tree species of the Bering group (Tikhomirov 1962). 1. *Chosenia macrolepis*, 2. *Pinus pumila*, 3. *Betula Ermani*, 4. *Populus suaveolens*

Chertovskoi et al. (1987) stated in their description of the forests situated close to the tundra in Russia that *Chosenia* occurs east of the River Lena in the form of small stands in the valleys of the Yana, Indigirka and Kolyma. In the northwestern forest vegetation region, *Chosenia* occurs farther north than *Larix gmelini* in some river valleys, but it is hardly ever observed outside the river valleys. *Larix gmelini* covers 42% of the forest area in the Magadan region, *Pinus pumila* 54% and deciduous trees only 4%. The biomass production of *Chosenia* and the poplars on rich soils in valleys outside the permafrost zone is many times greater than that of the *Larix gmelini* forests in the highlands. Nikolov and Helmisaari (1992) considered the northern boundary of *Chosenia arbutifolia* to be continuous, approximately in the same way as did Tuhkanen (1993a), stating that this species occurs mainly in river valleys and does not thrive in the permafrost region.

Parmuzin (1979) described the diversity of nature in sub-areas of northeastern Siberia in considerable detail, emphasizing the special character of the river valleys and the occurrence of both *Chosenia* and poplar in them. According to Aleksandrova (1980) the timberline on the Chukotsky Peninsula is formed by *Larix cajanderi*, whereas *Chosenia arbutifolia* and *Populus suaveolens* have spread far into the tundra along the rivers. Yurtsev (1973) considered these occurrences in the local continental climates of the inland valleys to be relicts from an earlier period of warmer conditions (Fig. 17).

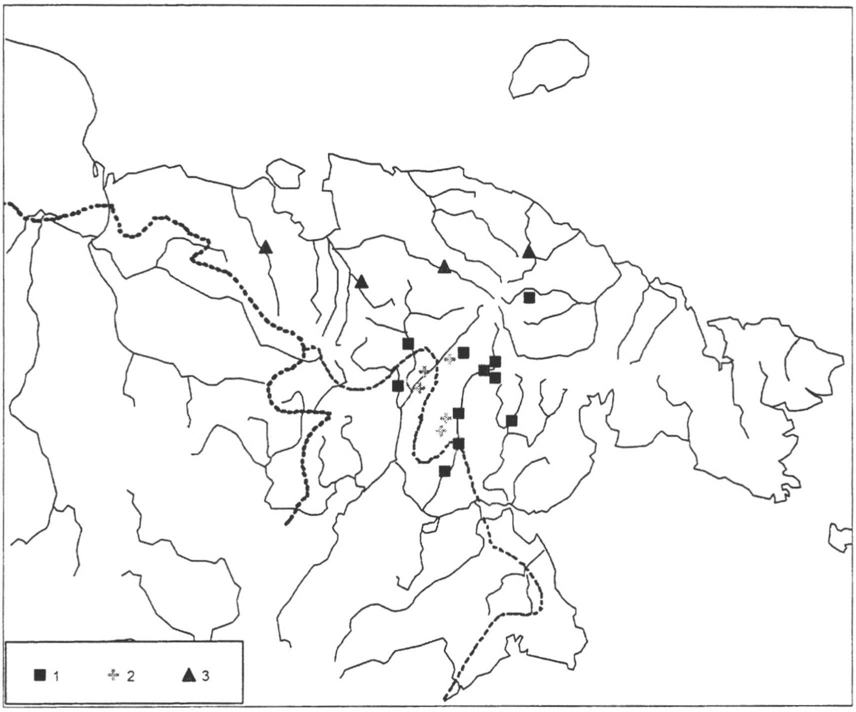

Figure 17. Species occurring in the Chukotska tundra (Yurtsev et al. 1985). 1 = Stand of *Chosenia arbutfolia*, 2 = Stand of *Chosenia arbutfolia* and *Populus suaveolens*, 3 = Individuals of *Chosenia arbutfolia*. Dotted line = timberline formed by *Larix cajanderi*, thin dotted line = limit of *Pinus Pumila* and other large brush species

The example of northeastern Asia shows that in areas of variable altitude and soils it is possible to arrive at diverse interpretations when describing timberlines and treelines formed by species that differ greatly in their site requirements and distribution.

2.5. Conclusions

Systems of concepts used for describing timberlines and treelines vary greatly, and the same term may even be used in different senses. Any examination of the frequently complex phenomena connected with the timberline requires exact definition of the basic concepts, and the conclusions are greatly influenced by whether the observations are made directly at the timberline or below it. The system of concepts presented by Hustich (1966) has been largely accepted and it is being used in a modified form not only in Fennoscandia but also in North America in particular. Special terms are available to describe distinctly altitudinal timberlines, e.g. in the Alps.

The Russian terminology has been built up from the definitions of vegetation zones, in which the concept of forest tundra occupies a central position. The term forest tundra is also widely used in North America, but opinions differ as to whether it is applicable to Scandinavian conditions.

The predominant approach to the timberline in North America and the arctic timberline of Russia involves the notion of ecotone. The arctic timberline is frequently compared with the southern boundary of the boreal zone with the steppe regions. The alpine timberline is generally considered an ecotone, although smaller in areal extent than the arctic timberline zone.

Mountain birch is the dominating tree species in the northern part of the Fennoscandian timberline ecotone, and numerous interpretations have been put forward of the status of these forests in relation to the vegetation zones. According to the most recent one, that of Oksanen and Virtanen (1995), the mountain birch forests belong to the northern boreal zone and to some extent to the hemiarctic zone. The northern coniferous timberline in Finland, which has traditionally been considered arctic-alpine, may be interpreted as hemiarctic throughout with the exception of the Muotkatunturit fell area, where it is altitudinal.

There has been very little discussion of the timberline as an ecotone in Finland, especially in the field of forest ecology, apparently because there are no extensive coniferous forests of the 'Krummholz' type, for instance. The mountain birch forests have not generally been regarded as true forests in Finland, certainly not in forestry circles, because of their minor significance for timber production, although their ecological significance is great and they are distinctly different from the barren areas.

The ecotone viewpoint and the connection with general landscape ecology theories gives us an opportunity to achieve a deeper understanding of timberline phenomena. Finnish timberline research has long been characterized by an approach which sets out 'from the direction of the forest', there has been less interest in approaching from the direction of the barrens or tundra. In North America, and even more so in Russia, timberlines are frequently studied in connection with the tundra. Findings that shed new light on the concept of the timberline and its ecology are readily available in papers chiefly devoted to the southern parts of the tundra.

As shown by the example of Northeastern Siberia, there may be surprisingly great differences even between commonly used references in the general descriptions they give of the arctic treeline and timberline, and different interpretations can easily be arrived at in areas of variable relief and soils featuring a number of tree species. The Russian view, that the actual 'front line' of the forest is defined in the 'placor' regions and that the occurrences in river valleys are to be regarded as extrazonal, differs from that espoused in Finland, for instance. A description of the distribution of tree species and a general determination of the timberline or treeline do not always lead to the same result. Generalization is necessary in the description of the timberline over extensive areas to such a degree that no far-reaching conclusions may be reached on the basis of such general accounts. The additional information provided in connection with maps is therefore of great importance for interpretation purposes.

3 Mapping of the timberlines in Scandinavia

3.1 General

The mapping of timberlines and treelines is an essential part of the study of nature in arctic regions, especially the flora and vegetation. For the very earliest times, expeditions carried out in Scandinavia, Russia and North America had mapping of the timberline as a part of their activities. Mapping of the timberline is a necessary prerequisite for other timberline studies (Kallio and Sonesson 1979), and the lack of adequate maps made this work considerably harder in the early days. Even in Finnish Lapland, the topographic map to a scale of 1:20 000 was completed as late as the 1970's.

Despite the inadequacy of the maps and the transport difficulties encountered in timberline regions, a fairly correct picture of the position of the timberline in Scandinavia was formed as early as the 19th century, whereas the same stage was not reached in the vast territories of North America and Siberia until greater technological progress was made in the 20th century. The general features of the history of mapping of the Fennoscandian timberline will be examined in the present connection, whereas more recent, regionally restricted studies of the timberline will be included only when they are of significance for mapping.

3.2 Finland

3.2.1 Early expeditions and research

Although the earliest information on the flora of Lapland dates from the late 18th century (Mäkinen 1981), research proper and mapping of the timberline began in the 19th century. Wahlenberg (1812) defined the following forest vegetation zones in Fennoscandia (from south to north): regio sylvatica, regio subsylvatica (pine zone) and regio subalpina (birch zone), with three zones of fell vegetation situated above these. The northern boundary of the regio subsilvatica on Wahlenberg's map deviated from the present pine timberline mainly towards the south in Enontekiö and towards the north in the Petsikko area. The occurrences of pine in the Teno, Karasjoki and Utsjoki valleys and beside the fjords of Finnmark in Norway were shown extremely accurately considering the scale of the map.

From the extensive notes of Jacob Fellman, vicar of Utsjoki (Reuter 1909) selected notes concerning the forests of the area around 1830, including detailed information about the timberline regions. This material does not give an overall picture of the timberlines, however. von Berg (1860) compiled a map of the distribution of trees and shrubs in Norway, Sweden and Finland on the basis of a journey made in 1858 and employing information obtained from local experts. The limits of birch, pine and spruce are in principle correct, but the pine treeline in Finland is clearly located too far north. He defined the treeline as the last point at which most of the trees are still of a usable size.

The travelogue of Middendorf (1864) ovbviously extends to Finland, and he describes the shapes of the trees at Maanselkä, but does not give any exact information on timberlines in Finland. He mentions the pine forests of Alta as the northernmost occurrence, in the same way as the stem-formed birches of the Rybachi Peninsula in Petsamo. In the summer of 1867 Norrlin, Palmén, Malmberg and Sahlberg made a natural history expedition to western Lapland and recorded observations on the timberline and the vegetation zones (Norrlin 1873), stating that the last occurrence of pine was close to the village of Maunu in the Könkämäeno valley, while birch grew in the river valleys up to Lake Kilpisjärvi. The situation is the same today. Norrlin (1873) analyzed the differences between the spruce zone and the pine zone, for example.

Blomqvist made a journey to Lapland 1868, although his report was not published until nearly a century later (1959). The focus of attention was on central Lapland, but he also presented detailed observations on other areas, including the timberlines on the fells of western Lapland. Kihlman (1884) made a botanical expedition to the Inari region of Lapland in 1880 and described the vegetation zones from this area in commendable detail, including an account of the most significant fells. Hult (1887), who had accompanied Kihlman on his expedition in 1880, also published observations of his own, concentrating on the alpine vegetation. He suggested only minor revisions of Kihlman's map (1884).

In his description of the tree species of Finland, Blomqvist (1881) included a concise, accurate account of the northern tree line and altitudinal limits of pine. Lindén (1943) made a journey in 1888 up the Lätäseno river to Lake Porojärvi in Enontekiö and to the Arctic Ocean, making observations on the occurrence of pine and birch. The pine treeline in the river valley is still to be found at present in the same place on Isokurkkio where Lindén described it. Sandberg (1898) made a journey to northern Lapland in 1892, one of the aims of which was to determine the positions of the timberlines. His descriptions of the timberline regions of Utsjoki and Inari in particular are highly detailed and apparently correct. He compiled a map which shows the limits of pine and spruce both as 'sporadic occurrences' and 'forming stands', and also pondered over the difficulty of determining the timberline, although his map shows that his conclusions were quite correct. The pine treeline had been determined quite accurately with the exception of the occurrence in Utsjoki, which was marked on the map as being too extensive.

Hult (1898a) summarized the vegetation zones of Lapland in a paper read to the Geographical Society of Finland in which he gave accounts of the expeditions he had made and assessed their results (Hult 1897). In the publication by Hjelt (1897) on the distribution of the trees, bushes and dwarf shrubs in Finland, there is a map of the northern limits of the trees and of the northern vegetation zones: the pine zone, birch zone and fell zone.

Among the early writings that concentrate mainly on alpine timberlines, one that is particularly worth mentioning is the detailed account of the vegetation and treelines of eastern Lapland and the fells of the Kola Peninsula by Borg (1904), based on research carried out in 1898 and 1901 and including maps and measurements of altitude. Borg's map shows the southern limit of the birch zone from the Teno valley to the western part of the Kola Peninsula in adequate detail. Nyholm (1903) presented corresponding altitudinal data for the treelines in the fells of Saariselkä. Cajander (1903) described the ground vegetation of various vegetation zones in the fells of western Lapland as a result of his journey in 1902, while the description of pine forest formations in Finland provided by Kranck (1907-1909) also included a description of the latitudinal and altitudinal timberlines for this species along with altitude data for the timberline and treeline.

The report of the committee for protected forests (Komiteanmietintö 1910) includes a map on which the timberline regions are shown in great detail. It is based on the zones recognized by Wahlenberg, denoted as a zone of open fells and mountain birch, a zone of scattered pines, a zone of scattered pine stands and a zone of continuous pine forests. The map is a result of fieldwork carried out in the summers of 1906 and 1907, supported with local knowledge acquired by the district offices of the National Board of Forestry. Olli Heikinheimo, secretary to the committee, played a major part in compiling the report and the map. The report explains the course of the timberline in detail and provides estimates of the areas of the zones.

The main object of criticism in the map is the width of the zone of scattered pines, which is exaggerated in northern Inari and in Utsjoki, and the excessive emphasis placed on scattered pine stands in relation to continuous pine forests. On the other hand, it is possible that the area of scattered pine stands was actually larger in the early 20th century than it is today. Ilvessalo (1927) also made a remark to the same effect stating that a part of the zone of scattered pine stands as described by the committee could with some justification have been included in the zone of continuous pine forests. He assumed that one reason for the discrepancy was a lack of comprehensive forestry maps at the time when the committee was carrying out its work. It is probable that the differences between the map produced by the committee and the present state of affairs are attributable to both inaccurate mapping and subsequent development of the forests.

Appended to the dissertation of Renvall (1912a) dealing with pine seed years is a map of the area studied by him, showing the northern pine timberline in great detail. The occurrences along the River Inarijoki and in Utsjoki are accurately depicted, and the fell area of Vätsäri has also been taken into account. The map was at least partly based on the results of recently commenced forest surveys.

Tanner (1919) published a map and account of the vegetation limits in Enontekiö which gives quite an accurate picture of the sporadic occurrence of birch, pine and spruce, and of the northern limits of stands of these species. The contour lines, among other features, made this map considerably more advanced than the earlier ones.

The forests of the Petsamo area came under the jurisdiction of the Russian forest administration and were mapped prior to the time when the area became part of Finland. An account of the positions of the timberlines formed an important part of the report on the forests of the province of Petsamo produced by Pöyhönen (1921).

The publication by Heikinheimo (1921) on the timberline forests of Finland was for a long time the best source of information on these areas. It also contains a map, which is based not only on knowledge acquired by the author himself, but also on the report of the protected forests committee, several of the publications mentioned earlier and the reports of Renvall and Pöyhönen (Figure 18).

A fairly exact general picture had thus been obtained of the timberlines in Finnish Lapland by the early 1920's, mainly as a result of expeditions and surveys. The actual timberlines and treelines arrived at were naturally somewhat variable, but given the lack of topographic maps, the result may be considered very good. The scientists were probably aided in their fieldwork by the existence of traditional means of transport across the timberline, mainly along watercourses and by information gleaned from users of these, local people and the district offices of the National Board of Forestry. The picture was further filled out by the results of the forest surveys.

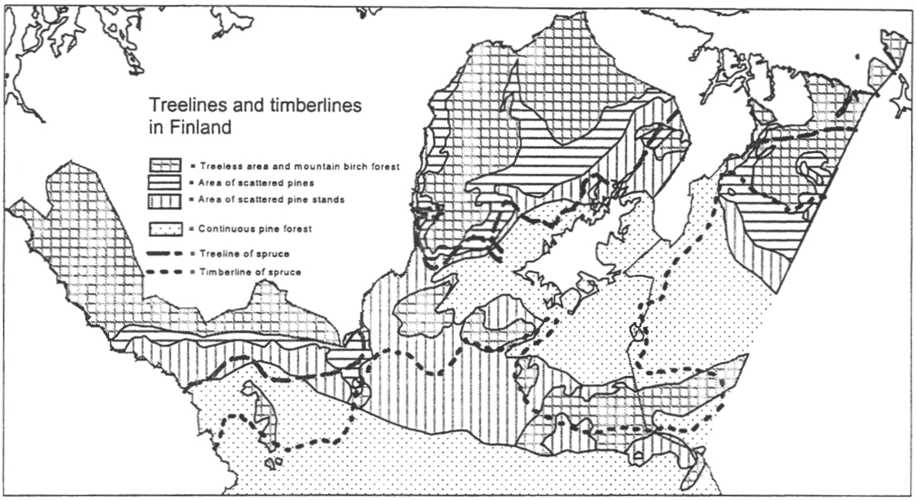

Figure 18. The arctic treelines and timberlines in Finland (Heikinheimo 1921).

3.2.2 Forestry maps

Since the earlier surveys of state-owned forests carried out in the 1860's did not give sufficient information on which felling plans could be based, new surveys were started in 1881 by hiring forest surveyors. In the extensive northern districts the work was carried out in the form of line surveys. Nearly all state-owned land had been surveyed by 1906 (Hertz 1934).

Surprisingly enough, this survey, which included assessments and maps, also extended to the timberline regions, even though these lay beyond the area where timber could be harvested. On the other hand, the exploitation of forests in the far north of Lapland was concentrated at the timberline itself, due to the needs of the local population and the demand for timber in Norway. It was also necessary to know the extent of the forest reserves, in view of continuing pioneer settlement and the coming enactment of the Great Partition in the region.

A line survey by taxation areas was carried out in the forest district of Inari in 1897-1915, and this work also covered the timberline regions of both northeastern and western Inari. The resulting maps depicted the vegetation zones after Wahlenberg (1812), and the limits of the pine and birch zones were regularly shown. The forest survey manuals also contain verbal descriptions of the timberlines.

The forest district of Utsjoki occupied in a special position on account of the scarcity of forest resources relative to the use habitually made of them. Senate decrees had been issued even in the 19th century to regulate the use of the forests in this area. The first comprehensive survey of forest reserves that included mapping of the timberline was carried out in 1911-1915, covering the valleys of the Rivers Teno and Inarijoki (Lakari 1912), Skietsim and Vaskojoki (Sammallahti 1913), and Utsjoki and Kevojoki (Renvall 1915). The relevant research served to a significant degree as the basis for a publication on protected forests by Renvall (1919). The survey of the local government district of Enontekiö in the forestry district of Muonio was made as early as 1899 (Lojander 1899).

The forestry plan with maps of the Utsjoki forest district compiled by the taxation official A. Hiilivirta is the most thorough and extensive account of the timberline and timberline forests ever made in Finland, extending down to stand level (Metsähallitus 1941). It also provided basic material for the Atlas of Finland and for forestry research. Maps to a scale of 1:100 000 covering the entire administrative district of Utsjoki and the northern part of Inari divide the birch zone into a stunted birch zone and a mountain birch zone, which also includes the zone of scattered conifers. The maps show the limits of continuous pine forests, scattered pine stands and scattered pines. Stand level information is also given for the mountain birch zone.

Sirén (1970) published parts of Hiilivirta's map in connection with the results of his own regeneration inventory (Fig. 19), and also presented preliminary findings on the later development of the timberline in the same areas (Sirén 1933b, 1994). In the more recent forest surveys conducted by the National Board of Forestry the mapping did not extend to the northern pine timberline nor to the mountain birch zone.

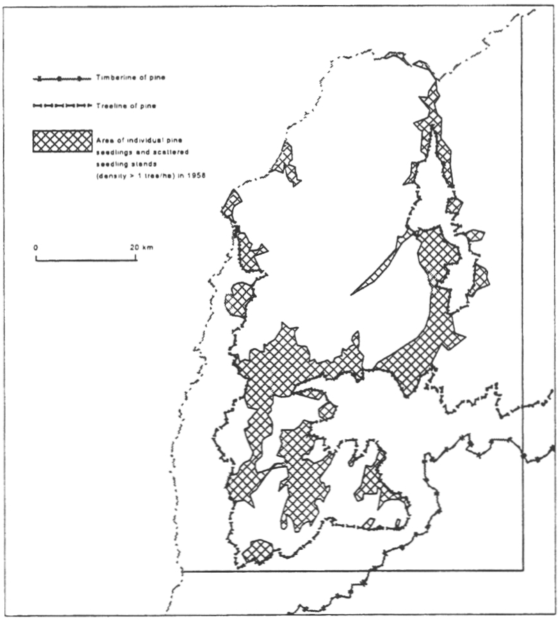

Figure 19. Results of an inventory of pine seedlings in western Utsjoki 1958 (Sirén 1970).

The timberlines in Saariselkä and the fell areas to the south have been thoroughly mapped in connection with forest surveys, a distinction being made in these surveys between non-productive land, including the barren fell zone and that possessing bush-formed birch stands, and low-productivity land, which consists of fell and highland forests, the latter including the main part of the mountain birch stands and the zone of scattered pines.

In their guide to the determination of forest types, Lehto and Leikola (1987) distinguished conceptually between low-productivity land, which includes highland forests and fell forests, and non-productive land, which includes the poorest highland forests of the fell tops, the poorest part of the birch zone on the fells, and the barren fells.

3.2.3. Atlas of Finland

The Geographical Society of Finland has published its Atlas of Finland at intervals since the late 19th century, and it is possible to gain an idea of how the description of timberline regions has developed at the level of general maps from the material related to the timberline that has been included in the various maps of the atlas.

The 'Atlas öfver Finland' of 1899 contains a short article by A. Osw. Kihlman (1899) on tree-formed plants ('Trädartade växter') in connection with a map of the limits of the tree species by Hjelt (1897), and an article by E. Sallmén (1899) on the forests connected with a map showing the abundance of forests. A zone is shown in the vicinity of the northern timberline where sawlogs are scarce but the volume of other timber is sufficient to meet the local demand.

The Atlas of Finland of 1910 includes an article on the flora and vegetation by J.P. Norrlin (1910) in which the northern zones are described in accordance with the system of Wahlenberg. This is accompanied by a map showing the zones of Lapland compiled by A.K. Cajander (1910) and covering the entire northern part of Fennoscandia, including the Kola and Kanin Peninsulas. The map shows the spruce zone, pine zone, birch zone and fell zone. In spite of its small scale, it is quite accurate as far as Finnish Lapland is concerned.

There is an article and map in the 1925 edition of the Atlas of Finland under the heading 'Vegetation and grouping of the population' (Granö and Cajander 1929). The map was compiled by J.G. Granö. The part on the vegetation was written by A.K. Cajander and that on the population was again the work of J.G. Granö. The map distinguishes between forest, mountain birch forest and barren fells, and a special marking is adopted to show the limit of coniferous forest.

A map of the vegetation zones of Lapland which has been widely used later was included in the Atlas of Finland edited by Aario (1960). This map distinguished the following regions: tundra and barren fell, birch scrub and birch forest, birch forest with small pine stands, pine forest and coniferous forest, which includes spruce. The birch forest with small pine stands was interpreted as being quite extensive in the Enontekiö and Muotkatunturi fell regions.

Part 141 of the newest edition of the Atlas, that devoted to 'Vegetation and flora', contains an article on the general features of the vegetation in Finland by Hämet-Ahti (1988) which includes Map 5a, 'Forests of Lapland', distinguishing barrens above the treeline, mountain birch woodland, birch forest mixed with pine stands, pine forest mixed with birch, and also pine, spruce and birch forest. Open peatlands are also shown. The map is exact, but the use of the terms 'mountain birch woodland' and 'birch forest' may cause confusion. The pine forest of Inari, which its admixture of *Betula pubescens*, is different from the mountain birch forest with small pine stands.

3.2.4. Special studies

Much important information on the timberline is to be found in reports of research carried out for various specific purposes, e.g. floristic research, regional vegetation mapping, geographical studies and land-use planning.

The mapping of the vegetation of Inari and Utsjoki carried out from the Kevo Research Station has produced detailed information on treelines. Kallio et al. (1969) described the starting points for this mapping and basic facts about the area, following which Kallio et al. (1971) published a detailed account of the occurrence of pine and spruce based on extensive field surveys (Fig. 20), maps and aerial photographs. Thus the determination of the limit of continuous pine forests and the description of scattered occurrences provided by this publication may still be considered the best and most thoroughly grounded interpretation of the pine treeline in Finland.

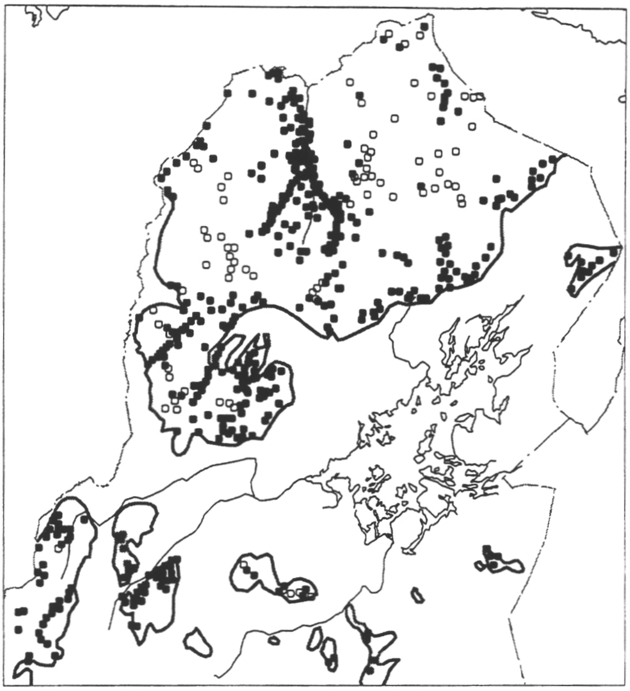

Figure 20. Occurrence of pine in Finnish Lapland (Kallio et al. 1971). The black line represents the limit of continuos pine forests. Black dots depict individual / isolated stands and trees, and circles represent saplings less than 2 m in height.

Timberlines are naturally also shown in the maps of the northern national parks and nature reserves. Heikkinen and Kalliola (1989) compiled a vegetational map of the Kevo Strict Nature Reserve to a scale of 1:50 000. Small pine stands are depicted precisely, and special attention in the mapping of birch stands is given to areas damaged by *Oporinia autumnata* (Bkh.). Eeronheimo et al. (1992) mapped the vegetation of the Pallastunturi-Ounastunturi National Park thoroughly on a scale 1:10 000. The results are available in the form of a database which can be printed out as required. This mapping gives a very detailed picture of the timberlines.

In the management plans for wilderness areas currently being compiled by the Finnish Forest and Park Service, the vegetation maps will also show the timberlines. This work is based on forestry maps and colour infra-red or false-colour aerial photographs. The biotope map of the Pöyrisjärvi wilderness area shows the treelines and timberlines for pine and mountain birch. The timberline ecotone is divided into the following groups: practically pure pine forest, pine-dominated forest with birch, mountain birch forest with pine, heavily forested mountain birch areas, mountain birch forest and low, partly bush-formed mountain birch forest (Metsähallitus 1994 b). In order to provide a basis for natural resource planning in Northern Lapland, the Finnish Forest and Park Service is planning to carry out biotope mapping, in which the timberlines will also be an object of comprehensive study (Metsähallitus 1995 a).

Using the Landsat-1 images, Seppälä and Rastas (1981) compiled a vegetation map of the Inari region of Lapland to a scale of 1:200 000, paying special attention to timberlines and areas damaged by *Oporina autumnata* Bkh. They also assessed the results of earlier mappings of the timberline and discussed the description of forests which are mixtures of pine and birch in various proportions, stating that it is extremely difficult to distinguish stands of *Betula nana* from mountain birch forests and shrub-covered peatlands. In some areas, e.g. east of the lake Inari, the map showed a high proportion of birch-dominated forests compared with the information given on forestry maps.

In his study of the geography of the Inari area, Piirola (1972) also examined the vegetation and timberlines and created a geographical division of the region into sub-areas. On his vegetation map of the area, based mainly on forestry maps, Piirola attempts to distinguish between arctic and alpine timberlines, considering the pine timberline between the River Inarijoki and Neiden to be arctic.

3.3 Russia

The research of Trautvetter (1849) into phytogeographical conditions in western Russia includes a description of the northern timberlines. Regarding the Kola Peninsula he referred to the information given by Wahlenberg, Fellman, Böthlingf, von Middendorff and Helmers. The history of research into the vegetation of the Kola Peninsula is well described in the comprehensive work of Regel (1935-1941).

Jacob Fellman, vicar of Utsjoki, published the first botanical observations on the Kola area in 1831, and then a more comprehensive description in the 1860's. Members of the St. Petersburg Academy of Science, among them von Baer and von Middendorff, made expeditions to Kola in the early 19th century, leading von Middendorff (1864) to claim that total misconceptions prevailed around the middle of the century concerning timberlines in the Kola Peninsula. He stated that fairly exact information was given in the official sources about the forests of Archangel, but that only stunted forests were said to exist in the Kola area. Correct information was given by von Middendorff on the timberlines of the Kola Peninsula, although he laid too much emphasis on the role of spruce in forming the timberline east of the Kola Fjord.

Finnish scientists made expeditions to Kola from the 1840's onwards. The first journeys were made by Fredrik Nylander in 1842, 1843 and 1844, during which he collected an extensive herbarium. In his report on an expedition made in 1867, the Norwegian Professor J. A. Friis (1872) published a map, based on those possessed by the forest administration in Russia, showing 'the northern limit of continuous deciduous forest' and 'the northern limit of continuous coniferous forest'. He described the area north of the birch limit as 'forestless tundra or peatland and willow steppe', and described the main fells separately. The timberlines were mainly correct, but the birch occurrences extending north in the direction of the river valleys were lacking.

As a result of an expedition made to the Murmansk coast in 1880 by some natural scientists from St. Petersburg, Kudryavchev published information on the forests and the timberline in that region. A Finnish expedition was arranged to the Kola region in 1887 (Kihlman and Palmén 1889), and Kihlman (1889) also made a separate journey later. The main publication by Kihlman (1890) remained for a long time the most significant achievement of timberline research in Fennoscandia, and is still considered valuable today. It includes a coloured map by A. Petrelius which gives a very accurate picture of the northern timberline on the Kola Peninsula and of the relation between the mountain birch forests and coniferous forests. The most obvious mistake was made in the area near the White Sea, which was also regarded by Kihlman as covered by continuous coniferous forest.

Especially worth mentioning among the other Finnish studies are those of Borg (1904) on alpine timberlines and Tanner (1913) on an expedition to the watersheds the Rivers Luttojoki and Paatsjoki. Regel was of the opinion that it was in general the work of the Finnish scientists that had led to the Kola Peninsula being among the best known parts of northern of Russia.

The map of J.A. Friis (1872) contains a special mention, the only one of its kind, that 'there is rather luxuriant birch forest' on both sides of the isthmus between Maattivuono and Pummankivuono on the Rybachi Peninsula, and he also describes these birch forests, which were later destroyed, in his commentary to the map. After Petsamo had become a part of Finland, botanists took a strong research interest in this area. The timberline was at least partly the subject of work by Auer (1927), Tanner (1927) and Kujala (1929). Tanner's paper is accompanied by a map which distinguishes between barrens, the birch zone, the zone of scattered pines and pine stands and the area of pine forests. The northern limit of spruce forests and spruce stands is also depicted. Kujala's map is almost identical to Tanner's. There was still time to make some forest surveys in Petsamo in the 1920's (Havas and Herold 1923, Lindström 1927), and Aario (1940, 1943) later continued the study of the timberline regions in Petsamo, compiling vegetation maps, among which that of forest zones before the influence of man is especially interesting. All the research points to a powerful human impact on the forests.

Tanfil`yev (1911) presented a general map of the northern timberline throughout Russia and a more detailed study of the area between the River Mezen and the Pechora delta, giving at the same time a detailed account of earlier research. Pohle (1917) described the northern timberline of Russia, stating that the Kola Peninsula is more closely related to Scandinavia than to eastern Russia. According to Regel (1935-1941), Russian scientists continued to study the forests of the Kola Peninsula in the 1920's, but conditions on the peninsula changed rapidly with the coming of industrialization, the increase in population and improved means of communication.

In his comprehensive basic survey of the vegetation Tsinzerling (1932) divided the Kola Peninsula into the forest zone, the forest tundra and the tundra, and entered into an extensive discussion of timberlines. Regel (1935-1941) analyzed earlier research and re-introduced the maps of Tsinzerling and Pryachin, in which the timberline and its surrounding areas were presented in more detail than before. He arrived at the conclusion that the northern timberline of the Kola Peninsula is of the atlantic-subarctic type, which grades to the eastern European type in the eastern part of the peninsula. Regel also paid attention to isolated patches of forest, which are an important factor further east. Solonevich (1940) compiled information on the pine timberline and treeline and described the occurrence of pine in the Kola Peninsula.

The picture of the timberline on the Kola Peninsula became more detailed on later vegetation maps, the latest of which is that edited by Lavrenko and Isachenko (1979). The general principles of this mapping were explained by Gerbikh et al. (1970). Regarding the plotting of the timberline, it is important that the zones are not drawn as lines, but that efforts are made to depict the vegetation of the ecotone in the form of separate units. This method gives a better picture of the natural conditions. In the new map a separate area of northern atlantic birch-dominated forest tundra is defined for the Kola Peninsula, denoting an area of birch forest with variable admixtures of spruce and pine. The birch forests are divided into two groups on the basis of the ground vegetation, in addition to which the birch forests of the plains and the fells are distinguished.

The timberline on the coast of the White Sea, which is covered by ice in winter, has a special structure on account of its isolated patches of forest. The timberline almost reaches sea level in places, and the characteristic fairly wide birch zone on the coast facing the Barents Sea is virtually absent on the White Sea coast. There are peculiar forms of wind-exposed pine forest on the coast, along with junipers. Strips of tundra occur on the outermost shore and on the capes (Payanskaya-Gvozdeva 1990).

Friis (1872), who based his knowledge on data from the forest administration, was quite right as early as 1872 when he said that the conifers come down to the very coast between Kandalaksha and Varsuga, and that the coniferous timberline from there eastward is less than ten kilometres away from the shore.

The limits of the vegetation zones are depicted in the form of lines on the basic maps of the flora of the Murmansk area (Gorodkov 1953), for instance, and in the newest textbook on the geography of this area (Kryuchkov 1993) (Figure 21). The northern limit of the forest tundra may be taken to represent the timberline for birch and its southern limit as the coniferous timberline.

The timberline regions in Russia were also mapped quite early in connection with forest surveys (e.g. Friis 1972, Pöyhönen 1921). A forestry map for the forestry district of Murmansk has been preserved from 1913, showing the coniferous stands later destroyed by man in the vicinity of the towns of Murmansk and Kola (Nechayev 1993). Kihlman (1890) also mentioned that significant pine stands were growing approximately 20 km north of the town of Kola, and that they were already being heavily used. At least on the Kola Peninsula the forest surveys extended to the northern timberline. The results of forest surveys still provide important source material for the compilation of general phytogeographical maps in Russia (Gerbikh et al. 1970).

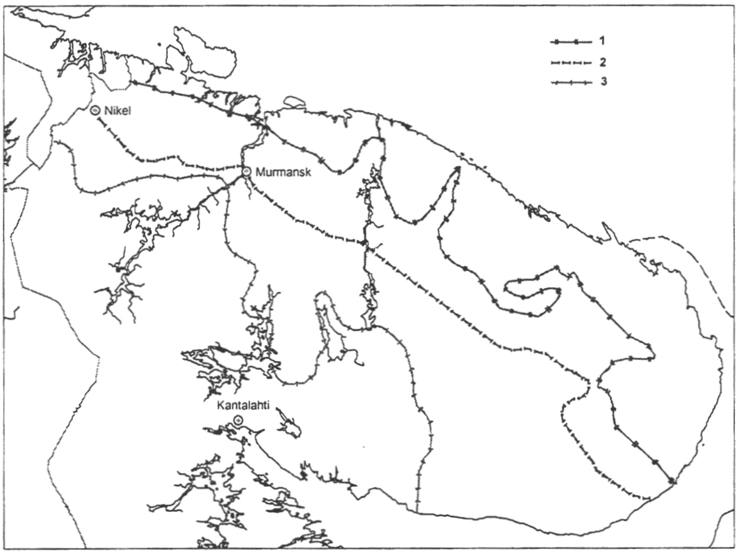

Figure 21. Timberlines and vegetation zones in the Murmansk area (Kryuchkov 1993). 1. northern limit of forest tundra, 2. souther limit of forest tundra, 3. southern limit of protected forests.

3.4 Norway

The conditions for timberline mapping in northern Norway differ from those in Finland and Russia. The forest areas are small and frequently clearly defined, and the steepness of the terrain means that the timberline is clearly visible. On the other hand, as Eidem (1956) states, the forested areas in northern Norway are so scattered that the concept of a continuous coniferous timberline does not apply. The birch forests are more extensive and continuous, however, so that a timberline may be determined for these. The northern timberline for birch runs across the northern peninsulas of Finnmark, while further south the line is alpine in character.

The history of utilization of the forests in northern Norway is to a large extent also the history of the timberline and thus Norway has an abundance of detailed regional timberline descriptions.

The notes made by Major Paul Schnitler pertaining to the demarcation of boundaries between Sweden and Denmark-Norway in 1742-1745 (Nissen and Kvamen 1962) constitute one of the earliest literary sources to include information on the forests and timberlines of Norway. Since the demarcation of such boundaries also took account of sources of livelihood and living conditions, the sufficiency of the forests was a significant issue.

Keilhau (1831) presented detailed information on timberlines in Finnmark, based on a journey made in 1827 and 1828. The first detailed survey of the forests of Finnmark was nevertheless that published by Barth (1858). Research on the forests of the Pasvik area is included in a work by J.A. Friis (1872).

At the turn of the century Amund Helland published an extensive work in Norwegian consisting of several parts, in which he gathered together existing information on the forests his country, presented area by area. In addition to information from local experts, he also used publications and archives as sources. Although the work is of a general character, the detailed descriptions of the forests take up numerous pages for each of the northern provinces. The first description to be concerned with northern Norway was that of the province of Troms (Helland 1899), followed by Finnmark (Helland 1905) and Nordland (Helland 1907). For Troms and Finnmark, Helland presented detailed figures on the altitude indicating the birch timberline in the archipelago, on the shores of the fjords, and inland. These figures, based on information obtained from a forest officer by the name of Norman, were arranged by local government district.

Among silvicultural studies proper, the first notable piece of work is that of Hagem (1917) on the seed crops of conifers. This includes a description of the pine areas of northern Norway, in which the pine timberlines and treelines are also indicated for each area. In connection with this publication there exists a map of the pine forests of northern Norway, compiled on the basis of the forest map of Norway by K. Gleditsch. The part of Finland included on that map is depicted according to Renvall (1912a).

Juul (1925) described the pine forests of Finnmark and Troms very thoroughly area by area on the basis of a forest survey carried out in 1916-1924, and he also gives detailed information on pine timberlines and treelines. The exact descriptions of scattered occurrences and remnants of dead pines are interesting with reference to the timberline. In the map appended to the publication, the probable earlier distribution area of pine is outlined on the basis of these remnants. It may be stated that the completion of Juul's work marked the first detailed mapping of the coniferous forests and timberlines.

Aas (1969) compiled a map of the entire Scandes showing the climatic timberline for birch. Among the most recent mapping projects, the Atlas of Norway is particularly worth mentioning. Its map sheet 8.2.1 'Areas of forestry and agriculture', 1:2 000 000, shows productive forests and low-productivity forests (Norges geografiske oppmåling 1983) and gives a good picture of the timberlines. The maps of reindeer pasturage and vegetation in Finnmark and Northern Troms give an overall view of the timberlines as well (Johansen et al. 1995). The estimated total length of the timberline in Norway is 47 000 kilometres (NOU 1989).

3.5 Sweden

The timberlines in Sweden are alpine in character and are located on the slopes of the Scandes. They differ markedly from those in Norway, however, in that the topography is generally gentler on the Swedish side of the mountains and there are extensive forest areas bordering on fells.

It was King Charles XI of Sweden who initiated research in Lapland. Olof Rudbeck made an expedition to Lapland in 1695, and inspired by him, Carl von Linné made his famous expedition there in 1732. The investigations at the initial stage were floristic (Andersson et al. 1985). The limit of the regio subsylvatica on Wahlenberg's map (1812) looks more schematic in Sweden than in Finland. Apparently it was not possible to take into account the effect of the numerous river valleys in Swedish Lapland. Laestadius, who was vicar of Karesuvanto in 1826-1849, was a student of Wahlenberg and published floristic and phytogeographical reports on the timberline regions in Latin. These were later published in Swedish, too (Laestadius 1993).

Nilsson (1897) assessed the 19th century timberline information on the basis of Wahlenberg's zonation, adding his own complementary notes. Of the earlier timberline studies, that of Gavelin (1909) on the lowering of the timberlines is particularly noteworthy. It contains abundant information, organized by river valleys, on the distribution and altitudinal limits of the tree species. This publication contained a good appendix map of the forest zones in Lapland, which also showed the coniferous timberline.

Fries (1913) studied the vegetation of the Torneå region of Lapland and compiled a vegetation map and a map of the altitude of the birch timberline. This research provided a detailed picture of the timberlines in the area between the Lake Torne and Lake Kilpisjärvi. Frödin (1916) studied the timberlines of the Luleå area in Lapland, including measurements of temperature and humidity. Smith (1920) carried out basic research on the timberlines of the fells in Central Sweden, and Hannerz (1923) ascertained the timberlines on the lower fells in Norrbotten. Enquist (1933) criticized the obvious faults in the way in which timberlines were depicted on general maps in the 1930's and published information on the altitudes of the timberlines and a map of the treelines and the distribution of pine in northern Scandinavia. The long-term research of Wistrand (1981) has resulted in a publication concerning the treelines on the lower fells in the Piteå area of Lapland.

On a commission from the Ministry of Agriculture, the Swedish government agency for nature conservation has been developing techniques of environmental management in the fell areas since the 1970's. In this connection the Department of Physical Geography of Stockholm University carried out vegetation mapping in the fell area based on aerial photographs. The 22 map sheets, published on a scale of 1:100 000, show the limits of the birch zone and the coniferous timberline. The project also resulted in four reports for individual provinces (Andersson et al. 1985). The mapping projects carried out in connection with forest surveys in Sweden have not in general extended to the timberlines.

3.6 Fennoscandia as a whole

Apart from maps depicting the phytogeographical zonation, there is no new, uniform, detailed map of the timberlines of Fennoscandia. It is not easy to combine the results of timberline mapping carried out in various countries, due to variations, especially in the description of scattered coniferous stands. The precision of the mapping of mountain birch forests is also highly variable. As far as pine is concerned, Hustich

(1958) combined information from throughout the northern part of Fennoscandia (Figure 22), using mainly the sources mentioned earlier for the individual countries, the most important of which were Juul (1925), Enquist (1933), the map of A. Hiilivirta (Metsähallitus 1941) and Kujala (1929). The information on the Murmansk area stems from the Flora of the Murmansk Area (Gorodkov 1953) and the works of Tsinserling (1932). Hustich had obtained oral reports on the scattered occurrences. He then published the same map in his timberline synthesis (Hustich (1966). This map is still regarded as the best general presentation of the distribution of pine in northern Fennoscandia.

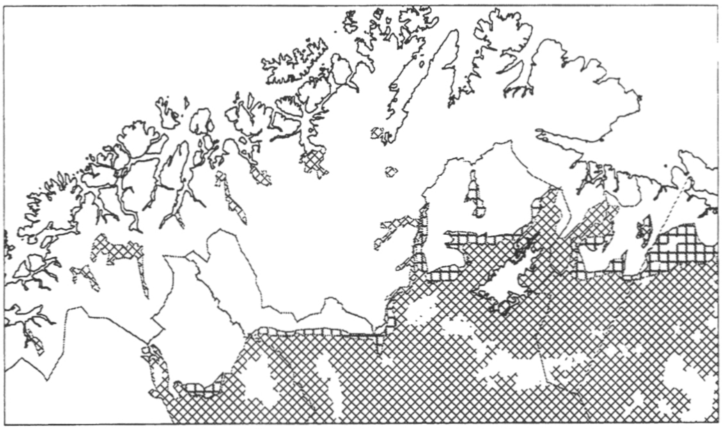

Figure 22. Preliminary map of the distribution of pine in northern Europe based on Hustich (1958). Coarse hatching represents more or less closed pine forests. Fine hatching represents (in general) areas where pine stands have an admixtur of the dominant birch. White pathces in the pine area depict alpine altitudinal belts.

3.7 Conclusions

A surprisingly detailed and correct picture of the position of the timberlines in Fennoscandia was formed as early as the 19th century, thanks to the work of Wahlenberg (1812), Barth (1858) von Berg (1860), Friis (1872) and Kihlman (1890). The fact that the areas were small and fairly easy to reach made it possible to form a good picture of them. The proximity of the Arctic Ocean and the routes leading to it were early causes of traffic, settlement and trading. The distinction relative to the timberlines of Siberia and North America is clear.

The timberline regions of Finland were studied intensively from a scientific viewpoint in the late 19th century, and the majority of the scientific expeditions also made observations on timberlines. The work of Kihlman (1884) in the Inari region of Lapland already gave quite a correct idea of the forest vegetation zones, and Hult (1897) was able to analyze the results of research carried out until then and the factors affecting the timberline. The Finns also made a significant contribution to the study of the Kola Peninsula.

Forest surveys were carried out in timberline areas from 1896 onwards, giving supplementary information on the timberlines and their forest resources. The work of Juul (1925) on timberline forests in northern Norway, based on the forest surveys, was especially important, and a very comprehensive picture of the timberlines in Finland was given by two papers, one published by the Committee for Protected Forests (Komiteanmietintö 1910), and the other, partly based on it, by Olli Heikinheimo (1921).

The map produced by Hustich (1958) indicating the distribution of pine in Northern Europe was a compilation of the information accumulated until then, and it is still the best general treatment of the pine timberline in northern Fennoscandia.

Later work based on aerial photographs and satellite images has provided a still more accurate picture of the timberlines. The vegetation mapping of the Kevo Strict Nature Reserve and the Pallas-Ounas National Park give an exact picture of the timberline ecotone.

The description of a timberline ecotone extending from the closed coniferous forest to the birch timberline is still problematic, since the combinations of birch and pine in variable proportions may be interpreted in different ways. Linear presentation, as is generally used to depict timberlines and treelines, is frequently an oversimplification of the conditions existing in nature. Separate representations of the various biotopes of the timberline ecosystem give a more diversified picture of the transition zone, e.g. Lavrenko and Isachenko (1979) and Hämet-Ahti (1988). It is surprising that a comprehensive mapping of the biotopes of the timberline regions in Finland is still only at the planning stage.

4 Factors affecting the formation of the northern timberline

4.1 General

Through the ages attempts have been made to explain the location of the northern timberline by various causes and the matter has been approached from the viewpoint of many different sciences. In early times the focus was on the general climatic parameters. With development, however, the advanced ecophysiological research has gained in significance, although the attempt to find general 'timberline theories' by which to explain the formation of the timberline is still evident (e.g., Daubenmire 1954, Stevens and Fox 1991).

Today the dominant view seems to be that the timberline is formed as a result of many unfavourable factors, although primarily connected with the temperature conditions of the growing season (Tuhkanen 1993a, b). As early as in the 1930's, Hein (1932) pointed out that many other factors of significance must be considered along with the temperature factor. Holtmeier (1974) emphasized the significance of regional and many-sided analyses, especially at the little-studied subarctic timberline. In his ecological study of the alpine timberline, Tranquillini (1979) distinguished a pioneer stage, started by Däniker in the Swiss Alps in the 1920's. Gradually, beginning in the 1950's, research stations and mobile laboratories came into the picture, not only in the Alps, but also in the USA, Australia and New Zealand. The field of modern phytogeography is also closely involved with the causes of timberlines and the relations between timberlines and vegetation zones (Ahti et al. 1968, Hämet-Ahti 1979a, Tuhkanen 1984, Haapasaari 1988, etc.).

In Russia the study of timberline regions and tundra is often considered a research field of its own, 'tundravedenie', the focus of which has for a long time been on phytogeographical research, however, with scientists representing numerous fields participating in the work. The literature of the field is very extensive and several interdisciplinary conferences have been arranged on matters related to the forest tundra (Tikhomirov and Norin 1967, Semyonov 1984, Kalabin 1993, etc.). Considerations of utilization are also associated with the Russian tradition, i.e., how the 'reasons of the forestlessness of the tundra', when known, can be conquered so that settlement and agriculture in the timberline region can be promoted (e.g., Tikhomirov 1953, 1955, 1962, 1967, Andreyev 1954, Norin 1974, Kryuchkov 1978). Lavrenko and Sochava (1956), in their overview of the phytogeography of Russia, stated that during the Soviet regime the object of phytogeography was to make quick surveys of the vegetation in order to improve the opportunities for its more rational and complete use.

4.2 Natural and anthropogenic timberline

The timberline and the treeline mostly form an ecotone, where the forest gradually turns from closed into open. On the other hand, especially in mountain regions, the timberline may be rather sharp. When studying the causes of the timberlines it is necessary to know which type is more original or whether both types occur also without human action. For a long time, two opposite theories have existed concerning this question (Tranquillini 1979). Ellenberg (1966) was of the opinion that distinguishing human action from natural factors is one of the most difficult tasks of timberline research.

According to one theory the gradual thinning of the stand is due to the deterioration in the environmental factors towards the tree line. The solitary trees get more light and heat, which helps them survive. However, the solitary position causes a gradual increase of injuries towards the tree line, and so the 'Krummholz' zone is formed. Taken as a whole the wide ecotone would represent the original structure of the timberline.

The alternative theory postulates that where a solitary tree can grow, forest can also grow. According to Ellenberg (1966, 1986) this theory is true for nearly all tree lines in the world, if the soil is homogeneous and human activity is not involved. As examples he mentions cases from the Dinaric Alps, Norway and the Andes. The forest climate prevailing on the forest side of the natural timberline forms a sharp limit against the climate of the open area on the other side. For this reason regeneration in the open area is prevented and the ecotone remains narrow. Slatyer and Noble (1992) were also of the opinion that the sharp line is caused by the contrast between the favourable forest climate and the climate of the open area. According to this theory the differentiation of timberline and tree line would always be an indication of human activities. Wardle (1981) arrived at the conclusion that although the sharp limit between different life forms in the vegetation is practically always associated with a steep gradient in environmental factors (e.g., a shore) or a change caused by some disturbance (e.g., a forest fire), the timberline is in this respect an exception, since at the alpine timberline the change from forest to open area is more abrupt than that induced by the environmental factors. Grace (1989) considered that the heat regime of the ground and the related tendency of the ground water to freeze might contribute to the formation of a sharp line, since in this respect the difference is great between nearly open area and closed forest.

Holtmeier (1985) arrived at the conclusion that both theories are possible considering the varied timberlines of the world. In general it seems that the shade tree species form sharp timberlines, whereas the light-demanding tree species frequently form wide transition zones at the timberline (Walter 1968). Armand (1992) studied the timberlines of the Caucasus and the Sajan Mountains and concluded that in the Caucasus a sharp limit is formed by beech, which is a strong 'edificator', controlling the development of the other vegetation. As a contrast, the timberline in the Sajan Mountains, formed by larch, which is a weaker 'edificator', is a gradual transition zone. This example also demonstrates the difference between shade trees and light-demanding trees.

4.3 Climatic factors

4.3.1 Climatic parameters as explanations for the vegetation zones

In phytogeography there is a firmly established conception that the vegetation zone limits are influenced primarily by climatic factors and only secondarily by soil factors. The climate of any area is a complex combination of all effective climatic factors, the most important ones being temperature, precipitation amount, humidity and wind velocity. The properties of the climate may be defined by various parameters, including averages, durations and extreme values.

In the comparison of coincidence between vegetation and climatic factors, various more refined indices are used. Tuhkanen (1980) has made an extensive general study of the use of climatic parameters and indices in phytogeography. He has also studied the coincidence between timberline and climate, concluding that the temperature factor is generally decisive, although other factors beside it may be of considerable significance regionally. The study of the relations between climatic parameters and timberlines is also influenced by differences in history of the timberlines and in tree species, as well as by differences in the effect of various disturbances. General worldwide comparisons of vegetation zones and climates do not give the sufficient basis for regional studies of the coincidence between timberline and climatic parameters, but the question must be studied in more detail on the basis of local information. Kryuchkov (1978) emphasized that utmost care must be taken when data obtained regarding different tree species in different climates are generalized to concern the whole subarctic area. Parameters and indices used in various parts of the world to describe the relations between the timberline and climatic parameters will be examined in the following.

4.3.2 Sun radiation and location of the arctic front

Larsen (1989) has examined the significance of solar radiation as a basic factor regarding both the biosphere and the atmosphere. In the biosphere the radiation is the energy source for the chemical reactions of the photosynthesis of the plants. It is also the driving force of the circulation of the atmosphere and thus the basis for regional climates. The solar radiation reaches the Earth irregularly. The energy transported from warmer zones by air and ocean currents is of great importance to the northern areas. The balance between incoming and reflected radiation represents the net radiation. In the north the balance is negative during most of the year, and so the significance of the energy brought by currents in the atmosphere and in the oceans is emphasized. Toward the north, at some point, i.e. the northern timberline, the radiation becomes the minimum factor for the trees.

Hare and Ritchie (1972) have shown that a distinct correlation exists between the annual net radiation and the location of the timberline. The main reason for the difference in net radiation is the greater albedo of the tundra in spring. Thus the structure of the vegetation affects the climate, which in turn controls the supply of radiation energy, an absolute necessity for the plants. In the timberline ecotone the radiation parameter values clearly change. The annual net radiation is at the northern margin of the forest tundra 15 Kly, at the southern margin 20 Kly, and in the southern part of the boreal coniferous forest 35 Kly. Larsen (1989) stated that later observations made by the Canadian climate programme support the above results.

It seems to be true that the vegetation limits of the northern part of the boreal zone are located according to the annual net radiation values in cases where the postglacial spreading of the trees has reached an equilibrium. The annual net radiation does not depend only on the distribution of the radiation according to latitude but also on such climatic properties as cloudiness, precipitation amount and prevailing winds. These in turn are associated with the movements of air masses and the formation of weather fronts. In North America the arctic front is in summer in its average frontal position, located at the forest tundra ecotone, separating the arctic air masses from the more southern ones (Larsen 1974, 1980, 1989). According to Krebs and Barry (1970) the situation is similar in the Eurasian forest tundra. In areas where the influence of mountains is distinct and the frequency of oceanic air currents is high, the regularity described above is not valid, e.g. in the western parts of North America and Eurasia (Larsen 1980).

Marr (1948) was of the opinion that although the gradient of climatic factors is generally distinguishable in the timberline ecotone, the local timberline is not controlled by this gradient. The intensity of the solar radiation depends on the altitude of the terrain and especially in summer it is considerably stronger in the mountains than it is in low-lying land. The radiation received by plants does not, however, consist of only direct radiation, but is affected by a complex combination of diffuse radiation, albedo and the heat regime of the ground (Ozenda 1988).

Yefimova (1971) has studied the amount and distribution of the radiation active with respect to photosynthesis. The active radiation accounts for approximately 50 % of the total radiation, during the growing season amounting to about 10 Kcal/cm^2 near the timberline and 20 Kcal/m^2 in the southern parts of the northern taiga.

4.3.3 Temperature

In principle, low temperatures affect the vegetation in two ways: indirectly through the length of the growing season and the possible supply of mineral nutrients, and directly by influencing the physiological growth processes (Körner and Larcher 1988). The idea of the crucial effect of temperature on the timberline is based on the fact that the timberline settles at the location where the temperature no longer permits the vital functions of the trees (Daubenmire 1954). Larsen (1989) summarized the three most central physiological processes that are temperature-dependent and are stopped or significantly slowed by low temperatures, i.e. transport of assimilation products, absorption of water, and photosynthesis.

Woodward (1988) has studied, on a general level, the effect of the heat factor on the distribution of plants, arriving at the conclusion that the northern distribution limit for annual plants is controlled by the climatic factors of the growing season, the most important of which is the heat sum. For perennial plants, including trees, the winter climate of the northern limit is equally important. According to Bliss (1981), not only one parameter, such as temperature, should be used in the definition of the vegetation zones associated with the timberline, but the effects of many factors should be examined at the same time. Several parameters have been used to describe the temperature, some of them general temperature parameters and others indices, developed expressly for the study of timberlines.

In the examination of the effects of temperature it should be noted that the temperature of leaves and meristematic tissue is different from that of the air. This difference is mainly caused by radiation, wind velocity, and height and structure of the vegetation. The difference generally increases with altitude (Grace 1989). As early as 1916 the phenomenon attracted the attention of Frödin (1916), who made temperature measurements. Langlet (1935) also considered the temperature difference as an important factor. According to Kryuchkov (1978) the difference between the temperature of the plants and that of the air is significant when the weather is sunny but not when it is cloudy. He presumed that this difference is of great importance in the subarctic area where the day is long during the growing season.

The temperature gradient in relation to the altitude of the terrain is a significant parameter. Bergan (1974) stated that in the Troms area the temperature change per 100 m was 0.6°C in June and July and 0.4°C in September. The annual average air temperature in the Alps decreases linearly with altitude, on an average 0.55°C per 100 m (Ozenda 1988).

The +10°C isotherm of the warmest month of the year. The +10°C isotherm is the oldest and still the best known and most extensively used indicator of the timberline and tree line (Tuhkanen 1993a). Cajander (1933) was of the opinion that this parameter in general describes the crucial significance of the summer temperature but he stated that locally other factors, such as the soil or wind may be decisive. According to Arno (1984) the correlation is true at cold timberlines in various climates of North America and north of the tropics in Eurasia. This parameter is to be considered as general and indicative, suitable for the geographical examination of extensive areas (Holtmeier 1974). On the basis of a study by Mikola (1952) of the correlation between the radial growth of pine and temperature, Grace (1989) concluded that the radial growth of pine requires an average July temperature of +8°C.

Average temperature of June - September. In Norway Helland (1912) stated that the tree lines of various species are controlled by the average temperature of June - September (the tetratherm). The minimum tetratherm for pine and spruce is +8.4°C, for *Betula pubescens* +7.5°C, for *Betula verrucosa* +10.5°C, for *Populus tremula* +7.6°C, and for *Alnus incana* +7.7°C. In the same connection Helland compiled a map of the climatic timberline of pine in Norway. He found the temperature change to be the most probable cause for past changes in the timberline of pine. Hagem (1917) stated that for pine a distinction should be made between the growth limit presented by Helland and the maturation limit of the seed, which is +10.5°C. In Norway the limits of Helland are still considered correct (Mork 1968, Børset 1988). Slettjord (1993) presented the tetratherms of numerous tree and shrub species, stating that the tetratherm, used with modification, is a reliable parameter of potential growth for most of the plant species at the timberline in cold climates.

Correlation between daily mean temperature of growing season, soil temperature and phenological development stages of trees. Kryuchkov (1967, 1975, 1978, 1987) has in the subareas of the Eurasian forest tundra made extensive studies of the correlations between air temperature, temperature of various parts of trees and shrubs, soil temperature and the phenological development stages of the plants. In the Kola Peninsula he concluded that the normal growing season development of birch, spruce, rowan and alder is possible if the daily mean temperature is +8-9°C. At the same time the day temperature has to be over +11°C for 3-5 hours, and these temperature conditions must prevail for at least 28-35 days. In addition the soil temperature prevailing in the root layer is of great importance, the minimum requirement of timberline trees being +5°C at a depth of 15-20 cm and below that +2-3°C.

Kryuchkov concluded that the present timberline is in many areas located farther south than the temperature requirements would allow. Walter (1979) has suggested approximately the same minimum temperature requirement for the existence of trees at the northern tree line: a period of at least 30 days, during which the daily mean temperature is above +10°C. In Kola the minimum requirements of this temperature are met as far as to the coast of the Arctic Ocean. Wardle (1993) stated that the photosynthesis begins to decrease if the soil temperature sinks below +5°C, probably due to decreased water absorption and closing of the stomata. Bonan (1992) considered the soil temperature to be the crucial factor influencing the tree growth in the permafrost area of the interior of Alaska. He described the temperature of the soil at a depth of 10 cm as the temperature sum of d.d. units over 0°C.

Length of growing season. When a threshold value of +5°C for the daily mean temperature is used, the timberline is approximately where the length of the growing season is 105 - 110 days. This is true both for the northern timberline and the Alps although the radiation conditions and thereby the effects on the physiological processes are different (Holtmeier 1974). According to Ellenberg (1986) the timberline of the outer Alps in a marine climate is located at an altitude of 1800 m and in the continental inner Alps at an altitude of 2200 m. In both cases the length of the growing season (threshold value +5°C) was 100 days.

Puzachenko (1985) suggested that with a threshold value of +5°C a growing season of less than 60 days does not permit the presence of trees. Forest, forest tundra and tundra may be present when the length of the growing season is 80-110 days and the presence or absence of forest is explained by factors other than the length of the growing season. Tundra is no longer present in areas with a growing season longer than

110 days. Blüthgen (1942) emphasized the importance of the early part of the growing season at the northern timberline, since its weather conditions determine how well the plants will benefit from the long light period.

Duration of maximum temperature of growing season and length of winter. Enqvist (1933), a Swedish researcher, arrived at the conclusion that the limits of the tree species are determined by the duration of the maximum temperature of the growing season and by the length of the winter. He suggested that pine during the growing season requires at least 26 days with a maximum temperature above +17°C and that in maritime areas at least 90 cold days are required. During its growing season, spruce requires 65 days with a maximum temperature of more than +12.5°C and in winter 120 frost days. In summer again the daily maximum temperature may not rise above +24°C during more than 65 days. Birch requires 26 days during the growing season with a maximum temperature of at least +14°C. This definition has not been used very widely although it has often been emphasized that maximum temperatures are better parameters than mean temperatures. Langlet (1935) considered the frequencies of the minimum and maximum temperatures as poor parameters.

Growth unit. Mork (1968, 1970) has studied questions related to the timberline in the research area of Hirkjölen in southern Norway during the years 1932-1966. From his study of the height growth of spruce Mork concluded that the effect of the heat is best described by the concept of growth unit (vekstenhet), i.e. the effect of heat on the growth during the six warmest hours of the day when the mean temperature is at least +8°C. As approximate value it is possible to use, instead of the mean temperature, the temperature prevailing at one o'clock p.m. As the temperature rises the number of growth units increases curvilinearly so that, e.g. at a temperature of +20°C the number is four. According to Mork the tree line of birch at Hirkjölen is at a point where the length of the growing season is 109 days, its mean temperature +9.1°C and the number of growth units 222. At the tree line of spruce the length of the growing season is 112 days, its mean temperature +9.5°C and the number of growth units 242. Bergan (1974) obtained about the same number of growth units at the timberline of birch in Troms as did Mork in southern Norway. Bergan (1985) considered the growth unit to be the best temperature parameter in view of afforestation in the timberline region. Besides in Norway, the growth unit is to some degree used in Sweden, too (Odin et al. 1983). Later on another parameter was developed in Norway on the basis of this one, the respiration equivalent (Tuhkanen 1980).

Temperature sum. In Finland in the 1960's the genetic adaptation of pine to the northern climate was studied by Sarvas (1970a). In this connection he used the temperature sum as the parameter of the temperature so that the threshold value of the daily mean temperature was +5°C. Sarvas concluded that the adaptation of pine to the climate, at least regarding the anthesis, ends in a region where the temperature sum is about 950 d.d. Sarvas stated that the genetic adaptation does not control the timberline, which settles at the point where the carbon balance remains negative. Sarvas himself mentioned that the temperature sum is hardly suitable for describing the climate of the tree line, since assimilation and growth relate in a different way to temperature than they do to what is called the annual period.

The findings of Luomajoki (1993) support the opinion of Sarvas on the adaptation of pine although the effective temperature sum turned out to be a poorer parameter than what is named *the period unit temperature sum* and calculated on the basis of temperatures measured hour by hour. In Finland the view has later become established that the coniferous timberline is controlled by the amount of heat energy of the growing season at the 'starvation boundary' of the trees, which expressed in the form of temperature sum is about 600 d.d. and at the tree line about 550 d.d. (Norokorpi 1982, 1994). Norokorpi stressed that this correlation is not true in the area of crown snow load. Eurola and Huttunen (1984) mentioned that the climatic timberline in Finland is generally at the level of 400-500 d.d., but on the solitary fells south of latitude 68 lower due to the summit effect, which is caused by snow, wind and the properties of the ground.

In Finland the correlation between temperature sum and timberline has apparently been considered more distinct than intended by Sarvas. Elsewhere the temperature sum has not been used to explain the timberline nearly as frequently as in Finland. Tuhkanen (1984) stated that although the use of the temperature sum in phytogeography is accepted, it is also criticized, since the threshold values for the plant species and for various physiological processes are varied. Further it is assumed that each temperature sum unit would have the same physiological effect although the correlation between the temperature and the physiological processes of the plants is not linear (cf. Mork 1970). Kauppi and Posch (1985) were of the opinion that although the temperature sum is a simple parameter for describing the the regional variation in the productivity of the boreal ecosystem, it does, however, take into account the two main factors, the length of the growing season and the daily activity level of the ecosystem.

The comparison of temperature sums determined in different countries is complicated by the use of various threshold values, e.g. in Sweden the value +6°C was earlier in general use (Odin et al. 1983). In connection with recent Swedish studies of afforestation at high altitudes, Persson (1994) found the temperature sum to be a useful parameter of the productivity of the forest, emphasizing at the same time, however, the necessity of taking other factors into account.

In Russia again it is common to add the daily mean temperatures exceeding +10°C. In the general comparison of the climates and vegetation zones of Russia, Grigor′yev and Budyko (1960) stated that using the above criterion, the temperature sum of the tundra and the forest tundra is less than 1000°C and that of the taiga 1000-2200°C. Puzachenko (1985) stated that when the above definition of the temperature sum is used, forest occurs commonly from a level as low as 700°C. Woodward (1987) has studied the temperature sum necessary for the development of leaves and needles, concluding that with a threshold value of 0°C, tundra covers the area with a temperature sum of less than 600 d.d. In the area 600-950 d.d., larch forest occurs, and in the area above 950 d.d., evergreen conifers can grow. According to Malyshev (1993), the temperature sum values of the arctic timberline of Russia are varied (Table 1) and he considered the length of the growing season the best climatic parameter of the arctic timberline.

In Alaska Hopkins (1959) has studied the relation between temperature parameters and the timberline. He concluded that the most distinct correlation of the timberline is with the temperature sum of the growing season when a threshold value of +50°F (+10°C) is used. On the other hand the mean temperature of the coldest month of the winter also correlated clearly with the timberline. As a characteristic feature of the very oceanic area, the temperature sum of some of the stations on the tundra was higher than that of the forested areas. The +10°C isotherm of the warmest month of the year is in southeastern Alaska 250 miles north of the timberline (Griggs 1937).

Davitaya and Mel′nik (1962) have made an interesting comparison between the temperature sums of the arctic and the alpine timberline. The arctic study included 14 stations, located along the circumpolar timberline. The sums of effective temperature, calculated as the sum of daily mean temperatures above +10°C, were 600-700°C. The stations closest to Finland were Röros (600°C), Karesuando (600°C), and Murmansk (700°C). At the alpine timberline again, the corresponding temperature sums for 14 locations at altitudes of 2300-3000 m in the Caucasus and the Rocky Mountains were 200-300°C. The only possible explanation is the more intensive solar radiation at the alpine timberline. When the researchers measured the temperature of the air and that of the leaves separately, the temperature of the leaves in the Caucasus was 3.7°C higher than that of the air, and correspondingly in Murmansk

1.5°C higher. On the basis of this, the temperature sum as measured at the surface of the leaves was 800°C in the Caucasus and 880°C in Murmansk. Thus, as regards the plants, approximately the same temperature sum is prevailing at both timberlines.

It is clear from the climatic data on the arctic tree line presented by Elliott-Fisk (1983) that the temperature sum using 5.6°C as the threshold value is different at the tree line in various parts of the continent: in the west Doll Creek, Yukon Territory, 600 d.d., in the central part Ennadai Lake, 1000 d.d., and in the east Napaktok Bay, Labrador, 550 d.d. The annual net radiation is, however, nearly the same at all the above sites (18-20 Kly/a). Bonan and Sirois (1992) arrived at the result that nor the temperature sum nor the temperature of the growing season in general controls the northern limit of the distribution of *Picea mariana.* Obrebska-Starklova (1993) presented climatic parameters from the alpine timberline in the Tatra Mountains. Using a threshold value of +5°C the average temperature sum at the timberline was 600 d.d., ranging, however, from 375 to 750 d.d.

Ebeling (1979) has reported the coincidence between temperature sum and altitude of the terrain in various latitudes in northern Sweden, stating that the continental or oceanic character of the area also has its effect. E.g., the temperature sum level of 590 d.d. (with a threshold value of 6°C) generally prevails at an altitude of 440 m a.s.l. in latitude 65 in Norrbotten, but at 500 m a.s.l. in the locally continental area of the inland and at 350 m a.s.l. in the locally oceanic area of the Scandes.

Laaksonen (1977) has made a clear description of the variation between continentality and oceanity in northern Fennoscandia during the growing season. The oceanity is pronounced in the eastern part while the most continental conditions prevail in the west, around the Tornio river valley. Laaksonen (1979) also found the cold air currents from the Arctic Ocean and the White Sea to have a decreasing effect on the temperature sum in eastern Finland. In the most recent numerical climatic model (Ritari and Nivala 1993) the effect of lakes and oceanity has been taken into account in the calculation of the temperature sum.

Nikolov and Helmisaari (1992) have studied the most central parameters of the main circumpolar tree species for simulation models of the boreal forests. One of the parameters presented is the annual minimum effective temperature sum for each tree species, which represents the temperature conditions at the northern limit of occurrence of the species. For the temperature sum a threshold value of +5°C was used and the calculation was carried out on the basis of monthly average values (Table 3).

Table 3. Temperature sum minima and mean temperatures of coldest month at northern limit of distribution area for main tree species growing at the arctic timberline and in its vicinity (Nikolov and Helmisaari 1992).

Tree species	Minimum temperature sum,>5°C, d.d.	Mean temperature °C of coldest month
Abies sibirica	510	-35
Betula pendula	410	-40
Betula pubescens	340	-40
Chosenia arbutifolia	240	-45
Larix gmelini	250	-45
Larix sibirica	300	-33
Larix sukaczewii	390	-22
Picea abies	470	-17
Picea obovata	320	-40
Pinus pumila	240	-45
Pinus sibirica	490	-35
Pinus sylvestris	450	-40
Populus tremula	400	-40
Abies balsamea	560	-25
Betula papyrifera	500	-28
Larix laricina	280	-29
Picea glauca	280	-30
Picea mariana	247	-30
Populus balsamifera	440	-30
Populus tremuloides	500	-30

For explaining the regeneration results of northern pine stands, Haila and Levins (1992) considered the temperature sum a 'sufficient parameter', which reduces the original group of parameters, representing several environmental factors separately, into one, more easily measured. This interpretation fits well with the fact that the temperature sum is generally used to describe many phenomena of the northern ecosystems. The temperature sum describes the timberline of pine by explaining the generative regeneration, but it may not be used to describe the timberline in general, since the temperature sum values for different tree species and in different climates are different, as shown in Tables 1 and 3. In the examination of vast areas it should be noted that the effect of the differences in threshold value used for calculation of the temperature sum is the greater, the greater the variation in continentality. In addition, the differences in temperature distribution during the growing season required by the continental and oceanic plant species are of importance (Tuhkanen 1980).

Frost. The frost resistance of trees varies greatly with the seasons. Trees normally hardened for the winter can tolerate low temperatures. The hardiest tree species of the European Alps is *Pinus cembra.* Also *Picea abies* and *Pinus mugo* tolerate temperatures of -36 ... -38°C. In the Rocky Mountains and in Japan some tree species have been found to tolerate cold temperatures down to -70°C. During the summer, however, the same tree species are damaged by a frost of only a few degrees. According to Tranquillini (1979) the frost does not endanger the presence of trees in the timberline ecotone but it is the factor inducing the 'Krummholz' forms. According to Stushnoff et al. (1983) the 'black heart' damage, visible in certain deciduous trees in the form of darkening of xylem damaged by the frost, is a factor contributing to the formation of the arctic tree line of the species concerned. On the basis of an extensive provenance experiment in Sweden, Eiche (1966) has concluded that during the period 1953-1964 frost injuries occurred especially in the ten year old planted stands of pine in the high-altitude regions of the inland. The injuries consisted in strangulation of the base.

Sakai and Eiga (1983) found that the hardiest conifers in the genera *Pinus, Larix, Picea* and *Abies* tolerate cold temperatures down to -60°C. In conifers the most critical factor is the frost tolerance of the shoot and flower buds. In the coldest areas of Alaska and Siberia the conifers except the genus *Pinus* have a survival mechanism of extraorgan freezing. A long history of phylogeny forms the background for the adaptation to the cold of the hardiest conifers. According to Ohsawa (1990), latitude 20°N in the mountains of southern and eastern Asia is the limit north of which the timberline, mainly controlled by the temperature of the growing season, is formed by conifers or deciduous trees, while the timberline south of this limit is formed by evergreen trees, which are less resistent to the cold, since here the temperature of the coldest month does not drop below -1°C. Thus the minimum temperature of the year also has its effect on the tree species of the timberlines.

Potential evapotranspiration. Larsen (1980) was of the opinion that of the climatic parameters correlating with the limits of the northern vegetation zones, the significance of the potential evapotranspiration is comparable with the annual mean temperature and the length of the growing season. In the example presented by Larsen, the PE values in Labrador-Ungava rise from the about 310 mm of the tundra to the about 360 mm of the forest tundra and further to the 420-480 mm of the boreal coniferous forest. In his circumpolar zone division, Tuhkanen (1984) used the potential evaporation presented by Thorntwaite as one of the parameters. The advantage of this parameter is that it reflects directly the short, warm summer of the continental parts and the long, cool growing season of the oceanic areas.

4.3.4 Other climatic factors

Precipitation. In cold timberline regions the precipitation is hardly ever the minimum factor. Treter (1984) has examined the timberlines of Scandinavia and found that in oceanic areas, excess water is rather an adverse factor. On the other hand, in the most continental parts of the inland, drought may for short periods be the minimum factor, which is reflected in the radial growth of timberline pines. Tranquillini (1979) was of the opinion that at alpine timberlines drought only rarely forms a growth-limiting factor. Frödin (1916) found that in the Scandes, in the same latitude, the timberline of birch rises higher in the high fells due to the moisture of the soil than it does in the low fells, where the drought of the soil in summer is the minimum factor. In Khibiny, Kryuchkov (1957) arrived at the result that the drought of the soil is the crucial factor for the tree line of spruce. He considered the formation of altitudinal belts in the vegetation as a hydrothermal phenomenon, and not only as controlled by the temperature. In Yakutia Zukert et al. (1995) considered the precipitation important for explaining the latitudinal timberline of *Larix gmelini* whereas the altitudinal timberline was more clearly affected by the hydrothermal regime.

Physiological drought. Especially in Russia, physiological drought has been considered an important reason for the absence of forest in the tundra. Kihlman (1890) based this theory on his studies on the Kola Peninsula, showing that under cold conditions especially the cold meltwaters are not available to the plants, which would cause the physiological drought. Grace (1989) pointed out the high viscosity of cold water and its effect on water uptake. Tikhomirov (1953) and Andreyev (1954) mentioned this theory in addition to other reasons, emphasizing, however, that practically no experimental studies have been carried out on the subject of physiological drought. Tikhomirov (1962) stated that Kihlman was the one who clearly brought the view of plant physiology into the discussion of the reasons of the timberline. Norin (1974) related the results of experiments, in which the water regime of plants in various parts of the forest tundra ecotone were studied with the result that in the timberline region, no general change occurred in the water regime of the plants. Instead, the differences were between species and species groups. The theory of physiological drought is closely related to the problem of frost drought.

Humidity. Humidity and aridity is a pair of terms lacking generally accepted definitions and so they may denote relative or absolute humidity of the air, precipitation, or the combined effect of either precipitation and temperature or precipitation and evaporation. For these, various indices have been developed (Tuhkanen 1980). In Russia, the isoline of Kaminski, which represents the relative air humidity, was earlier used as a general parameter in the same way as the +10°C isotherm of July. This isoline is the limit, north of which the daytime air humidity is at least 70 % (Tikhomirov 1967).

Puzachenko (1985) has again brought up the significance of the relative air humidity, noting that the influence of this global factor is frequently ignored. Besides the heat factor, Malysev (1993) considered humidity, which varies according to longitude, as a significant factor influencing the timberlines. The alpine timberlines are in the continental areas of Siberia and Central Asia located higher than in the more temperate and oceanic areas of Europe and the Far East. Tuhkanen (1980) mentioned the humidity factor of Linsser and the aridity index of de Martonne among the indices describing the relation between precipitation and temperature.

Puzachenko (1985) arrived at the view that the hydrothermal coefficient (GTK) of Selyanikova, which represents the relation between precipitation and temperature, is of significance as a parameter explaining the location of the timberline. The hydrothermal coefficient is obtained by dividing the precipitation (mm x 10) of a period by the sum of the daily mean temperatures exceeding 10°C of the same period. With a GTK value below 5, the occurrence of forest is probable and with a value over 7, the occurrence of tundra. The picture of GTK values possible for forest is filled out by the result of Zukert et al. (1995), showing that at both the latitudinal and altitudinal timberline of *Larix gmelini* in Yakutia, the GTK value is 1. This result reflects the condition of a very continental area, where the temperature is the general factor for explaining the timberline.

Continentality - oceanity. Tuhkanen (1980) made a thorough alysis of the concept of continentality, finding it to be a complex combination of many factors, difficult to represent by one single index. It is a broader concept than humidity/aridity, including both the thermal and the hygric component, while humidity/aridity includes only the hygric component. The relative continentality index of Conrad, in which Torshavn gets the value 0 and Verhojansk the value 100, describes the annual temperature variation, included in the thermal component. Attempt have been made to describe the hygric component, e.g. by the ratio of summer precipitation and annual precipitation. As early as 1919, Brockmann-Jerosch presented the clearly grounded view that the timberline reaches farther north in continental than in oceanic areas. Dahl (1983) also considered the effect of continentality on the altitude of the timberline as a universal phenomenon, independent of tree species.

Dolukhanov (1978) found it a generally accepted view that in the same geographical area the altitudinal location of the timberline is the higher, the more continental the climate. At the same time, however, he presented the view, based on the situation in the Caucasus, where abundant tree species grow, that different species relate in a different way to continentality. The timberline of species belonging to the humid flora element, such as *Betula medwedegii* and *Quercus pontica*, is located at higher altitudes, the lesser the continentality of the climate. Some of the tree species again do not at all react to continentality, such as *Abies nordmanniana* and *Picea orientalis*, whereas certain species originating in the zonal taiga, e.g. *Pinus sosnowskii* and *Betula litwinowii*, react positively to increasing continentality.

The timberline of fell birch in the slightly oceanic 'Arm of Lapland' in northern Finland is at an altitude of 550-700 m (Mikkola and Sepponen 1986), but in the Muotkatunturi fells in the subcontinental sector of the inland at an altitude of 400-430 m in approximately the same latitude 69 (Kallio et al. 1978). The altitude of the pine timberline again correlates positively with an increase in continentality due to the increase in temperature sum (cf. Ebeling 1972).

The phenomenon of 'Massenerhebung', traditionally discussed in Central Europe, is related to the same whole as is the continentality. Originally it was in a way used to describe the average altitude of the mountain area, and it was observed to be connected with a rise in timberlines (Brockmann-Jerosch 1919). Mainly in the Alps this phenomenon has later been understood, on the whole, as the fact that in the same latitude, the timberline is located higher in the interior parts of the mountains than in the marginal parts. The same phenomenon is true in other major mountains as well, such as the Himalayas and the Rocky Mountains (Arno 1984), and also in the Scandes (Blüthgen 1960). Kalliola (1939) considered the 'Massenerhebung' phenomenon the reason for the location of the birch timberline distinctly higher in the fells of the Arm of Lapland than farther south. The reason suggested for this phenomenon is the warming of the central parts of a great mass of land compared with the margins. Mayer and Ott (1991) presented results showing that the daytime temperature in the Central Alps is 1-2°C higher than at the same altitude in the Outer Alps. The reason was found to be the 'Heizflächeneffekt', which is related to 'Massenerhebung'. As a whole, however, the phenomenon concerned is probably the influence of the warmer summers of a more continental climate (Holtmeier 1974, Wardle 1974, Arno 1984).

In northern Norway the effect of the increasing oceanity is clearly visible, since the altitudinal location of the timberlines is lower towards the coast than it is in the more continental parts of the inland. On the coast, however, the strong anthropogenic effect makes the examination difficult (Holtmeier 1974). Elven and Vorren (1980) observed that the altitude of the pine timberline in the area of central Troms sank from 400 m in the inland to about 150 m at a distance of 100 km towards the coast. In Sweden, attention has been paid to the local lowering of the timberline caused by oceanic climate (Ebeling 1972, Kullman and Hofgaard 1987). The reason is the relatively lower growing period temperature of the oceanic areas. In Sweden this factor has also been noted in the practical forestry instructions (Ebeling 1979). In Finland Laaksonen (1977) has clearly brought up the decreasing effect of the Arctic Ocean on the temperatures of the growing season in northern and eastern Lapland. According to Haapasaari (1988), the growing season in the interior of Fennoscandia is shorter than that on the coast and that the timberline is controlled more by the maximum temperatures of the growing season than by its length. The upper parts of the southernmost fells in Finland are more oceanic than the lower areas. This contrast is visible, besides in differences of vegetation, also in the occurrence of crown snow load (Hämet-Ahti 1979b).

Snow. The snow cover is one of the most important bioclimatic factors affecting the timberline ecotone (Holtmeier 1974). The snow protects, but on the other hand it may shorten the growing season and keep the site cold for a long time. Ellenberg (1986) found that the snow becomes a crucial factor to the plants when the forest becomes so open that the wind can affect the snow cover without obstacles. The accumulation of a snow cover according to the terrain and the climatic factors may have a decided effect especially on the formation of the timberline. Holtmeier is of the opinion that the combined effect of landforms, wind, radiation and snow cover and its melting clearly requires more research. Holtmeier (1974) and Treter (1984) have studied the significance of the snow cover in various terrains. Arno (1984) also mentioned the beneficial and adverse effects of the snow, showing that the snow situation, on an average, is in balance at the northern timberline, whereas at the alpine timberline it often becomes crucial. The main point is whether there is enough snow but not too much of it. An excessive amount of snow may prevent forest growth in an area where it would be possible otherwise, considering the air temperature. Years with less snow than normal may make episodic regeneration at the timberline possible. Kullman (1979, 1981, 1983) has thoroughly studied the significance of the snow in the timberline dynamics of the Scandes. Holtmeier and Broll (1992) have examined the important effect produced by the differences in snow distribution, caused by microtopography and forest islands, on the long-term development of the timberline vegetation and soil.

In mountain regions with abundant snow, avalanches have a certain effect on the timberline which can also be observed in Fennoscandia, e.g. in the Norwegian fells and in the vicinity of Kilpisjärvi (Holmgren 1912, etc.). The most recent example of the effect of avalanches in Finland is from the spring of 1995, on the Ailigas fell in Nuvvus, Utsjoki. Crystals of snow and ice, carried by the wind, also influence the the trees at the timberline. The snow cover also affects the occurrence of fungi, and Ellenberg (1986) presented the hypothesis that the vulnerability of conifers to fungus attacks in an oceanic climate with abundant snow might be the cause of timberline forests being formed by deciduous trees.

The phenomenon named crown snow load is formed by snow, ice and hoar frost. In Finland, it is considered a factor of crucial effect on the timberline south of the Saariselkä fells (Heikinheimo 1920, Norokorpi and Kärkkäinen 1985, Norokorpi 1994). A corresponding phenomenon, 'snow ghost' trees, occurs in the oceanic mountains of North America (Arno 1984). In humid mountains, Malyshev (1977) considered abundant precipitation and thick snow cover as factors lowering the timberline. In Japan, observations show that in the regions with the most abundant snow, the stand of the subalpine zone is formed by brush-formed deciduous trees instead of by conifers (Sakai and Larcher 1987).

Wind. In earlier studies the wind was assigned an important role in controlling the timberline. As early as 1864 von Middendorf emphasized the significance of cold, humid winds in the control of the timberlines on the coasts of cold seas. Kihlman (1890) stressed the importance of the wind, including besides its mechanical influence on the shapes of the trees, also its effect on transpiration and frost drought. Referring to the treeless areas of the North Sea coast, he was of the opinion that the temperature had been too much emphasized. Renvall (1919) also considered the wind as influencing the drying of timberline stands. According to Kryuchkov (1978) the contribution of the wind to the frost drought is the most important factor controlling the growth of trees in what is called the zone of relative forestlessness. Daubenmire (1954) mentioned that in the northern hemisphere, ecologists have for a long time considered the influence of the wind as crucial for the formation of alpine timberlines. He based his argument on the following observations: asymmetric shape of the trees related to the prevailing wind direction; dense crown along the ground surface - a favourable form considering the frost drought; the last trees are frequently located in wind-sheltered places; the timberline is located much higher on the wind-sheltered side; at sites open to the wind the timberline is located lower than normal. He further found that as the temperature falls towards higher altitudes at the same time as the velocity of the wind increases, a critical combined effect will be formed at some level, turning the forest into tundra.

Grace (1977) has discussed the influence of the wind in the formation of timberlines in the mountains, concluding, however, that the temperature factor is decisive. In the Alps it has been studied whether the 'Krummholz' forms are actually caused by the abrasion of windblown ice particles, as earlier was supposed. According to Tranquillini (1979), the effect of the wind is mainly indirect, since by removing the snow, the wind promotes frost drought. Arno (1984) considered the wind to have a direct effect by causing mechanical damage and an indirect effect via frost drought. In the mountains there are windblown summits and passes, where the timberline has been clearly lowered due to the wind. In his opinion the effect of the wind is small at the northern timberlines compared with the alpine ones. Perttu (1972) showed that in the fells of Norrbotten, the velocity of the wind in the open fell region is sometimes double that in the forest. According to him the wind, which is probably one of the most important limiting factors in the fell region, has an indirect effect, e.g. by lowering the maximum temperatures, and a direct mechanical effect.

Robertson (1993) made a comprehensive study of the effects of the wind on boreal forests, showing the effect on the timberlines of changing wind relations connected with climatic changes. The direct effect of the wind can be seen as 'Krummholz' forms, of which he mentioned as an extreme example a vegetation at the timberline of eastern Canada consisting of about 15 cm high, dense, carpet-like *Picea mariana* forma *semiprostrata* (Peck.). Robertson also emphasized the physiological effects of the wind. The mechanical shaking by the wind decreases the growth of the roots. The cooling effect of the wind decreases photosynthesis and slows the development of the needles, increasing the risk of frost drought. In addition the wind-blown ice crystals abrade the cuticula. According to Grace (1989) high winds break young shoots, which is one of the most important causes of the formation of the crown forms typical of windy areas.

The importance of the wind as a modifyer of the forest ecosystem is pronounced in humid areas, where the frequency of forest fires is low (Canham 1984). In Finland Sirén (1994) has emphasized the importance of storm damages in the development of timberline forests. Opinions differ as to the significance of the wind in the formation of oceanic timberlines. Grace (1977) represented the opinion that the effect of the salts transported by the wind is more important than that of the wind itself. On cold costs the decreasing effect of the wind on the temperature and length of the growing season is pronounced. In his comparison of the oceanic timberlines of Europe and Alaska, Faegri (1968) also arrived at the conclusion that in natural conditions the effect of the wind and the salts transported by it forms the central factor in the formation of oceanic timberlines.

Solar radiation. Mountainous regions are characterized by a high radiation intensity, which is further increased in late winter by the reflection of the snow cover, up to twice that of lower altitudes. At the same altitude the proportion of ultraviolet wavelengths is high, and it has been suspected that excess radiation might be an adverse factor to the trees. On the sunny side of the crowns the colour of the needles may change, especially at the timberline, due to the photochemical altering effect of the radiation on the chlorophyll molecules. In spring the chlorophyll deficiency is compensated and generally no actual damage is caused (Tranquillini 1979). Daubenmire (1954) also mentioned excess light as a possible timberline theory.

Combined effect of climatic factors. As early as 1864 Middendorf discussed the combined effect of several climatic factors on the timberline. Brockmann-Jerosch (1919) arrived at the conclusion that neither the alpine timberline nor other vegetation zone limits can be explained by the mean temperature isotherms, since the 'Klimacharakter', i.e. the combined effect of the climatic factors is crucial. Tuhkanen (1980) has thoroughly examined the significance of the various factors, clearly bringing up the primary role of the temperature but also emphasizing the importance of taking the other climatic factors into account.

Puzachenko (1985) studied the importance of several climatic factors and their combined effect for the explanation of the northern vegetation zones. The material consisted of about 800 sites from northern Russia. The parameters to be examined were the temperature sum of days with a daily mean temperature of over 10°C, the length of the growing season (threshold value +5°C), mean temperature of January, precipitation of the growing season, thickness of the snow cover, relative air humidity at 1 o'clock p.m. in July, and the hydrothermal coefficient of Seljanikova. He mentioned that additional data on wind velocity and ground temperature would have been required, but sufficient observation data were not available.

By these parameters he attempted to explain the presence of various vegetation forms: tundra, mire, forest tundra or forest. The results show that the greatest explanatory value is possessed by the temperature sum, length of growing season, hydrothermal coefficient and relative humidity. A growing season shorter than 60 days does not give the opportunity for trees to grow and in areas with a longer growing season than this, the lack of trees is caused by factors other than the temperature. All the vegetation types studied were possible where the length of the growing season was 80-110 days and forest tundra occurred only in this area. The correlation with the temperature sum was similar to that with the length of the growing season. The correlation between hydrothermal coefficient and vegetation type was clear. The adverse effect on the trees by the high relative humidity of cold oceanic areas was also pronounced, which is evident e.g. on the coasts of the White Sea. Puzachenko stressed that in different areas the effect of climatic factors and their combinations is different. There may also be differences in the reactions of various tree species (Dolukhanov 1978).

Puzachenko (1985) divided the timberline of Eurasia into three sectors. In the oceanic sector of Europe-West Siberia the change of forest tundra into tundra is best explained by the increase in the hydrothermal coefficient northward and by the increase in relative humidity. In Kola these factors are also the most important ones for explaining the change of forest tundra into tundra. In the western sector the temperature would be sufficient for the growth of trees north of the present tree line. A nearly identical situation is prevailing on the opposite side of the continent, in the Bering oceanic sector. In the Central East Siberian sector the situation is different, as the location of the timberline is here controlled mainly by the temperature. Under these conditions the forest continues northward as far as the temperature factor permits, to the limit of 'absolute forestlessness' (cf. Kryuchkov 1978). Within these vast sectors the regional factors cause many kinds of variations. Puzachenko mentioned that floristic as well as dendrochronological studies support his findings.

4.4 Geological factors

Rock and soil. Relatively little attention has been paid to the properties of the rock and the soils at the timberline, as they have been considered secondary compared with the climatic factors. The soil factors have a clear effect on the alpine timberlines, since frequently the question is whether the amount of soil is sufficient for the trees to attach their roots. At the northern timberlines of Fennoscandia the sufficiency of loose soil is also a crucial factor (Kryuchkov 1978). In alpine terrains, the timberline location caused by rockiness and boulders should be distinguished from that caused by the climate. According to Holtmeier (1974), the timberline on many of the Finnish fells, e.g. Pallas and many of the fells in the Tana river valley, the timberline is clearly lowered due to rockiness and boulders.

The underlying rock types naturally influence the properties of the soil, such as its nutrient content. In this respect there are great contrasts, e.g. in Scandinavia between the timberlines of the Precambrian bedrock area and those of the Scandes. Generally the rock type and the resulting fertility of the soil are not minimum factors, although they do have a distinct influence on the flora.

Mäkitalo et al. (1994) arrived at the conclusion that in Finland the northern timberline of spruce is not explained by the temperature sum, but is controlled by soil factors. Bystrov (1939) was of the opinion that the forestlessness of the valley floors in Khibiny is caused not so much by the temperature or wind conditions as by the unfavourable nutrient and water regime of the soil, due to the scarcity of fine material in the young soil cover. Marr (1948) considered the scarcity of loose soil in Labrador as the main local reason for the formation of the northern timberline. In the Bol′shezemel′skoi tundra in Western Siberia, P′yavtsenko (1955) studied the significance of the soil, concluding that the layer of organic material in the soil is of crucial significance to the trees due to its influence on the water, nutrient and heat regime of the active soil layer. The layer of dwarf shrubs, especially that of dwarf birch, is of great importance as it forms tundra raw humus, and in addition the dwarf shrubs protect the tree seedlings. P′yavtsenko also came to the conclusion that in afforestation of the tundra, sowing should be used, in order for the root system to settle naturally in the active surface layer of the very thin soil.

At dry timberlines the water regime of the soil is of great importance, although the soil moisture is rarely the foremost limiting factor at the cold timberlines, where the humidity is sufficient (Arno 1984). The northern soils have been fairly thoroughly studied in North America and Russia. There is a difference in views as to how the podzols change towards the tundra and whether the forest-tundra ecotone has a soil profile entirely of its own. The properties and classifications of the soils of the tundra and timberline are examined by, e.g. Everett et al. (1981). In the podsol area the soil is modified by chemical processes, whereas the arctic soil of the tundra is mainly affected by mechanical phenomena such as mechanical weathering, erosion and the effects of wind and frost (Larsen 1989).

The influence of freezing phenomena such as patterned ground and solifluction increases in the vicinity of the timberline even south of the permafrost area. According to Troll (1973b), the lower limit of solifluction in a humid, cool climate is approximately at the alpine timberline. In the Canadian classification of soil types, the soils occurring from the northern part of the boreal zone northward form a main group of their own, named 'cryosols' (Pettapiece 1984).

Sveinbjörnsson (1992) emphasized the significance of the temperature of the ground, including its influence on the supply of nutrients. In an experiment carried out in the Swedish fells, the trees reacted more distinctly on fertilization near the timberline than at lower altitudes, which possibly indicates a problem regarding nutrient supply at the timberline. According to Sveinbjörnsson et al. (1993) the nitrogen deficiency is a notable factor in timberline afforestation. Skre (1993) was also of the opinion that the amount of nitrogen and phosphorus available to the plants is a growth-limiting factor under timberline conditions. Kullman (1981) considered the cold meltwater in the soil, coming from melting snow, a significant factor, since it may prevent the germination of birch seeds and the development of seedlings.

Topography. The effect of the topography is related to the bedrock and the soil cover, since on steep slopes the influence of the rock and soil types is at its most pronounced. At the flat northern timberlines again, the topography is interlinked with mire formation. Especially at alpine timberlines the topography influences the temperature conditions. The exposition, i.e. the direction of the slope, affects the amount of solar radiation. Arno (1984) considered the effect of the exposition significant, especially north of 40 degrees northern latitude. On steep slopes the effect of the exposition may be crucial: on slopes facing south, timberline forest occurs, while slopes facing north are treeless (Figure 23). Mayer and Ott (1991) reported that in climatically and geologically uniform forest areas in the Alps, the altitude of the climatical timberline may vary 50-100 m upwards or downwards from the average location, depending on the exposition. In the Alps the topography of the valleys have a great influence on the formation of the timberline (Holtmeier 1974). The differences in microclimate depending on the direction of the slope have a surprisingly great effect on the photosynthesis of *Pinus mugo* and *Larix decidua* in the Alps (Grace 1989). Ellenberg (1986) found exposition to be a common reason for the extrazonal occurrences of vegetation zones in the Alps.

Obrebska-Starklowa (1993) has in detail specified the effects of topographical and related topoclimatic factors at the alpine timberlines of the Tatra Mountains. Perttu (1972) has studied the altitudinal location of the timberline on slopes facing in various directions in the fells of northern Sweden. He found that the coniferous timberline on the western slopes is, on an average, located 25-30 m higher than on the eastern slopes.

The influence of the topography is also closely related to the snow and wind. Kryuchkov (1957) found that in Khibiny the timberline formed by spruce and birch is at an altitude of 470 m on the southern slope and at 400 m on the northern slope. Holtmeier (1979) emphasized strongly the significance of the small-scale topography for the timberline ecotone vegetation. Holtmeier and Broll (1992) have studied the influence of the small-scale topography on the timberline ecotone in the Rocky Mountains. They reported that a distinctly developed patchiness of the properties of the vegetation and site depends on the distribution of the snow cover, which in turn is controlled by the effect of the microtopography and the forest islands on air currents close to the ground. Ground vegetation, soil formation and soil properties differed within the forest islands, on the windy side and on the leeward side.

On mountain tops and steep ridges the effect of topoclimatic factors appears in the form of the 'summit effect', due to which the actual timberline is located lower than the climatic timberline. Many ecological factors contribute to this phenomenon: strong radiant emittance from the ground surface, the effect of the wind, cooling in summer and thinning of the snow cover in winter, and drought (Troll 1973a).

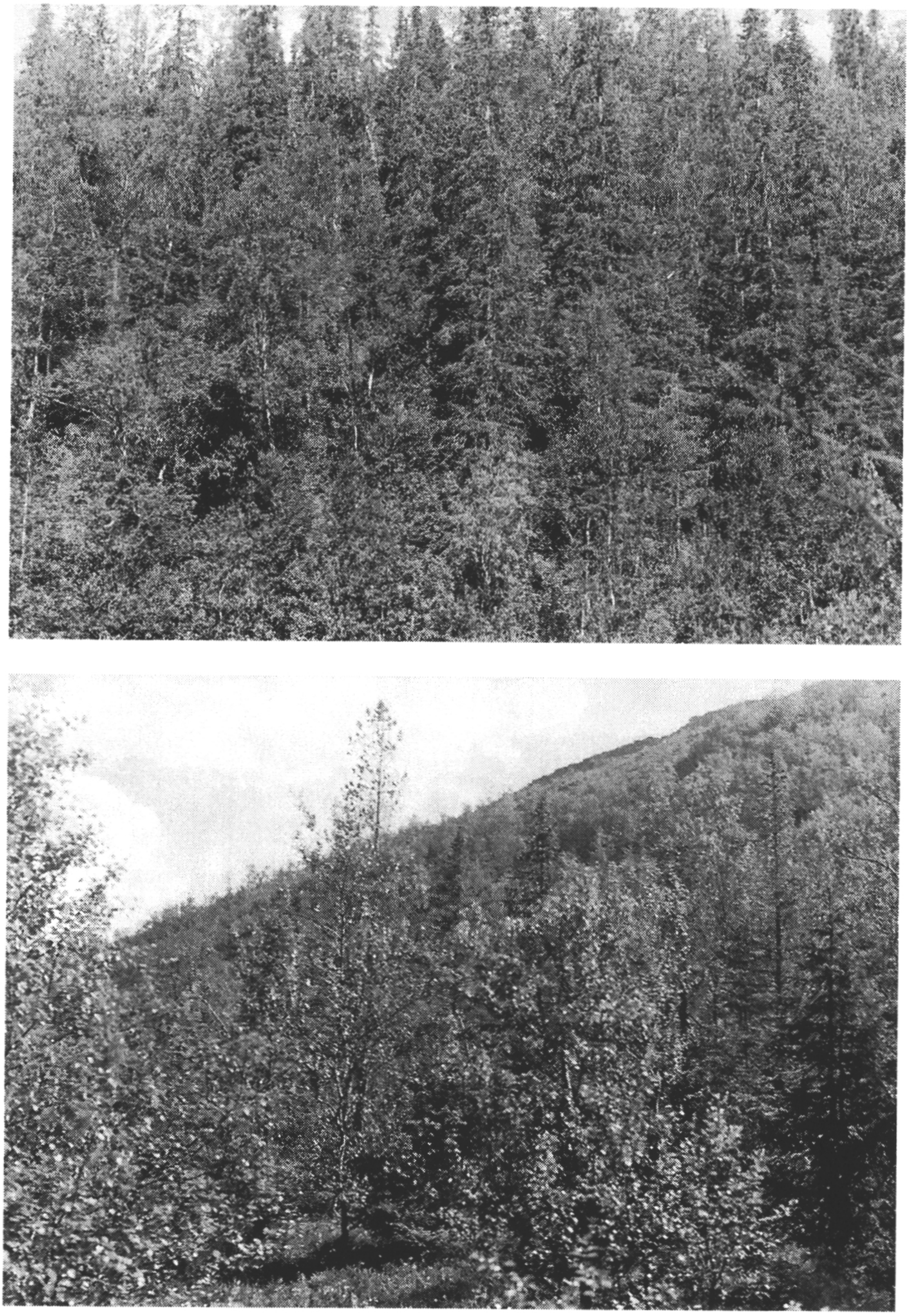

Figure 23. Exposition has effect on the level of timberline. Upper photo: Spruce forest on the slope exposed to south in the valley of the fell Khibiny. Lower picture: Birch-dominated brushformed vegetation in the same valley on the slope exposed to north. Photo: Pertti Veijola 1995.

In the southernmost fells of Finland, additional factors are block fields and steepness of the slopes (Autio 1993), and probably many of these fells are treeless only due to the 'summit effect'. Dahl (1983) emphasized that scattered, low felltops should be excluded from studies of the altitude of the climatic timberline and its causes in more extensive areas. In his own studies, he included only fells, the tops of which are 200 m or more above the tree line.

Paludification. The climate of cold timberlines is generally clearly humid, and so the conditions are favourable to paludification. Along the regular northern timberlines of both Eurasia and North America the proportion of mires is large. Paludification is also closely related to permafrost, since the state of melting at the ground surface has a crucial effect on the water regime of the ground during the growing season. At the alpine timberlines of the northern mountain regions, sloping mires and wet meadows are common. Removal of the timberline forest favours paludification, and thus the view has been expressed that human activities have favoured the paludification of the timberline regions.

Formerly in Russia, paludification was considered one of the basic causes of the treelessness of the tundra, and at the same time it was suggested that the situation may be amended by drainage (Andreyev 1954). Tikhomirov (1962) reported that Middendorf in the 1860's and further Tanfil´yev in the early 20th century have expressed the idea of ground vegetation succession in the timberline regions, in which the moss cover grows and paludification progresses, while due to these processes the temperature of the ground decreases. The location of the timberline would be controlled by this natural succession. Kryuchkov (1976) and Tyrtikov (1995) still considered these phenomena important in the long-term dynamics of the ecosystems of the northern timberline, especially in the flat terrain of West-Siberia.

Permafrost. Permafrost is related to the temperature and humidity of the soil, but since it is such an important factor, it is usually examined as a separate phenomenon (Brown 1970). According to Pruitt (1970) the term 'permafrost' is a paradox, since it is neither permanent or frost. According to the common definition permafrost is ground which has been frozen for at least two growing seasons. It may consist of any type of soil or even rock. Permafrost is a complex, dynamic whole, which is influenced by the history of climate and vegetation, the present climate and vegetation, soil, topography and fauna (Pruitt 1970). Permafrost has a crucial effect on the arctic timberline ecotone and tundra, whereas at the alpine timberlines extensive permafrost does not generally occur (Arno 1984).

In the continental parts of Eurasia the permafrost extends deep into the boreal zone (Parmuzin 1979). Of the forest-covered area in Russia, about 60% is in the permafrost region (Pozdnyakov 1983). In the northern parts of Alaska and in northwestern Canada the southern limit of permafrost coincides approximately with the northern timberline (Arno 1984) and roughly with the -1.1°C isotherm of the annual mean temperature of the air (Bonan 1992). In Scandinavia permafrost occurs in the upper alpine belt of the Scandes (King 1986). The southern limit for the palsa mires coincides approximately with the pine timberline (Kallio et al. 1969). The permafrost prevents the warming of the ground during the growing season and keeps the temperature of the root layer below optimum, which in turn makes the water uptake and metabolism of the roots difficult (Larsen 1989). The annual melting and freezing as well as the presence of snow keep the ground very moist, causing solifluction, which leads to damage of roots and inclination of trees. On steep slopes, solifluction may be the cause of extensive erosional landforms.

Trees adapted to these conditions have a superficial root system. In Canada *Picea mariana* and in Siberia *Larix gmelini* succeed in the area of permafrost, where the ground surface melts to a depth of about 0.5 m, and under these conditions the microtopography and the small variations in the melted layer affect the occurence of trees (Arno 1984). In Russia permafrost was earlier considered the crucial reason for the formation of the timberline (Blüthgen 1942). The removal of forest growing in a permafrost area causes a fundamental change in the temperature conditions of the ground, giving rise to a thermokarst phenomenon, in which the structure of the ground surface is definitely changed. In the Russian timberline regions the formation of thermokarst is considered a serious environmental problem (Kryuchkov 1984). Permafrost is not always, however, an adverse phenomenon to the development of forests, as in areas of very low precipitation, e.g. Yakutia with 190 mm a year, the permafrost makes the presence of forest possible by retaining water in the surficial soil layer during the growing season (Kryuchkov 1987).

4.5 Biological factors

Fungi. Although fungi may be of great local significance, they are not usually, over extensive areas, factors that crucially influence the location of the timberline. In the early 20th century the fungus *Cronartium ribicola* was accidentally brought from Europe to the Rocky Mountains, where it has caused significant damage in forests of *Pinus albicaulis* (Arno 1984). The same fungus is common in the old timberline pine stands of Scandinavia, occasionally killing trees. Holtmeier (1974) mentions the fungus *Herpotrichia juniperi*, which causes considerable damage in the Alps. In his opinion the significance of fungus damage to the afforestation and natural forest regeneration in the timberline region may exceed that of climatic factors. In Scandinavia the most common fungus of pine plantations is *Phacidium infestans*, which has been considered to be of significance, especially in Sweden. Holtmeier (1979) has found the damage caused by this fungus in Utsjoki to be the greatest in the areas where the snow melts late in summer. The clearly most disastrous of the fungus diseases in the planted stands of the high-altitude areas in Lapland is *Gremmeniella abietina* (Jalkanen 1989). During a study of the natural regeneration of timberline pine, Osmonen (1985) observed significant damage caused by *Gremmeniella abietina* and *Lachnellula pini* at the alpine timberlines, whereas at the polar timberline this type of damage was fairly rare.

Insects. Plant-eating insects damage plants in all climates. The relative significance of the damage to the plants is, however, frequently the greatest in suboptimal environments, such as at the timberline. Leaf damage is repeatedly caused to the fell birch, *Betula pubescens* subsp. *crepanovii* (Orlova) Hämet-Ahti, by *Oporinia (=Epirrita) autumnata* (Bkh.) and two species of *Operophtera* (Haukioja et al. 1983). Nuorteva (1963) found that mass occurrences of *Oporinia autumnata* (Bkh.) in Finland are known since the beginning of the 20th century. He has studied the effect on fell birch of the damage that occurred 1927 on the Ailigas fell in Karigasniemi, concluding that the recovery from serious damage may last a century. Nuorteva (1966) considered *Oporinia autumnata* (Bkh.) to be among the most important factors that affect fell birch, along with man and reindeer.

Helland (1905, 1907) mentioned the *Oporinia* damage observed in northern Norway in the 19th century. Holmgren (1912) gives a detailed account of the damages in the provinces of Norrbotten and Troms. In the years 1964-65, extensive *Oporinia* damage occurred in Utsjoki and the northern parts of Inari, covering an estimated area of 1210 km^2 (Seppälä and Rastas 1980). At the Kevo research station of the Turku University, the causes of the damage and the relation between *Oporinia* and fell birch have been thoroughly studied (e.g. Haukioja 1981, Haukioja et al. 1980). The research carried out at Kevo as well as the results of Tenow (1983) from Finnmark show that the birch stands in the valleys were spared damage due to the low winter temperature of the valleys, which destroys the eggs of the insects. Kallio et al. (1983) emphasized that a factor most probably contributing to the extent of the damage was the energy shortage of the trees, since the catastrophy was preceded by two extremely cold summers.

Lehtonen (1981) has studied the changes in vegetation after the damage, concluding that about half of the damaged area will lose its trees entirely, changing into barren area. After the damage the ground vegetation grows vigorously at first, then gradually changing, however, into a vegetation dominated by dwarf shrubs, corresponding to the properties of the site and resembling alpine vegetation (Lehtonen and

Yli-Rekola 1979). This development is unfavourable to the reindeer herding. The effect of reindeer grazing may prevent the regeneration of fell birch from shoots (Treter 1984). On the other hand, the results obtained by Lehtonen (1987) indicate that reindeer do not significantly hinder the regeneration of fell birch in the damaged areas. Results obtained by Lehtonen and Heikkinen (1995) show that in the damaged areas regeneration from seed is in theory possible, although the grazing of reindeer prevents the development of the seedlings. The development of shoots was not affected to the same degree by the grazing, whereas rot spreading from the mother tree played a certain part (fig. 25 Appendix 1)

The destruction of birch has locally favoured the regeneration of pine and the development of young stands, probably due to the end of the competition and the fertilizing effect of the decaying birch. This phenomenon is clearly visible, e.g. in the eastern Inari area. Hoffman (1984) has concluded on the basis of the forest inventories carried out in the Paatsjoki river valley in 1960 and 1975 that the amount of deciduous trees was reduced by 80 % due to the *Oporinia* damage. Effects of the same damage are also visible on the Finnish side of the border within the pine region.

Oporinia damage was observed in the summer of 1992 in the northern parts of Sodankylä, and extending into the municipality of Inari. The damage was most evident in forests at an altitude of over 300 m a.s.l. and the total area of damage was about 37 000 hectares (Metsähallitus 1992). In 1995 damage was reported in an area of about 4000 hectares in the 'Arm of Lapland' (Olli 1995).

Koponen (1983) has studied the leaf damage on fell birch and related birch species during the years 1971-1980 in Fennoscandia, Iceland, Scotland, Greenland and eastern Canada. He arrived at the conclusion that besides *Oporinia*, many other insects may also cause damage. The areas of damage were small. In the fell birch stands on the coast of northern Norway in the 1990's, the larvae of a moth species, *Argyresthia retinella* Zell. (Lepidoptera: Yponomeutiadae), were found to dry birch shoots by eating them hollow (Elverum 1995).

Birds. Birds use seeds of conifers as food and may thus contribute to the spreading of the seeds. The best example is probably the case of the nutcracker *Nugifraga caryocatactes*, which spreads the seeds of *Pinus cembra* above the timberline, storing them on ridges with a thin snow cover. As a result, plant stands are formed parallel to the ridges (Holtmeier 1974). The nutcracker also plays a role in Siberia in the regeneration of *Pinus sembra* and *Pinus pumila*. The crossbill *Loxia* is known to use and spread considerable amounts of pine and spruce seeds (Tikhomirov 1962).

Other wild animals. Many mammals may cause damage on small areas in the timberline forests. This damage is, however, of little consequence. The influence of wild deer species on the vegetation is smaller than that of the reindeer. Tikhomirov (1962) mentioned the effect of rodents that eat seeds, such as chipmunk. Kallio and Mäkinen (1978) and Haapasaari (1988) also mentioned the adverse effect of voles during the peak population years.

Mycorrhizas. Andreyev (1966) considered the lack of mycorrhizas in the ground as one of the reasons for the poor success of trees in the tundra. According to his opinion, it is as important to safeguard the presence of mycorrhizas as it is to use seeds of good quality for he planting of timberline stands. The growing season of the root systems of timberline trees starts later and the growth is slower than at lower altitudes. According to Tranquillini (1979) many studies show that the formation of mycorrhizas is an absolute prerequisite for the function of the root systems of timberline trees. It has also been found that mycorrhizas have forms that are adapted to cold environments. The symbiosis between ectotrophic mycorrhizas and roots is considered to be a combination, which enables the tree to take up sufficient water and nutrients in a cold environment. According to Moser (1967) the ectorophic mycorrhizas of the timberline stands makes it possible to take up nutrients so effectively during the short growing season that it safeguards the development of new shoots until they are frost resistant. The mycorrhizas are also important for the regeneration of timberline forests. Especially in grazing areas and forest fire areas at a distance of 50 m or more from the timberline, the insufficient mycorrhiza formation may limit the natural regeneration of the trees (Mayer and Ott 1991). According to Wardle (1981) all significant timberline trees have developed an ectotrophic mycorrhiza, which is important for the uptake of nutritients, especially where the ground is poor in phosphorus.

4.6 Anthropogenic factors

4.6.1 General

Degree of naturalness. When examining the effect of anthropogenic influence on the vegetation it is essential to understand what is meant by anthropogenic influence and, on the other hand, by naturalness. Peterken (1996) has recognised several qualities of naturalness: original-, present-, past-, potential- and future naturalness. He analysed the level naturalness of forests using an eight-point scale from virgin forests to immature plantations with native tree species. Westhoff (1983) has presented the following general outline for description of the degree of naturalness:

- Natural: a landscape or ecosystem, unaffected by man.

- Subnatural: a landscape or ecosystem, affected by man to some degree, but still belonging to the same structural type of vegetation that it originates from.

- Semi-natural: a landscape or ecosystem, the flora and fauna of which is natural but the flora of which belongs to a structural type other than the original one (e.g., pasture or heath, formed from a forest).

- Cultural landscape or ecosystem: by the influence of man the flora and fauna has been replaced by new species (e.g. a field or a forest of foreign species).

At the timberlines, all the situations mentioned above may occur. At the timberlines of sparsely inhabited regions there are very virgin forest areas, as shown e.g. by the concentration of protected areas in the timberline regions of Finland and Sweden. Cultural ecosystems are represented, e.g. by the areas of planted foreign tree species in Iceland and Norway. The heaths formed at the oceanic timberlines are mainly semi-natural areas, and so are the meadows and pastures in the mountains. Apparently the main part of the present northern timberline of Scandinavia is of the sub-natural type, in which various degrees of human activities have been present for a long time, however, with the original forest vegetation structure remaining in a dominant role.

Long-term anthropogenic effect and natural processes. The timberlines are influenced both by human activities and natural processes, the time spans of which overlap so that it is often hard to distinguish these two. The anthropogenic effects may be of a very long duration. The study of the oldest ones is closely related to the study of the timberline dynamics caused by climatic fluctuations. In Central Europe anthropogenic effects on the vegetation are known also from the mountains from as far back as 6000 years ago (Bortenschlager 1988). The changes caused by man in the forests of the Alps have been studied extensively, starting with the semi-nomadic agriculture of the Roman time, and ending with the effects of today's ski resorts and other recreational use (e.g. Stern 1983, 1988). Plesnik (1978) considered the activities related to the ski resorts as significant factors in lowering the timberline in the Carpathian Mountains. According to Obrebska-Starklowa (1993), 64 % of the timberlines in the Tatra Mountains have been lowered due to the anthropogenic factor. Ozenda (1988) estimates that in the northeastern Alps the timberline has been lowered on average 400 m, about half of which is due to the cooling of the climate and half to the anthropogenic factor. Gorchakovski and Shiyatov (1978) were of the opinion that human activities have influenced the alpine timberlines of the boreal zone of Russia fairly little.

Hustich (1966) found that pre-historic man already lived in the vicinity of the northern timberline, clearly influencing the forest. He was of the opinion that man has through the ages accentuated or decreased the effect of climatic changes on the timberline. Haila and Levins (1992) arrived at the conclusion that it is practically impossible to distinguish between natural disturbances and anthropogenic effects in the analysis of factors influencing changes in the timberline. Human activities have influenced northern Lapland for thousands of years already, and thus man affects the ecosystems as an integral part of them.

Tikhomirov (1962) concluded that the anthropogenic effect has lasted for thousands of years and that in the struggle between tundra and forest, man has always supported tundra. Kryuchkov (1990) estimated that the extent of the tundra formed due to anthropogenic effects is 400 000 - 500 000 km^2 between Kola and Chukotska. The reasons for this development have been the use of forest resources, which in many areas has exceeded the growth for thousands of years, and above all, the forest fires. The effect of the Sàmi and other arctic indigenous peoples on the timberline is mainly related to reindeer husbandry.

In Fennoscandia and generally in the region of the North Atlantic, timberline forests have been under significant strain due to utilization. On the coast of northern Norway, agriculture and animal husbandry began considerably before the Christian Era, and even the marginal areas were taken into use during the period 100 - 400 A.D. The forests were affected by clearing and grazing and by leaf foddering for the winter feeding of the animals (Vorren 1979). A strong demand for forest products was caused by taxation, trading, fishing, settlement and growth of the densely populated areas on the coast extending to the White Sea, starting at the time of the raids of the Viking chief Ottar around 890 A.D. (Helland 1905, 1907, Homén 1918, Sveli 1987, Slettjord 1993, etc.). Olafsen (1911, 1912) compiled a thorough account where the disappearance of the forests is examined as a part of the forest history of Norway.

Iceland is one of the best-known examples of the long-run influence of man on the timberline forests. According to Loftsson (1993) about 30 % of Iceland was covered by birch forests at the time of settlement of the country. Due to felling and grazing the proportion of forests at the end of the 19th century was only about one percent. The influence of the Norwegian settlement from the 11th to the 16th century was disastrous to the birch forests of southern Greenland, which, however, recovered when the utilization ended (Fredskild and Ødum 1990).

The study of the long-term influence of man on the timberlines may be based besides on historical facts, also on pollen analyses. According to Hicks (1992) the effect of a climatic change is generally evident from the tree pollen ratios over extensive areas. The change is also in general of long duration. The anthropogenic change again is frequently local with visible changes only in the field layer and ground layer. Usually its time of incidence and duration also vary from place to place.

Anthropogenic influence during the last few centuries. Abundant historical, regional accounts exist of the anthropogenic influence on the timberlines of Fennoscandia during the last few centuries. In Finland the effect of the settlement spreading from the south began in the 18th century, adding to the earlier influence on the timberline by the Sàmi and from the direction of the Arctic Ocean. In Sweden, too, the settlement spread towards the fells during the same period, whereas in Norway and Russia the spreading of the settlement was mostly confined to the coast of the Arctic Ocean. Olafsen (1911) considered the 16th century as the turning point in the history of devastation of the Norwegian coastal forests, since from then the export of timber started to become an important factor affecting the decrease in forest area. According to Olafsen the main influence was Dutch, although the domestic use of wood was crucial in the devastation of the forests.

According to the opinion of Blüthgen (1942) the anthropogenic effect on the timberlines near the coasts, such as on the coasts of Kola and the White Sea, has been much greater than on the timberlines of the interior of Lapland. Kihlman (1890) gave a thorough description of the anthropogenic effect on the timberlines of Kola, estimating that the timberline regions of the Kola Peninsula were the last remaining actual wilderness areas (Urwald) in Europe. The utilization of natural resources from northern areas has been intensified during this century in Russia. E.g. the oil and gas industry and related changes in economic and population structure have caused significantly increased pressure on the timberline forests (Chertovskoi et al. 1987, Kryuchkov 1987, etc.)

Massa (1979) found that Northern Lapland was overpopulated as early as in the 19th century and that the felling and forest fires caused by the Finnish farmers were the main cause of the lowering of the timberline. However, the earlier effect of the nomadic Sàmi on the timberline had also been distinct, especially in Utsjoki. The following examples of more extensive studies concerning the anthropogenic effects in Fennoscandia are worth mentioning: Sandberg (1898), Renvall (1919) and Tanner (1927) from Finland, Gavelin (1909), Holmgren (1912) and Fries (1913) from Sweden, Olafsen (1911, 1912), Juul (1925), Hvosleff (1956) and Sveli (1987) from Norway. On the basis of an abundant source material Mattsson (1995) arrived at the conclusion that the pine timberline in northern Fennoscandia has shifted on average 30 km towards the south due to the anthropogenic influence during the last two centuries. In his interpretation the timberline was considered to be formed by the northernmost isolated pine stands.

Figure 26.The northeastern Inari is a good example of an area where human impact on the timberline has been heavy. As result the treeline ecotone is wide and dispersed. Last pines near the Arctic Ocean about 4km from Neiden. Photo: Pertti Veijola 1995.

In Russia, the anthropogenic influence on the northern timberline has also been extensively studied. As early as 1864, Middendorf could clearly observe the influence of man during his expeditions to Siberia, and he wrote as follows: 'Carelessly they fell the remotest islands of stunted forest, which would serve as natural shelter against the winds. Man is rapidly promoting the spreading of the tundra.' Pohle (1917) and Regel (1935-1941) have also described the anthropogenic effects on the timberlines of Russia. Kryuchkov (1978) presented as his estimate that the annual use of phytomass of trees and shrubs by the traditional means of living is 200-400 kg/ha and the corresponding annual growth is in the forest tundra on an average 200-500 kg/ha and in the birch forest 500-900 kg/ha. Still today, the anthropogenic effect in favour of the tundra continues (e.g. Kryuchkov 1988). Hustich (1966) estimated that in the 20th century the anthropogenic effect on the forest tundra had decreased due to urbanization and the development of the trades.

In superficial studies of short duration the anthropogenic effect on the timberline is frequently underrated. On the other hand the effects of climatic changes may purposefully be presented as caused by man. This was the case in Norway in the late 19th century during a conflict concerning the right of pasture in Norway of Swedish nomadic Sàmi. The disappearance of pine from the fell highland was claimed to be caused by the activities of the reindeer herders (Juul 1925, Sveli 1987). The effects of natural processes and of human activities, including their duration, have also frequently been mixed in the discussion of the timberline forests during the last few years (e.g. Wahlström et al. 1992).

In the estimation of the anthropogenic effect on timberlines the basic assumption is in general that the effect is negative. On the other hand it is worth remembering that many landscapes, experienced as esthetically valuable and frequently also rich in species, were formed as a result of forest devastation. Examples of these are the heaths of Britain and the varied landscapes formed by forest islands and meadows at the timberlines of the Alps. Even under the austere conditions of the Finnish timberlines, the open patches or homesteads cleared by man in the forest are considered as valuable factors, increasing the biodiversity. Westhoff (1983) found that the essential is the time span of change, as a slow change allows organisms and people to adapt. The other extreme is represented by clear fellings in timberline regions, erosion areas caused by anthropogenic factors, or forests destroyed by air pollution. The slow changes caused by traditional forms of use represent the basic attitude of cooperation with nature, and the rapid changes caused by industrial activities an attitude of exploitation.

4.6.2 Fire

Fire is a natural part of the ecology of the pine forests. Man has for so long used fire by purpose or by accident that the consequences of fires caused by lightning are difficult to distinguish from those caused by man. According to the view of Arno (1984) extensive, destructive fires are rare at the alpine timberline due to the scarcity of burning material. At the arctic timberline again, fires have played an important role in Canada (Payette 1980, 1983, 1992, Larsen 1980, 1989), in Scandinavia (Sandberg 1898, Fries 1913, Renvall 1919, Juul 1925, Heikinheimo 1921, Hustich 1966, Sirén 1961, Zachrisson 1977), and in Russia (Kihlman 1890, Pohle 1917, Regel 1940, Tikhomirov 1962, Kryuckov 1968, Andreyev 1981).

Fire stimulates the regeneration of many conifer species, also in the timberline regions. The serotine cones of *Picea mariana* (Larsen 1989) and the adaptation of *Pinus sylvestris* to repeated fires may be mentioned as examples. The fire may be disastrous to a tree species that normally regenerates well in connection with forest fires, if the climate allows the formation of germinating seeds only rarely. This was the case in the timberline regions of Lapland and Russia in the late 19th and the early

20th century. From this time, numerous and detailed regional descriptions of the effects of the forest fires exist. In Finland, a clear picture of the consequences of forest fires is obtained from the results of the earliest forest surveys of the northern areas, carried out 1897-1915, and the research work of Renvall (1919). It is evident that if the regeneration of the conifers is very slow, *Betula pubescens* will take over the areas. Especially with the better forest types this development is common (Lakari 1915).

In the forestry plan for the Inari district, Lauri Ilvessalo (1927) has made a good summary of the effect of forest fires on the basis of his own studies and earlier forest assessments. Taken as a whole, the forest fires that occurred in the 18th and 19th centuries had a crucial effect on the state of the forests in Inari. Ilvessalo wrote: 'Regarding the state of the forests, one cannot omit the fact that vast areas, comprising a total of thousands of hectares, due to destruction by forest fires, have become entirely forestless or grow at the most extremely scattered birches of poor quality. Judging from charred stumps and remains of charred trunks lying on the ground, these lands have, at least in numerous cases, been covered by fairly dense pine forest.'

In 1936, Mikkola (1954) made observations of the extensive birch forests in burnt areas south of Saariselkä, where formerly coniferous forests grew. Tynys (1995) has studied the forest fire history of the Hammastunturi wilderness area, concluding that the more extensive forest fires of the 19th century may be located. He also estimated that in the 18th century the fires were more common and more violent. In general the fire areas were covered by forest in a reasonable time. The pine-dominated forests had partly turned into birch-dominated ones after the fires (fig. 27, 28 Appendix 1).

Hustich (1966) and Sirén (1961) were of the opinion that the 'pseudotundra' of Utsjoki is the result of a succession where birch has invaded the site after a forest fire. Thus at least part of the fell birch zone would have formed as a result of birch invasion after forest fires. Massa (1979) considered the 'pseudotundra' to be caused by the activities of the nomadic Sàmi. In earlier times, forest fires have been considered the cause of the presence of the northern pine zone and the absence of spruce in northern Lapland (Kihlman 1890, Fries 1913).

Payette and Gagnon (1979) arrived at the conclusion that at the timberline of northern Quebec, fire and climatic changes together control the population dynamics of *Picea mariana*. Johnson (1992) found that although the area of forest fire risk moves toward the timberline with the progress of the growing season, the fire risk remains clearly smaller at the timberline than in the interior of the boreal zone. Johnson (1979) was of the opinion that the timberline may roughly be considered the line that separates the ecosystem susceptible to forest fires from that of low fire risk. According to Payette (1992) the fire cycle is decidedly longer in the northern part of the Canadian forest tundra than in the southern part. However, the proportion of taiga forest, thinned as a result of forest fire, decreases while the proportion of open lichen heath increases correspondingly. This subarctic deforestation is caused by failure of regeneration from seed after forest fires. According to Auclair (1983) the fire risk of the tundra and forest tundra depends on the ground vegetation, since the scattered trees of the forest tundra would not maintain a fire. The fire susceptibility of the ground vegetation is caused mainly by quickly drying lichens and dwarf shrubs containing abundant etheric oils, such as various species of *Empetrum, Ledum* and *Vaccinium*.

According to Zackrisson (1977), regeneration does not always occur immediately after a fire in the high-altitude areas of northern Sweden, and so the forest fire areas may degenerate into open *Cladonia* heaths for decades. The same phenomenon may be related to the formation of the lichen heaths in Finnish Lapland (e.g. Aaltonen 1919). Sirois (1992) pointed out that in the southern forest tundra repeated fires cause thinning of the stand, while in the northern part one single fire may be sufficient to destroy the stand completely. Information is also available on the disastrous effects of forest fires in e.g. the Rocky Mountains (Agee and Smith 1984).

Andreyev (1981) examined the significance of forest fires in Siberia and found that in the tundra proper the fires are in general small in extent, while in the forest tundra they may be quite extensive. Due to a fire the forest tundra may turn into treeless 'pyrogenic tundra', a type that is common in the continental parts of the tundra zone, as e.g. in the area between the Ob River and the Chukotska Peninsula. After a fire various species of *Salix* and *Betula nana* are dominant in the shrub layer, *Eriophorum vaginatum* etc. in the field layer, and various species of *Sphagnum* in the ground layer.

Kryuchkov (1968, 1978) described the powerful effect of the forest fire, which may change the entire ecosystem, in the permafrost area of the northeastern Siberian forest tundra. Regardless of the short period of forest fire risk, only from mid-July to early August, numerous fires occur. A forest fire changes the heat conditions of the ground surface, causing melting of frozen ground and formation of thermokarst. The moisture of the ground increases, and during the following years the frozen layer melts slowly, and the process of paludification begins. The depth of the surficial layer that stays unfrozen during the growing season decreases and the temperature of the ground sinks. Due to these factors the regeneration of the trees is not successful even when germinating seeds are present. According to Kryuchkov the 'pyrogenic tundra' formed by this mechanism forms an irregular zone, from 1-2 km to 60 km wide, north of the timberline in northeastern Siberia.

Pettapiece (1984) found that in the subarctic *Picea mariana* forests of Canada the development of the post-fire tree generation is successful, since by removing the thick humus layer the fire improves the heat and nutrient conditions of the site. However, the effect of the fire may be unfavourable in the vicinity of the timberline, resulting in 'fire-induced' tundra. Sirois (1993) concluded in summary of findings from throughout the subarctic area that under these conditions, post-fire regeneration is not generally able to maintain the stable state of the forests for a long time. In early times fire has also been used purposefully in order to stimulate the growth of food plants for game animals and to improve the pastures in boreal forests (e.g. Blomqvist 1959, Barrett and Arno 1982).

4.6.3 Felling

Wood harvesting for forest industry and corresponding use of wood. There are no documented cases from the northern timberline of displacement of the timberline as a result of felling that can be considered as serving the industrial wood supply. In Fennoscandia forestry and commercial felling is carried out closer to the timberline, in 69 degrees northern latitude, than elsewhere on the Eurasian continent or in North America. The reasons are the accessibility and the properties of the forests due to the favourable climate of Fennoscandia.

According to available information from central Siberia, felling for local purposes to be considered as forestry, is carried out as far as north of 70 degrees latitude in *Larix gmelini* forests. The average volume of the forests concerned is 20-40 m^3/ha, at its best 60-80 m^3/ha (Abaimov and Bondarev 1992). According to Chertovskoi et al. (1987), significant felling to cover the local demand is carried out in the industrialized areas in the timberline forests of eastern Siberia. These fellings are extensive due to the small percentage of merchantable wood. In Yakutia forestry is concentrated in the middle taiga and the northern taiga is mostly outside of forestry operations (Timofeyev et al. 1994).

Many research workers have expressed their concern regarding the commercial fellings in Canada, which are also approaching the timberline forests (e.g. Hämet-Ahti 1983). Mackay (1985) reported that views have been expressed in Newfoundland according to which the areas of clear felling will turn into tundra for a long time. In the plans for conservation of the arctic environment, forestry and deforestation are considered a hazard factor in Finland, Iceland, Norway, Sweden and Russia, but not in Canada nor in the USA (Directorate for Nature Management 1994).

Permanent settlement and household use. The felling affecting the timberline has usually been related to household use and traditional means of living. In earlier times, the supply of firewood and construction wood was crucial for the location of permanent settlement, and the acquisition of firewood seems to have been a problem in all northern areas (Massa 1979). According to Pohle (1917) the population density in the timberline areas is frequently so low that the anthropogenic effect cannot be significant over extensive areas. However, considering the long time of this effect, in addition to the slow growth and regeneration of forest, the significance of even small-scale, long-lasting felling may be considerable. Paine (1957) described how the supply of fuel had a crucial effect on the living and housing of the coastal Sàmi of western Finnmark. Due to the wood shortage, peat was taken into use in the 1870's, and in the 1930's coal entered the picture. From the 1890's the forest authorities of Finnmark promoted the use of peat in order to save the forests (NOU 1994).

Holmberg (1912) made a thorough study of the household use of wood and its effect on the timberlines in the Troms province and the fell valleys of Norrbotten. He concluded that the effect of the reindeer-herding Sàmi on the timberlines had earlier been exaggerated. The winter villages of the timberline Sàmi population were located in coniferous forests or in the best birch forests (Hultblad 1968, NOU 1994). Rikkinen (1981, 1983) described how the location of a winter village of the Sàmi on the Kola Peninsula had to be shifted at intervals of 15-20 years due to the lack of wood. The same was also true for winter villages located in the coniferous forest area (Paulaharju 1921). According to T. I. Itkonen (1991) the Skolt Sàmi of Suonikylä moved their village to a new place at intervals of 40-50 years, when the lichen heaths had been consumed by the reindeer and the firewood and bark bread trees by the people. Hustich (1946) quoted the explanation to the map of Sàmi villages from 1642 by Olof Tresk as follows: 'The village of Inari is located north of the fell ridge by the Inari Lake and will now be moved 10 km from the place where it has been so far, since both firewood and reindeer lichen now are beginning to run out'. Using archeological and historical information as well as pollen analyses, Hicks (1995) studied the environmental impact of the Sàmi winter village in Inari, describing the change in the adjoining forests from pine to birch forest and then back to pine forest. She concluded that people in a hunter-gatherer economy are capable of changing their environment quite dramatically over restricted areas.

In Finland, the sufficiency of the forest resources and the household use of wood in the timberline regions has been thoroughly assessed in connection with settlement plans. The most difficult situation was encountered in Utsjoki and northern Enontekiö (Komiteanmietintö 1910, Renvall 1919, Heikinheimo 1921). According to Mattsson (1987) the birch forests of Utsjoki are affected by selection felling and grow in bushlike fashion due to the gathering of firewood, which has continued for a long time.

Tikhomirov (1962) mentioned the town of Dudinka by Yenisei as an example of the effect of the forest utilization of a densely populated area.

The town is located at the very timberline, after being in the middle of a larch forest still a century ago. According to Kryuchkov (1988) the deforestation has continued up to the present around many densely populated areas in the north. Detailed descriptions exist of the devastating use of forests to meet the demand of the coastal population in northern Norway (e.g. Helland 1899, 1905, 1907, Sveli 1987).

Seasonal dwellings. In many timberline areas of mountains and fells it was earlier common to have a system, mainly pertaining to animal husbandry, of moving to a place near the timberline for the summer. In Sweden this system is known as 'fäbodväsende', in Norway as 'seterdrift'. In some areas this activity has clearly increased the use of wood from the timberline forests (Kullman 1979, Lykke 1988). A related system exists in Siberia (Hämet-Ahti 1983). In the Alps a similar seminomadic form of agriculture has had a distinct influence on the forests of the subalpine zone (Stern 1983).

Selling of construction timber and other commercial timber. The good accessibility of some timberline regions has made it possible to sell timber, which has clearly had its influence on the timberline. The valleys of the floatable waterways in Fennoscandia that drain into the Arctic Ocean are the best examples. Even ready-made cribs of timbered houses were dismounted and floated to the coast, where they were sold. In Finland the selling of timber to Norway has affected the timberlines in the river valleys of Tenojoki, Näätämöjoki and Pakanajoki (Sandberg 1898, Renvall 1919, Sveli 1987). From the birch forests in the fell region of northern Sweden, sheets of birch bark were during long periods exported to the Norwegian coast for use as roofing (Campbell 1982). For centuries, firewood has been sold from the coast of Petsamo and Näätämö to the area north of the Varanger fjord (Andresen 1989).

Use of wood in handicraft and small-scale industry. Besides as raw material for carpenter work, quite significant amounts of timberline wood has locally been used as fuel for small-scale industries. On the coasts of the White Sea, such amounts of firewood were required for salt-making that this use affected the timberline (Pohle 1917). Tsvetkov et al. (1983) reported that salt was made on the coast of Murmansk, too, and that the number of salt-works at the end of the 16th century on the Kola Peninsula was more than 20. Their total annual firewood consumption was estimated to be more than 100 000 m^3. According to Wallenius (1994), the coniferous forest once reached down to the sea shore on the Poluostrov Rybachi of Petsamo. In the 1920's the villagers in Pummanki still used roots and stumps from the ground as firewood. The firewood consumption for salt-making has affected the timberline in Petsamo, too: 'The salt ate the forest, it needed enormous amounts of wood'.

The cheese making connected with the 'fäbodväsende' system has affected the use of wood both in Norway and in Sweden (e.g. Kullman

1979). Charcoal burning and tar burning were carried out even in the northernmost areas of pine occurrence in Norway, and in the 19th century the firewood need of the train oil cookeries was significant on the coast of northern Norway (Sveli 1987).

Bark bread. According to Renvall (1919) the use of phloem, i.e. inner bark, as raw material for bark bread, has been of importance in the pine forests of Utsjoki. According to the estimate of the Lapland Committee (Komiteanmietintö 1905), 2 150 000 pines were felled for the making of bark bread in Utsjoki alone during the years 1740-1880. In northern Norway, too, the making of bark bread has affected the forests during earlier centuries and the best pine forests were in use (Helland 1907). The circular letter from the National Board of Forestry (Metsähallitus 1918) shows that this form of use was important as late as during the beginning of the 20th century. It points out both the disadvantages of the felling of trees for bread making and the need for supervison, since trees had been felled without permission and bark had been used as food for animals.

Cattle feed. In Finnmark, twigs and bark of deciduous trees and pine were commonly gathered as cattle feed for the winter. In the northernmost occurrences on the coast this practice contributed to the disappearance of the forests, and the forest recovered visibly when cattle was no longer kept there (NOU 1994).

Traditional routes. Before the modern means of communication, traditional routes served the inland traffic of the northern areas, in summer using watercourses as much as possible. Winter was generally the period of maximum traffic. The winter routes often differed from those used in summer. The most important effect of the summer routes on the timberline forests was the increased fire risk. Sandberg's (1898) description of the condition of the forests along the route from Inari to the Arctic Ocean is a good example of this fact. In winter again, the consumption of firewood and the effect of the reindeer were of significance. According to Pohle (1917) a much used winter route followed the timberline from Mesen by the White Sea to the Ob river delta in the 17th century. The effect of the large numbers of travelers and reindeer on the forests along the route was evident. The condition of the forests along the ancient route between Kandalaksha and Murmansk, and along the present main road and railroad is a good example of the anthropogenic effect during various times. Chechott (1925) reported that during the construction of the Murmansk railroad, the forests were felled in a 2-4 km wide zone along the route. Today it is locally difficult to distinguish the secondary birch-dominated forests of the taiga from the fell birch forests proper. In Sweden vast fell birch forests were cut down during the construction of the Kiruna-Narvik railroad in the early 20th century (Emanuelsson 1987).

4.6.4 Grazing

The timberline forests of Fennoscandia are at present subjected to the extensive effect of reindeer herding and the limited, local effect of sheep and goats, mostly in the vicinity of farms in certain parts of Norway. The effects of grazing are frequently difficult to distinguish from those of other factors. According to Griggs (1937) a very small grazing pressure may already be enough to influence the timberline. The composition of the feed of the reindeer and its wild basic form is identical, but due to a higher population density the effects of reindeer on the vegetation are in general more pronounced (Helle 1994). During the last few years, the environmental effects of reindeer herding have become a subject of discussion. Excessive grazing is related to the problems of the whole reindeer economy in adapting to a changing environment (e.g. Prestbakmo 1994).

An estimation of the effects of reindeer husbandry on the timberline requires knowledge of the methods and extent of the trade. The northern part of Fennoscandia is almost entirely reindeer area. The systems of reindeer management show great variations according to area, and the methods have changed thoroughly since the 19th century. According to Skauge (1993) the reindeer numbers were as follows: Finland 410 000, Norway 220 000 and Sweden 295 000. In all these countries there is a problem of excessive grazing, and especially in Finnmark the situation is considered alarming.

The effects of reindeer herding on the forest may be divided into the immediate effect of the reindeer on the tree stand and the wood use of the reindeer herders. The influence of reindeer herding on the timberlines has been studied in the Troms area as early as in the early 20th century (Holmgren 1912, Barth 1915). Both wood use and grazing were found to affect the birch timberline, but the views of the total effect of the nomadic reindeer herding differed. Besides firewood and construction wood, the wood used for reindeer fences also had its effect on the timberline (Fries 1913, Emanuelsson 1987). Barth (1915) was of the opinion that grazing hampers the regeneration of birch significantly. At present the wood use of the reindeer herders is quite similar to that of the other local population.

<u>Finland</u>. As early as from the late 19th century, the effect of reindeer on the timberline was the subject of animated discussion. Ericsson (1888) quoted Silén, who had the experience of more than a decade as forestry officer in Inari, as follows: "If it is argued that the reindeer while digging destroys a tree seedling, I am sure that he, at the same time, sows a hundred". Ericsson himself shared this opinion on the basis of his experiences from Sodankylä, whereas Reuter (1907) in an extensive study of experiences so far gathered, emphasized the damage done by

reindeer. Fränti (1914) wrote that according to the earlier predominant view, reindeer have a positive effect on forest regeneration. However, he arrived at the conclusion that taken as a whole, reindeer have an adverse effect on the forest, although not to such a degree as is frequently suggested. Renvall (1919), like many other contemporary representatives of forestry, considered the adverse effect of reindeer significant, although the number of reindeer was much lower than the present one.

The reindeer pasturage commission (Komiteanmietintö 1914) also studied the influence of reindeer on the forests. It was found that the digging, trampling and shedding of velvet from the antlers of the reindeer affects planted stands, causing damage especially in the timberline forests, where regeneration is slow. Damage was also caused by the felling of lichen trees and by the taming of reindeer. The commission found, however, that the total significance of the damage is difficult to estimate. The examination was quite objective in comparison with many contemporary views.

Massa (1979) estimated that the damage to the young pine stands at the timberline was directly proportional to the number of reindeer. Today the areas of the reindeer herding associations are mostly separated by permanent fences. Each association follows its own annual herding cycle, based on traditions and circumstances, varying from clearly distinguished summer and winter pastures to nearly free grazing. According to the present view, the damage caused by reindeer to conifer seedling stands at the timberlines is occasional and of small extent, and as a whole, of small significance. Occasional damage may occur in places where the reindeer density is momentarily high, such as in certain parts of fence systems for reindeer roundups. Helle and Moilanen (1993) observed that the grazing intensity affected the damage frequency, whereas the grazing had no effect on the number of developable seedlings. Reindeer slow down or prevent the regeneration of birch in general, and in particular the recovery of birch forests destroyed by *Oporinia*. Helle and Kojola (1994) studied the effect of reindeer grazing on the vegetation and found it to weaken crucially especially the development of young birches. The effect on young pines was minor. According to Helle (1994) the grazing of reindeer increased the mortality of young birches at the timberline.

According to Oksanen et al. (1995) the grazing of reindeer has a critical effect on the timberline of birch in northern Fennoscandia. They found that in areas of low grazing intensity the timberline birches are brush-formed, polycormic, while in areas of more intensive grazing they are bigger, monocormic trees growing farther apart. The influence that the grazing of reindeer has on the fell birch forests is evident from satellite images and aerial photos from the boundary between Finland and Norway. In the Näätämö area, e.g., birch forests are present on the Norwegian side but scarce on the Finnish side, despite the identical history of *Oporinia* damage. Among the indirect effects of reindeer herding on timbnerline ecosystem, the cross-country traffic is at present the greatest problem. In the conclusions of the results of the Eastern Lapland Forest Damage Project it was stated that grazing which strongly affects the lichen cover may have a negative influence on the microbiology of the soil and on the frost resistance of the roots (Tikkanen and Niemelä 1995).

Norway. In Norway the system of reindeer management is mainly based on the cycle between the summer pastures on the coast of the Arctic Ocean and the winter pastures in the inland. Also in Norway it was earlier considered that the reindeer and the wood use of their herders caused damage (Juul 1925, Hvosleff 1956). However, both Juul and Hvosleff found that the Norwegian settlers affected the forests more than did the Sàmi. Schaanning Kollström (1987) studied the relations between reindeer management and forestry in the Pasvik river valley, concluding that the reindeer do not at present have an adverse effect on the planted pine stands. Earlier, in the 19th century, the large herds of the nomadic reindeer herders caused significant damage to the planted pine stands in the Pasvik valley (Wikan 1980) and as late as in the 1950's conflicts existed between the forestry and the reindeer management (Bakke and Jørgensen 1981).

Sweden. In Sweden the reindeer management is based on an annual cycle between the summer pastures in the fell area of the Scandes and the winter pastures in the coniferous forest area. According to Kullman (1979) the reindeer herding may locally have affected the fell-birch timberline. According to the estimate of Emanuelsson (1987) the reindeer management based on permanent grazing, which was common in the timberline region beginning in the 17th century, probably had a great effect at the time on the timberline in the vicinity of lake Torniojärvi. The change towards more extensive pasturing around the year 1900 took off some pressure, perhaps making it possible for the timberline to rise. In his comprehensive examination of the relations between reindeer management and forestry, Gustavsson (1989) makes no mention of the adverse effects of reindeer on conifers.

Russia. In Russia the reindeer management is generally based on the natural pasturing cycle, meaning that the reindeer are in the tundra by the coast of the Arctic Ocean during summer and in the forest tundra or northern taiga during winter. This is clearly the model also in the Kola Peninsula (Atlas Murmanskoi ... 1971). The greatest effect on the timberline forests is traditionally considered to be that of the migration across the timberline in spring and early winter (Tikhomirov 1962). Reindeer herding has generally been considered to have an adverse effect on tree seedlings. Andreyev (1954) studied the causes of death of larch seedlings at the timberline and found that reindeer are the most important factor, although their practical significance is probably quite small.

In 1980 it was estimated that the number of reindeer in Russia was about 3 million in a tundra area of approximately 3 million km^2 (Andreyev 1981). Rogingo (1992) estimated that the reindeer number of the northern regions had decreased to less than 2 million in the late 1980's due to the decline in pastures. According to Yurtsev et al. (1985) the reindeer number of the Chukotska Peninsula has increased clearly during the last decades, and the winter lichen pastures have at the same time become insufficient. The present number of reindeer in the Kola Peninsula is estimated at nearly 80 000 (Nieminen and Tervonen 1994). In his account of the effect of reindeer on the ground vegetation in the tundra, Andreyev (1981) did not mention the effects on the trees. Chertovskoi et al. (1987) were of the opinion that the safeguarding of the regeneration of larch in the timberline regions of the Komi Republic requires protection of regeneration areas from reindeer pasturing.

4.6.5 Erosion

The majority of the information available on the adverse effects of anthropogenic erosion in the tundra and timberline forests comes from Russia. Chertovskoi et al. (1987) reported that in about 9 % of the Russian forest tundra, erosion and formation of thermokarst is a problem. Parmuzin (1979) also pointed out the problems of solifluction and thermokarst, occurring mainly in the area of permafrost. According to Abaimov and Bondarev (1992) the felling of timberline forests in Central Siberia is combined with the risk of erosion. On the coast of Teri in the delta of the river Varzuga on the Kola Peninsula there is an eroded area of about 2000 ha, which has been formed as a result of felling and grazing, and may be mentioned as an example of erosion areas. When attempting to bring back vegetation to sandy soil, grasses are used at the first stage (Kazakov 1993). Kryuchkov (1968) described how in the permafrost area it takes only a short time of cross-country traffic, which destroys the ground vegetation, in order for thermokarst to form. Kryuchkov (1987) and Yurtsev et al. (1985) have emphasized that especially cross-country traffic on wheeled vehicles rapidly causes adverse effects to the tundra ecosystem. According to Kryuchkov (1968), forest fires contribute to the erosion in permafrost areas by changing the temperatures of the soil. Dryzhinina (1985) has studied the anthropogenic effects on the tundra in the Vorkuta area in Western Siberia. The connection between thermokarst and vehicle tracks in the terrain was evident. In general the anthropogenic effect causes the ground vegetation of the brush tundra, formed by shrubs, dwarf shrubs, mosses and lichens, to become dominated by *Carex* and grasses. The changes may in part be reversible.

At the timberline in Finland the risk of erosion is greatest in the sandy areas of Enontekiö, where the most distinct erosional landforms are visible at the lake Pöyrisjärvi. The sandy hills occurring there are nearly treeless due to the combined effect of wind, rain, ground frost, reindeer, and the anthropogenic factor. Judging from the present active wear of the vegetation and from the deflation, the climatic conditions have again turned worse (Punkari and Varjo 1977). Seppälä (1984) has studied deflation in the timberline region at the Hietatievat hills in Enontekiö. He found that annually a sand layer of about two centimeters is worn off the most exposed areas, and so the recovery of the vegetation is extremely difficult. According to Tikkanen and Heikkinen (1995), the effect of reindeer and terrain traffic may start erosion under the conditions that prevail in Enontekiö. The summer-time terrain traffic in areas susceptible to erosion requires strict supervision.

A factor that may be considered as related to erosion is the removal of vegetation and surficial soil layers for the purpose of mining or extraction of useful soils. In Russia the effects of these activities are extensive. Regarding the recovery of the vegetation, the tundra and forest tundra form a zone of their own, to which the Kola Peninsula belongs in the form of a subarea (Fedotov and Motorina 1978).

4.6.6 Air pollution

The most evident and extensive examples of the effects of air pollution on the timberline vegetation are found in Russia. Kharuk (1993) described the effects of the Norilsk smelting plant. In Norilsk, in 69 degrees northern latitude, timberline forests are formed by *Larix sibirica* and *dahurica* and by *Picea obovata, Betula tortuosa* and certain species of *Salix*. The smelting plant emits nitrogenous gases, heavy metals, and above all, more than 2 million metric tons of sulphur dioxide annually. This makes it the main source of sulphur dioxide of the northern areas. In the 1960's about 5000 ha of forest had died, and by the early 1990's the area of totally destroyed forest extended 50-60 km from the plant.

Tømmervik and Johansen (1992a) have used satellite images to study the impact of the pollution sources in Kola. Besides the completely destroyed vegetation in an area of 320 km^2 at the border between Norway and Russia, they observed effects in 2385 km^2 of meagre pine and birch forests. The impact of the Nikel smelting plant extends into Norway, where an area of over 250 km^2 is affected to various degrees (Aamlid and Venn 1992). In Russia the impact of the emissions of the

Severonikel (Monchegorsk) smelting plant on the environment, especially on the pine forests, was the object of study for a major project in 1981-1989 (Norin and Yarmishko 1990, Yarmishko 1992). It was found that visible damage to trees extended about 60 km from the plant and that young pines were more resistant to the emissions than were old trees. According to Kryuchkov (1992) the Severonikel area of impact on the vegetation increases 300-1500 m annually and that the total area of industrial desert on the Kola Peninsula is 1500-1600 km^2. In the Eastern Lapland Forest Damage Project was found that the forest death limit in the Montchegorsk area advances about 500 m per year (Tikkanen and Niemelä 1995).

Kryuchkov and Makarova (1989) described the environmental impacts of air pollution in Kola, dividing them regionally into five zones according to severity. The zone next after industrial desert is named 'dwarf birch-growing industrial-technogenic forest tundra', which reflects the fact that air pollution changes the northern boreal forest to resemble forest tundra. It may be concluded on the basis of available results that the northern timberline on the Kola Peninsula is clearly exposed to the effects of air pollution in the area Nikel′-Murmansk-Lovozero. The effects of the air pollution on the alpine timberline are most pronounced in the Petsamo fells, in Khibiny and especially in the fell area of the Monche and Chuna tundras west of Monchegorsk (Figures 29 and 30).

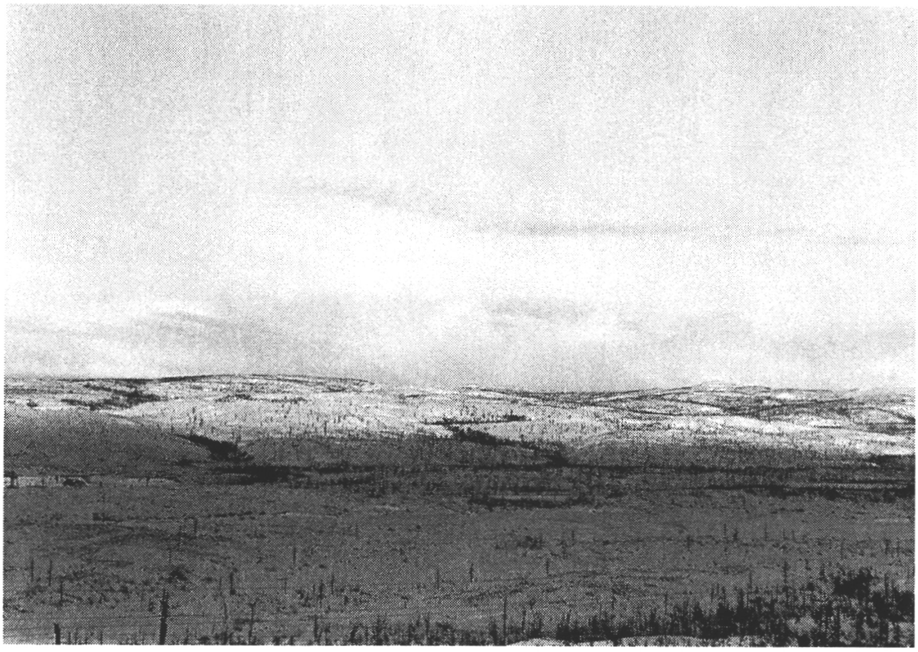

Figure 29. The valley, 3 km to the south from the nickel plant in Nikel. Originally there were timberline pine forests and fell birch forests. Photo: Pertti Veijola 1995.

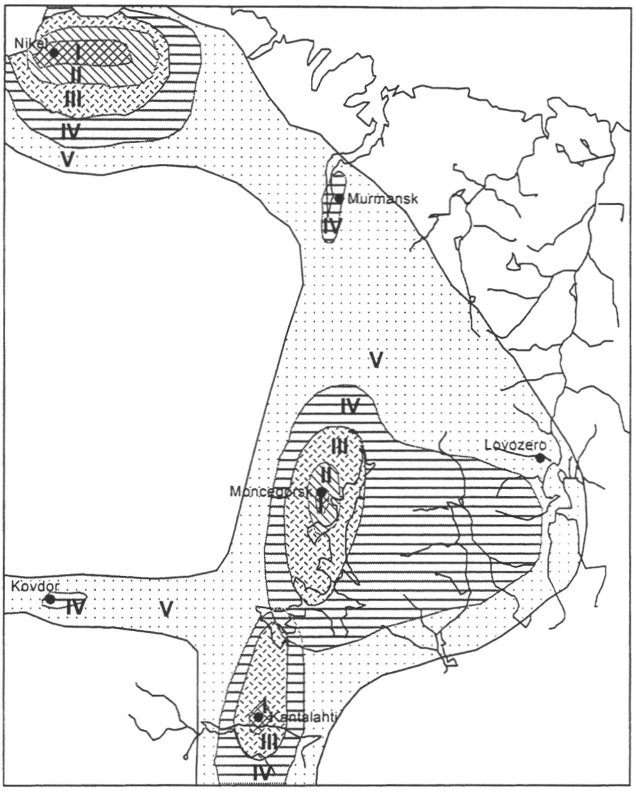

Figure 30. Zones of ecosystem degradation on the Kola Peninsula (Kryuchkov and Makarova 1989). I. Industrial desert, II. Industrial-technogenic forest tundra with dwarf birch, III. Fairly distinctly damaged ecosystem around industrial sites, IV. First stage of degradation, V. Earliest signs of degradation observable.

According to the conclusions of the Lapland Forest Damage Project, the outer visible-damage zone extends to northeastern Inari. In Finland, the inner non-visible-damage zone comprises northern Salla and eastern Inari and the outer non-visible-damage zone the entire eastern Lapland, Inari and Utsjoki. Within the impact zones, ecological changes and increased concentrations occur (Tikkanen 1995). Kryuchkov (1984) stressed that destruction of the vegetation by air pollution in permafrost areas inevitably leads to formation of thermokarst. At alpine timberlines and in mountain forests the fallout of pollution is greater than in equivalent conditions at lower altitudes (Grace 1989).

4.7 Combined effects and general theories explaining the timberline

4.7.1 General

In the foregoing, numerous factors affecting the timberline were examined. The combined effects of these factors and the possible general theories for explaining the timberline based on them may be analyzed in various ways. Stevens and Fox (1991) separated the stature-related hypothesis and the growth-related hypothesis from the materials of the traditional examination and presented a new hypothesis based on the size of the trees. The stature-related hypothesis is based on the fact that an arborescent plant cannot avoid the adverse effects of an austere climate in the same way as do lower plants, which take advantage of their position close to the ground surface. The growth-related hypothesis starts from the assumption that the non-assimilating mass increases with tree growth, and in difficult growth conditions at some point this relation becomes a critical factor. This theory includes the carbon balance hypothesis. The hypothesis based on the size of the trees starts from the idea that in timberline conditions the size of the tree becomes a limiting factor, whereas smaller plants are better able to make use of the microvariations of the site. E.g. the distance between stem and roots forms a risk factor and a burden as concerns the physiological processes of a tree.

Ellenberg (1986) considered the causes of the timberline to depend on an interaction between favourable growth conditions in summer and the drought caused by frost in winter. According to Wardle (1993) the entity of complex causes of the alpine timberlines is based on the view that the length of the growing season and the temperature at crown height determine whether the shoots can grow normally and become hardened against winter. In various conditions, numerous additional factors affect this starting point. According to Tuhkanen (1993b) the causes of timberlines have been studied extensively from the viewpoint of plant physiology, and on the basis of these studies two basic causes may be found. These are a negative carbon balance and the developmental phases of the plant, i.e. completion of annual growth and regeneration, which are related to poor climatic resistance in winter conditions. Tranquillini (1979) was of the opinion that the factors decisive to the existence of trees at alpine timberlines outside the tropics are the following: the carbon balance, a prevented cycle of annual growth or long-term development, and insufficient resistance to damage. He added that the above factors are interrelated, their combined effect ascertaining that the trees above a certain altitudinal limit cannot endure the stress of frost drought.

Taken as a whole, it is possible to distinguish from the general explanations and combined effects of the timberline the following interrelated factors, which may, however, be examined as separate phenomena: carbon balance, frost drought, regeneration, climatic hazard, and the theory of relative and absolute forestlessness.

4.7.2. Carbon balance

Tree growth decreases with increasing altitude or northern latitude due to the shorter growing season and lower temperature. The capacity of the trees for photosynthesis and carbon gain decrease since the time shortens during which the temperature of air and leaves is sufficiently high to sustain a level of photosynthesis that can replace the annual loss due to respiration. On the basis of productivity data concerning birch growing in plains and fell birch, Boysen Jensen (1949) concluded that the timberline might represent the altitude where the annual carbon balance no longer permits the arborescent growth. Besides the carbon balance, however, he considered the capacity for regeneration and for survival during unfavourable seasons and weather periods as general limiting factors.

At the point where assimilation becomes insufficient to keep up the treelike form, the site is invaded by species that are smaller in relation to the surface area of the leaves, and whose 'fixed costs' of respiration are thus lower (Larsen 1974). However, Wardle (1993) found that although some results show a barely sufficient carbon balance at the timberline, many studies show it to be distinctly positive, and so the alpine timberlines cannot be considered as the general altitudinal limit of the positive carbon balance in the trees. Tranquillini (1979) was also of the opinion that although fairly few studies have been made, it may be reliably concluded that the insufficient production of dry matter is not the reason of the alpine timberline. However, he added that the decrease of dry matter production has various unfavourable consequences, e.g. for the uptake, storage and transport of water and nutrients, and for the seed production.

Arno (1984) mentioned that most of the researchers dealing with the photosynthesis of timberline trees stress the importance of other minimum factors than the carbon balance in controlling the timberline. Holtmeier (1974) was of the opinion that although the limit of a negative carbon balance may be explained theoretically, it is hardly ever reached in nature. In their general review of the plant physiology of cold areas, Körner and Larcher (1988) concluded that the importance of the carbon balance to the physiology of plants is generally overestimated. They pointed out, however, that trees are in many respects different from other plants. Bonan and Sirois (1992) found that the carbon balance, which is mainly controlled by the temperature, does not explain the northern limit of *Picea mariana* in Canada.

In his study of anthesis, Sarvas (1970a) examined the adaptation of pine. The northernmost site in this material was located in Utsjoki, at the timberline, where the temperature sum was 605 d.d. According to Sarvas, the presence of the northern forests does not necessary require adaptation to the length of the growing season, but there is an absolute limit, which nor the forest nor other vegetation can cross: the limit beyond which the 'nutritive balance' is negative for several years. He continues that the temperature sum hardly offers any help in describing this limit, and that assimilation and growth depend in an essentially different way on the temperature than does the yearly period. Sarvas (1970b) considered the northern timberline expressly as a "starvation boundary", the position of which is hardly crucially affected by the capability of the forest to regenerate.

According to Norokorpi (1982, 1994) the pine timberline in Northern Lapland is located where the annual mean temperature sum is 600 d.d., and the tree line approximately at 550 d.d. Further he mentioned that the austerity of the climate shows itself especially as cooler than average summers, during which 'the energy balance of the trees may remain negative', the condition of the trees weakens and they are exposed to various types of damage. Norokorpi (1994) emphasized that the temperature conditions form the minimum factor, controlling the assimilation process of the trees and when the amount of assimilation products is insufficient to sustain the physiological processes of the trees, the closed forest ends and only the most resistant individuals may survive to the tree line.

In their explanation of the tree lines in Scandinavia, Kullman and Hofgaard (1987) found them to be controlled basically by variations on a theme, i.e. insufficient temperature/insufficient duration of the growing season. Above the tree line the temperature sum is too low for the net photosynthesis to compensate for the phytomass losses caused by the physiological and mechanical winter damage. Dahl (1983) presented the respiration hypothesis, which is linked to the carbon balance, and implies that the production of ATP, which is connected to dark respiration, is markedly dependent on temperature and constitutes the minimum factor at the timberline. On the basis of an extensive literature analysis, Skre (1991) concluded that in cold areas dark respiration is a limiting factor to tree growth. This view is supported by the existence of an alternative mode of respiration, independent of the ATP production.

It has not been possible to prove experimentally that the carbon balance is a crucial factor for explaining the timberline in general. In Scandinavia, however, the timberline is considered to be a "starvation boundary", caused by a negative carbon balance and related factors, and having the temperature sum as its best parameter. Although the temperature sum curve of 600 d.d. in Finland is located in the vicinity of the northern pine timberline, the actual meaning of this correlation remains to be discussed, since on the other hand it is known that anthropogenic factors of significance affect the pine timberline. In addition, some results of pine plantation north of the timberline (e.g. Sirén 1993b) and the minimum temperature sums presented by Nikolov and Helmisaari (1992) and by Malyshev (1993) indicate that the temperature sum values mentioned earlier should be considered only as approximate values for the "starvation boundary". Russian studies, e.g. those by Kryuchkov (1957) and Puzachenko (1985) indicate that besides temperature, the effect of the air humidity should also be taken into account.

4.7.3 Frost drought

Frost drought or winter desiccation, in German: Frosttrockniskomplex, is traditionally considered one of the central causes of the forming of the alpine timberline. Holtmeier (1974) defined frost drought as the combine effect of wind, radiation, transpiration, respiration and evaporation in a situation where the water-conducting tissues are frozen. He considered frost drought as an important growth-limiting factor both at the alpine and the northern timberline. According to Tranquillini (1979) the most common type of damage in the timberline ecotone is the slow desiccation of shoots of conifers extending above the snow. This phenomenon he considered as the key factor in the formation of the alpine timberline (Figure 31). Larcher (1985) emphasized the complexity of winter stress affecting the alpine timberlines, including the significance of strong UV and other radiation, and increased ozone concentration. Hadley and Smith (1986) found that in the Rocky Mountains, USA, the needle mortality of *Picea engelmannii* was primarily due to winter wind and cuticle abrasion. Inadequate needle maturation during summer contributed to the drought. In his examination of the mechanism of frost drought, Grace (1989) found that the water regime of the needle is more affected by the microstructure of the cuticula than by its thickness. He considered the damage of stomata and consequtive incomplete closure of them to be important causes of frost drought. According to the opinion of Wardle (1993) one of the most evident phenomena at northern timberlines is the change of colour and drying of needles and shoots; 'the most widely accepted explanation of timberline is that growing seasons are too short and too cool for shoots to fully develop and harden against winter conditions'. He considered the effects of frost drought in the European Alps especially evident concerning *Pinus cembra.* Sakai and

Larcher (1987) distinguished between chronical and acute frost drought. Chronical frost drought is typical of boreal conifers due to gradual water loss by cuticular and peridermial transpiration after 2-3 months of soil frost, despite of closed stomata. Acute frost drought arises from a breakdown of the water balance within a few days. Many plant species of warm-temperature areas are susceptible to this phenomenon, as they open their stomata during sunny weather and dry rapidly if the ground is frozen.

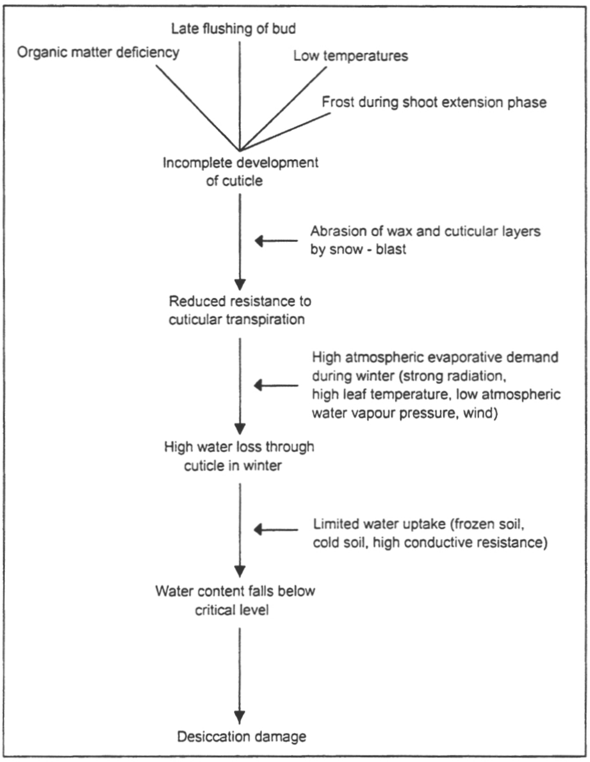

Figure 31. Factors affecting winter frost drought in shoots at the alpine timmberline (Tranquillini 1979).

Frost drought has not been ascribed as much significance as a cause of timberlines in Scandinavia as at alpine timberlines. This phenomenon has been known for a long time (Kihlman 1890), but it has been considered a type of damage mainly related to exceptionally cold years. According to Kallio et al. (1971), extreme cold in winter is not a limiting factor to pine, but extreme cold after too short a summer may cause disaster. Such a disaster occurred in 1902, extending over a vast area as far as northern Sweden and northern Norway (Andersson 1905, Venn 1970). Similar damage occurred in Northern Lapland as a consequence of the cold summer of 1968. Holtmeier (1971) studied the damage of 1968 on the spot and found it to be clearly caused by frost drought. The damage was most pronounced in the area of planted pine forest in the Utsjoki river valley, extending, however, into Inari as well. In the planted pine forests of the timberline regions in Inari and Utsjoki, frost drought was observed in the summer of 1995 following a long, sunny spring. No damage was found in the natural seedling stands of the same region, and the difference may be due to the more southern origin of the planted pine forests. Venn (1970) mentioned three known, extensive occurrences of significant frost drought in Fennoscandia during the years 1875, 1903 (1902) and 1963. In northern Norway, several additional damages of lesser extent have been observed, including that of 1969 (1968). At the pine timberline in Finland, frost drought is observable regularly.

Kullman and Högberg (1989) described a frost drought damage that occurred in the pine and spruce forests of the southern Scandes in 1987, caused by the thin snow cover and extreme cold during the winter. In their opinion the significance of frost drought damages in the ecology of timberline forests is frequently overestimated. In Sweden, Christersson and von Fricks (1990) have carried out laboratory studies of frost drought and hardening against winter. Clear differences in susceptibility to frost drought were found to exist between tree species, and *Picea mariana* was the most sensitive one of those compared. It was followed by *Picea abies* and *Pinus silvestris*, whereas *Pinus contorta* turned out to be the most resistant species. Kryuchkov (1975,1978,1987) considered frost drought, which is mainly controlled by the strength of the wind, to be the most important factor contributing to the formation of stunted tree forms and the area of relative forestlessness. He also emphasized the differences between tree species in sensitivity to frost drought.

Frost drought proper should be distinguished from the 'red belt' phenomenon, which is caused by pronounced temperature inversion and rapid temperature variations. The damage is generally local, occurring in a belt-like area and limited to a certain altitude level (Jalkanen and Närhi 1993). This phenomenon occurs regularly e.g. in the Rocky Mountains of Canada, where *Pinus contorta* is the most susceptible tree species (Sakai and Larcher 1987) (Figure 32 Appendix 1).

4.7.4 Reproduction

The reproduction process of the trees has a crucial influence on the tree species proportions and structure of the forest. The dynamics of regeneration varies according to the conditions prevailing in the forest ecosystem. The timberline forests represent an extreme, in which the reproduction is limited by many factors besides temperature. A fairly regular opportunity of generative reproduction controls the location of the rational timberline. At the climatic timberline a dynamic balance exists between advance and retreat of the forest. Although the timberline trees may be very long-lived, the timberline is basically always a result of the prevention of tree reproduction (Tranquillini 1979). Trees that produce germinating seeds are generally present closer to the alpine timberline than to the northern timberline. This may be the reason why more attention has been paid to the regeneration of trees in the study of the northern timberline in Fennoscandia, Russia and North America than in the study of alpine timberlines.

The regeneration of a forest from seed or the invasion of a new treeless site consists of a series of interconnected stages, which are controlled by various climatic factors. The generative reproduction of trees may be considered to comprise the following stages (Zasada et al. 1992): formation of flower primordia; flowering and pollination; seed maturation; quality and quantity of seed crop; seed distribution; seed stock on the ground; germination; and restocking with young growth. The timberline conditions naturally affect all stages of the generative reproduction, although the stages most crucial to the regeneration are seed crop and seed maturation, as well as distribution, germination and restocking. The reproduction must be examined species by species, since different factors may determine its success.

Seed crop and seed maturation. At the timberline, the seed crop and seed maturation vary greatly according to tree species. In nearly all tree species the development here differs from that of more normal conditions.

The process of generative reproduction in pine lasts for three growing seasons and is susceptible to disturbances caused by the strongly fluctuating climate. The seed crop of pine depends on the conditions of the flowering year and the previous year. The number of flower primordia formed during the year previous to flowering is considered to be favourably affected by a warm growing season. If the pollination is poor during the flowering year, most of the ovules do not develop into seeds and the conelet falls from the tree. The decisive stage, however, is the maturation of the seed. Renvall (1912a) showed that germinating seed is obtained only once in a century, on an average, in the timberline regions of Finland. Renvall's views, based on this result, influenced the discussions concerning the regeneration of timberline forests up to the 1980's. In Norway Hagem (1917) arrived at a similar view, showing that the maturation of the seed of pine requires a mean summer temperature of +10.5°C. Among the earlier studies regarding the seed years of pine, the works of Lakari (1915), Aaltonen (1919) and Lassila (1920) are also worth mentioning, although they do not specifically deal with the timberline. Hustich (1948) found that contrary to the views of Renvall and Hagem, germinating seeds had been formed to some extent at the timberlines of Utsjoki during several years early this century.

Sarvas (1962) found that the seed of pine matures fully in the area where the temperature sum is 950 d.d., while the degree of maturation decreases gradually north of this limit. According to Numminen (1989), fairly large quantities of insufficiently matured seeds, which germinate in favourable conditions, are formed at the timberline if the temperature sum exceeds 600 d.d., and the limit of total lack of germinability is not reached until at about 500 d.d. The degree of maturation varies from tree to tree and in various parts of the crown. Henttonen et al. (1986) found that a temperature sum of 890 d.d. is required for 50 % of the seed crop to germinate, and that the probability for this to happen in the vicinity of the timberline is 0.02-0.03. According to Koskesharju (1991) a distinctly lower temperature sum than that suggested by Henttonen et al. is sufficient for 50 % anatomic germination of the seeds. At the pine timberline in the Muotkatunturi fell area of Inari, Finland, Sirén (1993a) found that a cone year will also be a seed year in case the temperature sum exceeds 800 d.d. during three consecutive years. He also showed that at least 5 satisfactory seed years have occurred in this area during this century. Swedish (e.g. Ebeling 1979) and Russian (e.g. Beletski 1968) studies of the seed crops of pine in the timberline regions have also shown that the probability of obtaining germinating pine seed decreases with decreasing temperature towards the north and higher altitudes.

In the timberline regions of Finland, the seed crops of spruce have been studied much less than those of pine. According to Numminen (1989), good seed crops of spruce are distinctly rarer in northern Finland than in southern Finland, and the maturation of seeds from spruce and pine is controlled by the same factors. Nekrasova (1955) studied the regeneration of spruce in the Kola Peninsula, concluding that regeneration by seed is much poorer there than farther south and that the significance of vegetative regeneration is therefore correspondingly greater. Norin (1958b) presented a summary of the findings concerning the seed crops of spruce, clearly showing a decrease in both quality and quantity towards the north.

In Canada, Elliott (1979) has studied the regeneration of *Picea glauca*, *Picea mariana* and *Larix laricina* in the timberline region west of Hudson Bay. He arrived at the conclusion that the timberline stands of the study area are relicts from a warmer time, since regeneration by seed was not observed. In the forest tundra the germinability of all tree species was zero, and no seeds of conifers were found on the ground. All tree species were also found to form layers. Payette and Filion (1984) found that *Picea glauca* had regenerated successfully by seed at least three times during the last century in the timberline region east of Hudson Bay. Black and Bliss (1980) found that the seed production and germination of *Picea mariana* is limited due to the low temperature of the growing season in an about 40 km wide belt south of the timberline in the Mackenzie river valley.

According to Numminen (1989) the seed of the local races of birch and aspen matures almost every year in the zone of pine forests. In the fell birch zone, however, their seed may remain immature during a cold summer, and the aspens of Northern Lapland flower rarely. Kallio and Mäkinen (1978) observed that the seed production of fell birch varies greatly, and that the seed crop may be abundant during warm growing seasons. According to Nikolov and Helmisaari (1992), *Betula pubescens* produces seed every year and young trees produce abundant shoots. Norin (1958b) found that in the Yamal Peninsula, *Betula pubescens* does not produce germinating seed every year although this is the case farther south. According to Kullman (1979), fell birch in the southern Scandes has commonly regenerated by seed in the 20th century and the timberline has risen. In the timberline forests of the Kola Peninsula, Kihlman (1890) did not find regeneration by seed of birch. In Petsamo, Kontuniemi (1932) observed abundant birch seedlings of the same summer but very insufficient for the seedlings to root into the mineral soil during the growing season and so they die.

According to Norin (1958b), distinct differences in seed production exist between various species of larch. E.g., *Larix gmelini* has the shortest interval between seed years and and *Larix Sukaczewii* the longest. Chertovskoi et al. (1987) compiled an extensive material concerning the regeneration of various larch species, especially of *Larix gmelini* in its vast distribution area. The quality and quantity of the seed crop vary greatly with the conditions. Generally the seed crop is poorer towards the north and towards higher altitudes. A good cone crop does not nearly always guarantee a good seed crop, and e.g. seed damage may weaken the crop crucially. Inventories of undergrowhts show that the natural regeneration of *Larix gmelini* is satisfactory even in the northern parts of the forest tundra.

<u>Dispersal of seed</u>. The primary distribution of the seeds of timberline trees does not differ from the typical pattern of the tree species. The secondary dispersal, however, is affected by the timberline conditions. After coming loose from a cone, a seed may travel long distances with the wind, on the snow surface, with the water, or carried by man or animals (e.g. Tikhomirov 1962). The dispersal is affected by the time of seed shedding. As an example of the effect of the prevailing wind direction, Arno (1984) mentioned the east side of Hudson Bay, where the prevailing winds blow from the tundra towards the taiga, preventing the secondary dispersal of seed to the tundra. Andreyev (1954) related a similar example, regarding the dispersal of seed of *Picea obovata* in the vicinity of the Petsora river, where either calm or northeastern winds prevail during the seed shedding of spruce. In his opinion it cannot be assumed that major amounts of germinating seeds would be transported to the tundra. Andreyev emphasized the importance of isolated forest islands and 'nests', since they may occasionally produce germinating seed (cf. Sirén 1993a, 1994). According to the view of Renvall (1919), thinned-out stands at the timberline are of no significance to the

regeneration of pine. Forest islands in the tundra are frequently considered to have their origin in seeds carried by man or by animals. Birch seed is easily spread along the snow surface and during the melting stage (Kullman 1979).

Germination and restocking. The properties of the substrate are of crucial importance to the germination and restocking with seedlings. At the timberlines a soil with a minimum of competing vegetation is frequently available (e.g. Arno 1984). The low temperature of the soil is always an adverse factor, and so even minor factors with an adverse effect on the temperature may be crucial. Due to the cold soil, delayed germination is common (Renvall 1912 a, Tsvetkov and Semyonov 1985, Sirén 1993a, etc.). Besides the low temperature, competing vegetation and soil properties frequently contribute to the poor germination conditions. In Russia the effect of the ground vegetation has been studied and frequently a cover of mosses or lichens was found to prevent natural regeneration (Tikhomirov 1962, Chertovskoi et al. 1987).

In northern Sweden, Zackrisson et al. (1995) found that during a warming climatic stage the regeneration of pine in nonpyrogenic forests occurs with a delay of 20-30 years. This time period is required for the ground vegetation to change from *Empetrum hermaphroditum*, which provides poor conditions for restocking, to *Vaccinium spp.* and *Cladina spp.*, which favour restocking. Tikhomirov (1962) found the ground vegetation to have a positive effect on the seedlings. According to him *Betula nana* and other shrubs, by their protective effect, create the necessary conditions for the forest to advance to the tundra. Shiyatov (1967) found that the critical stages of *Larix sibirica* seedlings are the limit of the dwarf shrub layer and the limit of the snow cover. In Petsamo, Kontuniemi (1932) found that regeneration of birch by seed in untouched areas is successful only on lichen heaths. In other types the moss cover prevents the restocking.

In Sweden Kullman (1984) has studied the change in germinability of fell birch with altitude in the southern Scandes along lines extending to the tree line. In general the germinability decreased with increasing altitude. In Kevo, Northern Finland, Holtmeier (1974) has observed the favourable effect on the restocking of pine achieved by removing the ground vegetation. According to Kallio and Mäkinen (1978) the poor restocking of fell birch is caused besides by the competition of the ground vegetation, also by herbivores and birch rust (*Melampsoridium betulinum)*. During the peak years of voles, birch seedlings are eaten by *Clehtrionomys glareolus*, *C. rufocanus* and *C. rutilus*. Practical experience and results of forest cultivation experiments indicate that removal of competing ground vegetation and especially prescribed burning promote restocking with young growth (Chertovskoi et al. 1987).

In the forest tundra of northern Inari, Finland, Sirén (1993a) has found that the germination and restocking of of pine seed is possible on both sides of the timberline. Sirén (1993b) arrived at the conclusion that restocking of pine at the timberline is prevented by abundant birch-leaf litter, abundant occurrence of alleopathic *Melampyrum*, and a dense cover of dwarf shrubs and mosses. On the other hand, regeneration of pine is favoured by *Oporinia* damage to birch, forest fire, and removal of birch. According to Brown and Mikola (1974), a compound that disturbs the growth of the mycorrhizas of conifers is leached into the soil especially from *Cladonia alpestris* (L.). Kallio et al. (1983) concluded that lichens may have an alleopathic effect on fell birch as well. According to Scott et al. (1987), a dense, well-insulating lichen growth in the forest tundra has an adverse effect on the temperature conditions of the ground surface and thereby also on the restocking.

Vegetative reproduction. In timberline conditions, as generative reproduction becomes more difficult, the significance of vegetative reproduction becomes emphasized, and may for some tree species be more effective than generative reproduction. At the timberline vegetative regeneration is of importance to *Betula pubescens* (Norin 1958b, Kallio and Mäkinen 1978, Treter 1984, Nikolov and Helmisaari 1992), to *Picea obovata* (Kihlman 1890, Nekrasova 1955, Norin 1958), *Picea mariana* and *Picea glauca* Elliott 1979, Black and Bliss 1980, Larsen 1989) and *Picea engelmannii*, *Abies lasiocarpa* and *Abies balsamea* (Holtmeier 1993). Vegetative reproduction occurs in various species of *Larix*, but it is of lesser importance (Norin 1958b, Elliott 1979, Chertovskoi et al. 1987, Holtmeier 1993).

From the timberline ecotone of fell birch in Scandinavia Treter (1984) has described physiognomic types that differ as to stand structure. The formation of these types is a result of various factors, including snow conditions and the effect of grazing reindeer. Norin (1958b) described how on the Yamal Peninsula different forms of fell birch grow due to the influence of various environmental factors. In favourable growth conditions, such as in valleys on rich soil, a monocormic tree is formed, the development of which is affected by a thick, protective snow cover and the shading of other vegetation. In the most unfavourable growth conditions a shrub is formed, and the intermediate case is represented by a form in which an initial stage of slow growth is followed by rapid growth in only one of the shoots. According to Kryuchkov (1978, 1993), the stem form of fell birch on the Kola Peninsula varies mainly due to the effect of the wind. In the above examples, the possible effect of genetic factors has not been taken into account.

Kallio et al. (1983) again stressed the significance of genetic factors, such as hybridization, to the generation of various growth forms of birch. According to Kallio et al. (1983) and Valanne and Sulkinoja (1991) the central mechanism in the evolution of birch in northern Fennoscandia is introgressive hybridization. Larsen (1989) found that introgressive hybridization occurs between *Picea glauca* and *Picea mariana* at the arctic timberline of Canada. The most important components in the evolution of fell birch are *Betula pubescens* and *Betula nana*. The capability of a tree species to change growth form facilitates its adaptation to extreme conditions. The carpet-formed birch *Betula crepanovii* var. *appressa* at Kiilopää, Northern Finland, is a good example of this capability (Kallio et al. 1983). According to Kallio and Mäkinen (1978) both the monocormic and the polycormic fell birch are adaptations to timberline conditions. The monocormic form is more common in oceanic areas and cultivation experiments also indicate genetic differences between these forms. Monocormic fell birches grow root-collar shoots more rarely than do polycormic trees (Kallio et al. 1983). Oksanen et al. (1995) stress the effect of reindeer grazing on the generation of different forms of birch.

Significance of reproduction as an explanation of timberlines. A difference in views exists as regards the importance of the reproduction as a whole to the formation of the timberline. As early as in 1890 Kihlman arrived at the conclusion that the generative limit of spruce is in principle the limit of the distribution area of conifers. Hein (1932) considered the conclusion of Renvall (1912a) regarding the rarely occurring seed years as a valid explanation of timberlines in Finland. Tikhomirov (1962) considered the lack of regeneration by seed as one of the basic causes of the treelessness of the tundra although he emphasized the importance of taking all effective factors into account. According to Sarvas (1970b) again, the capacity for regeneration of the forest is hardly very crucial to the location of the northern timberline, although this capacity is poor at the timberline. In the opinion of Sarvas, even one favourable year in a century would be sufficient for regeneration.

According to Payette (1983), in northern Quebec-Labrador, the occurrence of various tree species in the direction of the latitudinal gradient seems to be a direct consequence of the regenerative properties of the tree species. The correspondence between the growth and reproduction of the trees is notable. Seedlings are always present where *Picea mariana, Picea glauca* and *Larix laricina* normally form arborescent growth, whereas seedlings are decidedly fewer in the 'Krummholz' region. This 'Krummholz' zone is a relic of a period of more favourable climate, when generative reproduction was successful. The present-day timberline and tree line are in balance with the present climate and the tree species have reached their limit of natural regeneration by seed.

Sirois (1992) concluded that in the Canadian forest tundra a general explanation of the timberline would possibly be found in the joint effect of forest fires and poor regeneration by seed. He found that in the Canadian forest tundra, knowledge of the reproductive biology of the trees is one of the keys to the timberline ecology. In summary of the vegetation zones of the North American timberline regions, Payette

(1992) suggested that the closed boreal forest as well as the open lichen woodland regenerate actively in connection with repeated fires. However, intensive fires occurring with long intervals cause thinning of the northern forests. The forest tundra again seems to be a relic of forest earlier capable of regeneration, which is now, due to fires, developing towards open land.

Elliott-Fisk (1983) arrived at the conclusion that differences exist between the various parts of the North-American continent. In eastern Canada the timberline is in balance with the present climate and the tree populations are capable of both generative and vegetative regeneration. In central and western Canada the timberline is not in balance with the present climate, and so generative regeneration does not occur. A timberline in imbalance is sensitive to possible cooling of the climate and to anthropogenic influence.

These Canadian studies show points in common with the situation at the Fennoscandian timberlines in the early 20th century, when fires and poor regeneration by seed were crucial factors. At present, however, regeneration occurs and the timberlines are in balance with the climate. In the southern Scandes Kullman (1987) has found that in the lower part of the subalpine timberline ecotone pine regenerates more regularly, even during unfavourable climatic phases, than at the timberline. The long life of the pine and the young growth forming in an open forest cause inertia and delay in relation to a possible cooling of the climate. Regarding its fire history, this altitudinal zone differs from the forests of lower altitudes by being a kind of fire refuge. In order to examine the results of the generative reproduction of timberline forests and make the correct conclusions one has to define the study area with sufficient exactness. Great differences may exist between the timberline proper and the forests immediately south of it and below it (cf. Renvall 1912a). In order to obtain the correct overall picture one must examine the significance of regeneration as an explanation of timberlines together with the questions related to forest fires and climatic fluctuations (Figure 33).

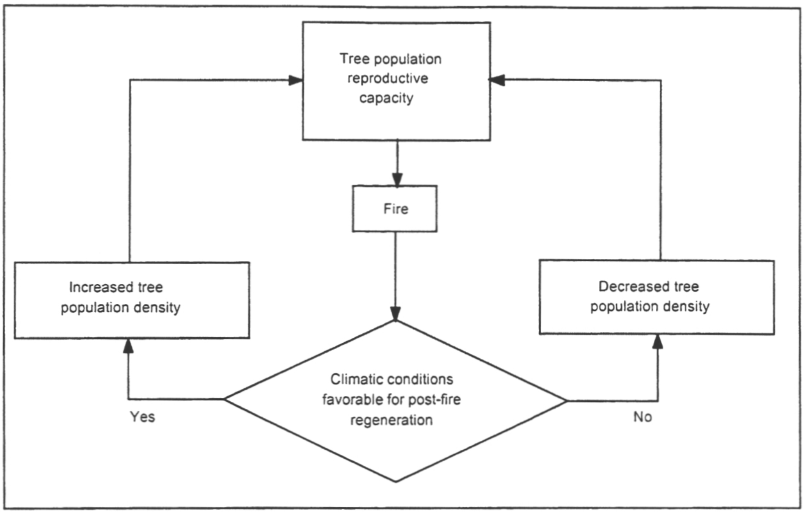

Figure 33. Estimated combined effect of fire and climate in the timberline forests of Canada (Sirois 1992). When other environmental factors are unchanged, the capacity for post-fire regeneration is related to the density of the stand before the fire. Repeated fires during climatic phases that allow effective regeneration maintain a forest structure with closed crown coverage. This situation prevails in the boreal zone. Repeated fires lead to the formation of open forest and open patches if the climate limits seed production and restocking with young growth. The soil conditions for post-fire restocking vary consiredably even within small areas. Thus the success of restocking is variable, as is the effect of fire on the density of subarctic forests at the landscape level.

4.7.5 Climatic hazard

All plant species have their characteristic tolerances of climatic factors, the central of which are temperature, precipitation amount and wind force. If these tolerances are exceeded, it leads rapidly to a disastrous situation, in which the reaction of the population, frequently devastation, differs entirely from that within the tolerances (Woodward 1987). The climatic hazard is closely connected to climatic fluctuations and timberline dynamics. As early as in the late 1940's Hustich (1948) in his timberline studies emphasized the significance of climatic hazard, which he describes by the term 'climatic hazard coefficient'. According to temperature statistics this coefficient increases northward in Finland, and the same is true for the grain crops and the increment of trees. According to Hustich (1978), the anthropogenic effect has been added to this combination of climate and natural environment during the last few decades. These three factors form an ecological triangle, in which the factors interact. Hustich stressed that the effect of the climate is often overemphasized, i.e., the variation of the crop or increment is relatively greater than the variation in climate. The climatic effect frequently occurs in the form of a 'lag effect'. Hustich divided the short-term variation into annual variation, which may be described by using a variation coefficient, and cyclic variation.

The concept of 'climatic hazard coefficient' has achieved wide recognition, and on its basis e.g. the examination of causes for climatic fluctuation has been developed (Pohtila 1980, 1993, etc.). The mechanisms whereby organisms adapt to northern conditions, where the variation coefficient is high, have been studied under Kallio's supervision at the Kevo research station (e.g., Kallio 1982, 1978, 1995). Mikola (1952, 1971, 1978) has examined the influence of climatic fluctuation on the forestry of the northern regions. In Sweden Kullman and Hofgaard (1987) have suggested a limit, 'klimatisk hasardgräns', in order to safeguard forest regeneration in the vicinity of the fell region. This limit, which is located 180-200 m below the tree lines of pine and spruce, is based on views similar to those of Hustich.

Seppälä and Rastas (1980) developed the hazard theory further in connection with the mapping of the vegetation of Northern Lapland. They concluded that in this area the timberline is significantly affected, besides by the long-term climatic fluctuation, also by short-term 'natural hazards', which are related to the weather and may influence the general picture of the vegetation for centuries. These hazard factors may be divided into climatic and biotic factors, the latter ones best exemplified by *Oporinia*. The timberlines may be explained by climatic parameters, but really critical factors cannot be described by mean values and they are difficult to recognize afterwards, although their effects are visible in the vegetation for a long time. Kullman (1989a, 1989b) also considered the short-term weather minima and maxima to be important at the pine and spruce timberlines in the Scandes. The perhaps most significant known hazard-type event in Fennoscandia is the extensive frost drought damage of 1902, which according to Mikola (1952) stopped the height growth at the timberline for about a decade.

Climatic hazard may not actually be considered an independent general theory explaining the causes of the timberline, because it is connected to frost drought and biotic factors as well as to climatic changes and their consequences. The hazard theory stresses the suddenness and unpredictability of the events. It is a useful approach, emphasizing safety and preparation for risks, to matters concerning the northern nature in areas where especially the variation coefficient of climatic factors is high.

4.7.6 Relative and absolute treelessness

Kryuchkov (1957, 1967, 1975, 1978, 1987, 1993), who has studied the timberlines in Russia extensively and for a long time, has presented a general theory explaining the circumpolar timberline by the concepts relative and absolute treelessness (Figure 34). This theory, which is little known in the western countries, is in Russia considered generally tenable (e.g., Kazakov 1995). The area between the tree line and the typical tundra is the zone of relative treelessness, which has many causes. This zone may be considered potential forest tundra. One group of causes comprises soil-related properties: paludification, rockiness and stoniness, and poor access to nutrients. In temperature-minima conditions the effect of the wind, contributing to frost drought, is crucial especially in winter. Especially in oceanic areas frost drought during periods of mild weather is disastrous to conifers, and a cause of dwarf forms of the trees. In addition there is the varied, long-time anthropogenic influence. The forest may be returned by afforestation to sheltered spots in the zone of relative treelessness. In the zone of absolute treelessness again the reason for the lack of trees is the low temperature, insufficient for maintaining their physiological processes.

Kryuchkov (1987) estimated that the circumpolar zone of relative treelessness is about one million square kilometres in extent. In Kola the area of the zone is approximately 40 000 km^2 (Figure 36). The circumpolar area of relative treelessness is distributed as follows:

	1000 km^2
Russia	450
Scandinavia	10-12
Greenland	2-3
Alaska	50
Canada	300-500
Mountain regions	40-60

Regarding alpine timberlines, Wardle (1981) made the conclusion that reproduction and biological factors affect the timberline structure and the way in which recovery takes place after disturbance, but that over long time periods the final limit is set by the physiological tolerance of the arborescent life form. This conclusion also fits in with the theory of relative and absolute treelessness, as do the results of Puzachenko (1985) concerning the effect of various climatic factors on the timberline. The concepts of relative and absolute treelessness permit logical analysis of the numerous factors influencing the timberline.

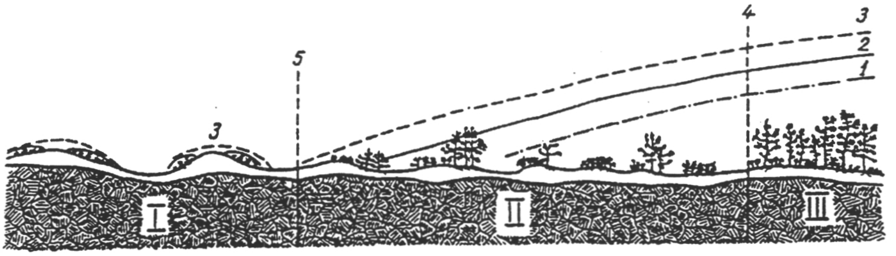

Figure 34. Relation between zones of relative and absolute treelessness in the tundra (Kryuchkov 1993). I. Zone of absolute treelessness (typical tundra). II. Zone of relative treelessness (brush tundra). III. Forest tundra. 2. Location of mean +10° C isotherm in July. 1. Location of the same isotherm during a cold summer. 3. Location of the same isotherm during a warm summer. 4. Northern limit of forest tundra. 5. Northern limit of southern tundra, mainly brush tundra.

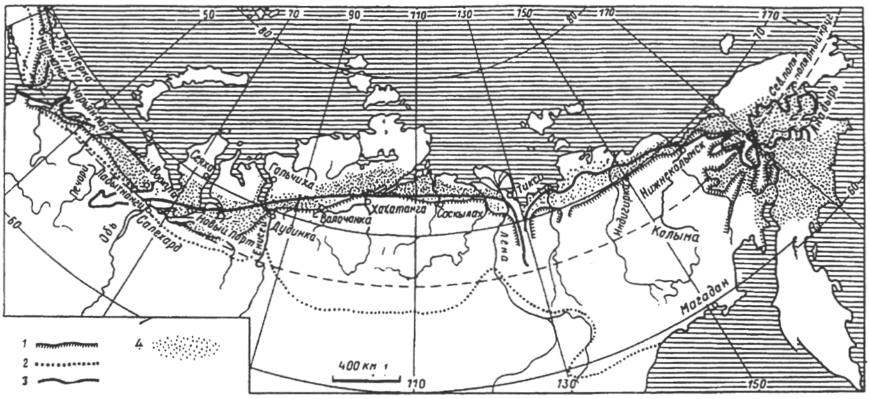

Figure 35. Zones of the timberline regions of Eurasia (Kryuchkov 1978). 1. = northern limit of forest tundra, 2. = southern limit of northern taiga, 3. = +10° C isotherm in July, 4. = zone of relative treelessness, and north of it, zone of absolute treelessness.

4.8 Conclusions

Through the ages, in various parts of the world, the timberline has been explained by various reasons, and efforts have been made to describe the determination of its location by various parameters. The development has progressed from explanation by general climatic parameters towards more accurate information based on plant physiology. In order to understand the relations between the effective causes one has to distinguish clearly between the examination of the bioclimatic reasons of timberline in extensive areas and the analysis of the regional and local causes of the timberline. The timberlines are a good example of the general determination of ecotones, where the broad-scale ecotones of the bioms are determined mainly on the basis of climatic factors, whereas the fine-scale ecotones are strongly influenced by site-specific characteristics (Gosz 1991). The timberlines may be either broad-scale or fine-scale ecotones, depending on the scale of examination.

The temperature is quite commonly considered as the crucial basic factor, but differing views exist as to its more detailed active mechanism. It seems that the parameters describing the maximum temperatures of the growing season (Enquist 1933, Mork 1970, Kryuchkov 1978) explain the timberline better than do the mean temperature parameters of the growing season (cf. Haapasaari 1988). Especially the Russian scientists also stress the effect of the continentality vs. oceanity of the climate as a general factor influencing the location of the timberline. Puzachenko (1985) expressed the opinion that in some area one climatic factor may be crucial whereas in some other area the sum of several climatic factors determine the location of the timberline. The smaller the area taken as object for the detailed analysis, the greater the number of factors to be taken into account.

Finnish scientists specialized in forestry have arrived at the view that the location of the conifer timberline may be considered as best described by the temperature sum. Elsewhere, however, this view has not been generally accepted. The connection between temperature sum and timberline suggested by Sarvas (1970b) has probably been interpreted further than intended by Sarvas himself. The timberlines of the southernmost fells in Finland are no vertical timberlines proper but caused by topoclimatic factors, mainly the so-called summit effect, soil factors and crown snow load. The crown snow load alone is not a sufficient explanation of these timberlines (cf. Norokorpi 1994). Elsewhere, too, the steepness and stoniness of the slopes have been found to lower the timberline.

Puzachenko (1985) brought up an interesting theory, which is supported by other Russian findings as well. According to it the change of timberline into tundra in the Eurasian western oceanic sector and in the Bering oceanic sector is best explained by the increase in the hydrothermal coefficient and in relative humidity in a northward direction. In the Central Siberian continental sector the timberline is mainly determined by the temperature factor. These findings indicate that in Fennoscandia more attention should be paid to the humidity of the climate as a factor influencing the timberline.

On the whole it seems that in the examination of the causes of timberlines one should take all effective factors into account. Lately the role of soil factors has been emphasized in addition to that of climatic factors (e.g., Bonan 1992, Sveinbjörnsson 1992, Tyrtikov 1995).

The correct estimation of the effect of anthropogenic factors requires detailed regional research work. The distinction between old anthropogenic influence and climatic variations is difficult to make. At the oceanic and northern timberlines of Fennoscandia the anthropogenic effect has been stronger than at the vertical timberlines of the inland. In Fennoscandia the anthropogenic effect has been strongest at the coasts of Troms, Finnmark and Kola, as well as in the river valleys of the interior of Enontekiö, Usjoki and northeastern Inari. The treeless heaths on the Fennoscandian coasts of the Arctic Ocean were partly formed as a result of anthropogenic activities. Many scientists also find anthropogenic influence a major cause of the formation of fell birch forests.

Regarding the general explanations of timberlines, the view prevailing in Finland is that of the timberline being a 'starvation boundary' (e.g., Sarvas 1970b, Norokorpi 1982, 1994). This view is based on conclusions, since results of empiric research are not available in Finland. Elsewhere the view is prevailing that the carbon balance is not a general explanation of timberlines (e.g., Holtmeier 1974, Tranquillini 1979, Wardle 1993). Neither has the frost drought theory, supported by Tranquillini (1979), been considered a general timberline explanation although e.g. Heikkinen et al. (1995) presented the conclusion that frost drought is a crucial cause of the formation of the tree line.

An interesting alternative explanation from the viewpoint of Fennoscandia is offered by the theory of reproduction of the trees. In both Russia and North America, the reproduction is considered an important explanation of timberlines. The most recent findings from North America emphasizes the combined effect of reproduction, forest fires and climatic variations on the structures and dynamics of the timberline (Payette 1983, 1992, Sirois 1992, etc.). In Fennoscandia the findings of Kullman (e.g., 1990) point in the same direction. Practical experience and descriptions from Finland support this explanation. The timberline ecotone should apparently be examined as a matter of population ecology of the trees.

The view presented by Kryuchkov (1978) concerning areas of relative and absolute treelessness offers a good opportunity to make a logical compilation of various effective factors. The limit of absolute treelessness is determined as a limit caused by the prevention of basic plantphysiological processes, related to temperature, and so it can be changed only by a climatic change of sufficient duration. Between the limit of absolute treelessness and the present tree line remains an area of relative treelessness, of varied width. At different spots within this area, various combinations of factors influencing the timberline occur, which for the examination of their mutual relations and significance require detailed regional studies (cf. Holtmeier 1974). The treeless part of the northern boreal zone, known from phytogeography, (Ahti et al. 1968, Haapasaari 1988) also fits in well with this concept (fig. 36 Appendix 1).

5 Timberline dynamics

5.1 General dynamics of vegetation and the timberline

The element of anthropogenic climatic change introduced into natural climatic fluctuation has aroused a great interest in timberline dynamics, since it is assumed that one can form an idea of the general trend in climate by studying changes in timberlines. The prevailing view is that the advance or retreat of the northern and alpine timberlines in the absence of anthropogenic influence is mainly due to climatic fluctuation, which must therefore be accurately reflected by the dynamics of the timberline (e.g. Grace 1989, Brubaker 1986, Woodward 1987).

According to Kullman (1993a) this idea of direct influence has recently been questioned, and Atkinson (1992) finds that many ecological mechanisms may make the timberline quite resistant to change. Slatyer and Noble (1992), for example, point out that timberlines offer many opportunities for analysing the variation caused by climatic fluctuation and disturbances, although at the same time the stabilizing effect of the forest climate, the slowing of the treeline advance and the stochastic character of the factors lowering the treeline contribute to the fact that these do not reflect global climatic changes very well. Bradshaw (1994) nevertheless expresses the opinion that the effect of climatic change on the vegetation dynamics is crucial, since possible delay and inertia in the reactions of individual species are factors that exercise an influence only for a short time or in a small area.

The notion of timberline dynamics as a whole includes the natural spread of tree species and the forest vegetation succession, the sum total of all these factors being part of the general dynamics of the vegetation. Vegetation dynamics has been analyzed in many ways. Van der Maarel (1988) distinguished between the following main forms:

- Fluctuation, denoting quantitative variations at the level of the individual plant, e.g. in the abundances of species due to ontogenic or external factors.

- Gap dynamics, denoting the deaths of individual plants and related changes, mostly qualitative, attributable to ontogenic or external factors.

- Patch dynamics, denoting the dynamics related to the disappearance of local populations or patches, involving changes of long duration.

- Cyclic succession, which differs from patch dynamics only in degree. In a plant community, for instance, it means a form of development during which the dominant species alternate cyclically. This process is also related to the regressive development of forests caused by external factors.

- Regeneration succession, denoting regeneration of a fully developed plant community changed by a disturbance. The regeneration of a forest after a fire, for instance, is included in this group.

- Secondary succession, denoting development of the vegetation in a cultural or semi-cultural environment towards a stage of maturity.

- Primary succession, denoting development of the vegetation in an area previously lacking any vegetation cover.

- Secular succession, denoting changes at the landscape level attributable to environmental factors, e.g. climatic changes. Van der Maarel considers the changes in the post-glacial forest vegetation to belong to this category.

In the classification of van der Maarel, the history of tree species distributions and changes in these caused by climatic fluctuation may be included in the concept of secular succession. They are not examined here under the heading of succession, however, but as separate concepts.

The general dynamics of vegetation may also be approached from the viewpoint of ecotone dynamics. Based on this view, Delcourt and Delcourt (1992) present a classification of vegetation dynamics into phenomena of various scales in relation to time and place as follows:

The *microscale* domain, including phenomena up to 500 years old and covering an area of up to 100 hectares, includes individual plants and isolated forest stands. The dynamics of disturbances operates on the level of patches, i.e. patch dynamics. Patches at various stages of regeneration form ecotones between adjacent plant communities.

The *mesoscale* domain, including phenomena aged 500 - 10 000 years and affecting an area of 1 - 10 000 km^2. The majority of these phenomena are included in landscape-level ecology, and the disturbances cause patch dynamics in which the ecotones develop within the landscape mosaic.

The *macroscale* domain, which comprises phenomena 10 000 to one million years old and with an areal extent of 10 000 to one million km^2, includes Quaternary studies.

The *megascale* domain comprises global phenomena on a geological time scale.

The complex landscape-level dynamics may be examined on the basis of patch dynamics by understanding the former as the total effect of the patches (see Shugart 1984). The phenomena of timberline dynamics may belong to all the domains mentioned above, although the focus of the present work is on processes in the microscale and mesoscale domains.

5.2 Methods of study

Eronen (1990), examining long-term climatic changes on a global scale and assessing at the same time the methods used to study vegetation history and climatic fluctuation, mentioned that although an abundance of exact information is available on the present climate and fluctuations in the weather, measurements have been made over quite short periods of time. Even the longest series of temperature measurements goes back only about 300 years, and information on earlier events has to be obtained by using what is called climatic proxy data, which require interpretation. Such data are available in Finland mainly for the post-glacial period (about 10 000 years). Following the ideas of Bradley, Eronen (1990) presents the following outline of proxy data on past climatic events:

1. Ice drill logs
    not possible in Finland

2. Geological sources
    a. Marine sedimentary sequences
    b. Terrestrial sequences

3. Biological sources
    a. Annual rings of trees: width, density and relations of stable isotopes - one of the most widely used methods for studying timberlines in Finland
    b. Pollen: species, relations and absolute influx figures - another method used widely in Finland

    - c. Plant macrofossils: age and distribution - closely related to studies of annual rings
    - d. Insects: species
    - e. Distribution of present populations: refugia, plant and animal relicts - regeneration and other measurements made on timberline forests may be included in this category

4. Historical sources
    - a. Written sources concerning environmental conditions - an important and frequently used method for studying timberlines
    - b. Phenological observations

According to Mayer and Ott (1991), the location of original climatic timberlines may be ascertained by the following methods: conclusions based on occurrences of relicts, comparison with other areas, use of archives, pollen analysis, soil analyses, and the analysis of plant communities, especially those dominated by dwarf shrubs. These methods have been used to study the history of timberlines in the Alps in detail, and it has become possible to distinguish between changes caused by climatic fluctuations and those caused by anthropogenic factors. Pears (1972) emphasized that in areas where anthropogenic influence on the timberline is very old, several parallel methods must be used to study climatic fluctuation and changes in the timberline in order to avoid erroneous conclusions. As an example, he mentions a case in Scotland where the lack of macrofossils in certain layers was due to anthropogenic influence. Kullman and Engelmark (1991) stressed in addition that one basic problem is that of distinguishing non-climatic migration lags from dynamic equilibrium processes in individual species in response to regional climatic patterns.

5.3 Distribution history of tree species

5.3.1 Interglacial forest succession

Constant change is one of the most important characteristics of the history of forests and of vegetation in general. The major changes over long time spans are connected with the ice ages and related climatic changes, while Korhola (1990) presents a general interglacial forest cycle which provides a good background for examining the distribution history of forests over shorter periods. The direction of development during the first half of an interglacial is called progressive and that characteristic of the later half retrogressive. The forest cycle comprises the following stages:

I. A rapid change from an open vegetation during the late glacial period to a closed forest community. Rapidly spreading tree species such as *Betula, Populus* and *Pinus* are dominant.

II. *Betula* and *Pinus* are gradually replaced by shade-tolerant, long-living temperate deciduous trees, i.e. the Quercetum mixtum species.

III. The mixed oak forest yields ground at a late stage to migrating forest trees such as *Picea, Fagus* and *Abies*.

IV. Pinus and Betula return as the dominant species and at the same time the number of temperate deciduous trees decreases. Picea is a significant tree species in some areas. The landscape starts to become more open and a new glaciation lies ahead.

According to Korhola (1990), the vegetation responds slowly to environmental change due to its low rate of reproduction and dissemination. He found that the postglacial history of the vegetation in Finland fits fairly well into this general framework. The rate of spread of the most common forest trees to sites emerging from the retreating ice has been about 100-1000 m per year, or 1-4 km per generation.

5.3.2 Postglacial history of the forests in Finnish Lapland

The recession of the ice margin in Finnish Lapland from east to west was fastest in Southern Lapland and in the north, close to the present Norwegian border. NE Lapland and the Utsjoki area began to emerge from beneath the ice nearly 10 000 years ago, and the whole of Lapland was ice-free by about 9000 years ago (Alho 1990).

The history of the forests and the timberlines in Lapland has been studied by many authors, among them Auer (1927), Aario (1940, 1943), Hustich (1948, 1958), Sirén (1961), Vasari (1978), Hyvärinen (1975, 1978) and Eronen (1979, 1981). The following summary of the general history of the spread of the forests into Lapland is mainly based on the works of Hyvärinen (1978) and Alho (1990). The changes in timberline will be examined separately in more detail. Hyvärinen (1978) distinguishes the following stages in the vegetation history of Northern Lapland:

1. Recession of the ice sheet and spread of birch forests (10 000 to 9000 years ago)

Birch scrubs and forests appeared in northern Norway immediately after the ice had receded in the early postglacial period, and birch forests spread to Finnish Lapland about 9000 years ago, after a short treeless phase following the ice retreat. These forests reached their maximum extent approximately 8500 years ago, after which they started to retreat, while pine advanced towards the north and west. The birch phase lasted the longest, about 2000 years, in Enontekiö, whereas in eastern Lapland it was considerably shorter (Alho 1990).

2. The spread of pine (8500 - 7500 BP)

Pine entered southern Lapland 8500-7500 years ago, at the same time as it migrated to the extreme margins of its postglacial occurrence at the Varanger Fjord. It then spread rapidly across the whole of Northern Lapland and invaded the last pioneering birch forests by about 7500 years ago. According to Alho (1990), it invaded the southern and northern margins of Lapland earlier than it did central Inari and Enontekiö. It advanced from the south, east and north, occupied the whole of the present birch zone and advanced along the valleys and fjords to the Arctic Ocean.

3. The pine maximum (7500 - 5000 BP)

After the end of the pine invasion succession the situation stabilized for a period of about 3000 years, with continuous pine forests prevailing in the present timberline area and the distribution of this species extending uninterrupted to the Arctic Ocean. There was apparently a narrower birch zone than at present beyond the pine timberline.

4. Retreat of the timberlines (5000 - 3000 BP)

At the same time as pine retreated due to the change in temperature, the birch timberline also shifted southward and the treeless zone expanded. According to Eronen (1979), the retreat of pine in Finnish Lapland was most distinct in Enontekiö.

5. Formation of the present forest zones (3000 BP -)

The timberlines were already close to their present positions when this period began, and it was around that time that spruce migrated into Lapland, reaching its present northern limit. According to Alho (1990), the slow migration of spruce was due to the excessively dry conditions, and it was not until the climate turned cooler and more humid during the Subboreal that conditions became more favourable for spruce. In western Lapland at least, spruce does not seem to have grown any further north at any time than it does at present, since by the time it reached its northernmost limit 2000 years ago, the climatic optimum, from which pine and birch had been able to benefit, was long past. This explanation may be regarded as a hypothesis of climatic equilibrium of distribution. Kullman and Engelmark (1991) arrived at the same conclusion, but found that in addition to short time scales, non-equilibrium responses are detectable.

Other explanations have also been presented for the northern spruce timberline in Fennoscandia. Mäkitalo et al. (1994) emphasize the importance of soil factors, while according to Oksanen (1995) the distribution of spruce is affected by three factors simultaneously: qualitative differences in climatic continentality, the capacity of spruce to maintain a position reached during a temperature maximum, its capacity to expand its distribution under current climatic conditions and the distribution barriers existing between the present timberline and potential sites lying further north.

The distribution history of the tree species of northern Fennoscandia as far as the countries bordering on Finland are concerned follows the outline described above. According to Nilssen and Vorren (1987), pine was growing in Varangerbotn as early as 8800 years ago, but it was a long time before races suited to the maritime climate of Troms and Western Finnmark developed. The species spread into the Alta valley 7500 years ago, but it was not until 5000 - 4000 years ago that it reached the outermost coast. Further south it spread more rapidly, either along the coast from the south or across the Scandes from the east. Mørkved (1987) studied the spread of spruce into Norway and observed that it has not spread naturally any further north than Saltfjellet. Some minor spruce stands in Finnmark are connected with the occurrences of spruce in Inari, Finland.

It is surprising that approximately correct estimates of the earlier, more extensive distribution of pine and of the effect of climatic change on the decrease in this distribution area could be arrived at early in the present century (Gavelin 1909, Juul 1925), although Renvall (1912b) had some reservations regarding climatic change as an effective factor in Finland.

The forest history of Petsamo has been studied more thoroughly by Finnish researchers than any other area in the present territory of Russia (Auer 1927, Aario 1940, 1941a, 1943). Aario (1941a) demonstrated the advance of pine, interpreting the numerous occurrences of spruce in Petsamo as signs of an advance as well. Russian pollen analyses suggest that pine spread along the Kola Peninsula from west to east, which is considered the reason for its northernmost occurrences being in the western part of the peninsula (Orlova 1972). Spruce, in turn, spread from the east, taking over the area from pine, which had earlier been more widespread, during a phase of climatic cooling (Solonevich 1940). Pine succeeded in keeping its position only at warm, dry sites on the plains (Solonevich 1940, Tsvetkov et al. 1983). Kozhevnikov and Ukraintseva (1992), studying the history of the vegetation during the early Holocene (12 000 - 10 000 BP), found that, in contrast to the situation in Fennoscandia, some species of *Picea* were the first to invade the ice-free area in Asia and NE Europe.

In summary, the present area of pine-dominated forests in Fennoscandia is located between Lake Torne in Sweden and the central part of the Kola Peninsula, with the main proportion of the pine forests located in Finland. The distribution area of spruce has not reached this area either from the south (Mørkved 1987, Alho 1990, Kullman and Engelmark 1991) or from the east (Solonevich 1940). Scattered spruce occurrences among the pine forests are more numerous in the direction of the eastern distribution limit of spruce than in that of its southern distribution limit.

5.4 The forest vegetation succession

Two types of forest vegetation community are traditionally considered to exist in every area of uniform macroclimate within the boreal zone, a small number of permanent climax communities and a large number of succession communities. In the permanent ones the vegetation has reached an equilibrium, while in the successional ones a development is taking place towards the climax community for each site (see Kalela 1945, 1960).

The crucial factors in the development of a forest vegetation are the competitive characteristics of the tree species. These may be grouped as follows: genetic plasticity, regeneration strategies, light demand, tolerance of competition, growth and capacity for phytomass production, tolerance of fire and biotic damage, and capacity for creating an environment unfavourable to competing species (Kuusela 1990). It is mainly light demand, reproduction and growth rate that distinguish the pioneer tree species from the climax species. The former are generally deciduous trees, while the best example of the latter in a Finnish context is spruce. Pine has both climax and pioneer characteristics.

It is an established view in Finland that the succession on mesic and semi-dry heaths in the middle and south boreal zone proceeds towards spruce forest, which is the climax stage community, where with site types that are poorer in nutrients the climax tree species is usually pine. In the northern boreal zone the trend operates in the same direction, although not as clearly. The succession of tree species described above is assumed to take place under approximately stable climatic conditions, where normal growth and development are possible. The succession has generally been examined in Finland over a fairly short time-span of one to three generations of trees. The developments of the other vegetation layers depends to a crucial degree on the tree species succession.

Our view of the forest succession has changed during the last few decades. Simberloff (1982), in his analysis of the development of ecological paradigms, found the first one to be the notion put forward by Clements of a plant community as a superorganism developing deterministically towards a climax. A real change came about in the 1950's, when this idea was replaced by a materialistic view based on probabilism, namely that the stochastic occurrence of disturbances plays an important role in the development of plant communities. The holistic view has nevertheless lived on in a new form, being related to interpretations of ecosystems in the terms of cybernetics and systems analysis.

Walter and Breckle (1983) maintain that the concept of primary succesion should be abandoned and the notion of zonal vegetation should be used instead of that of climax plant communities. They denote zonal biotopes by the term 'Eu-Klimatope', which is related to the Russian concept of 'plakor'. In addition to these, there also exist soil-related pedobiomes, the vegetation of which is azonal. Local factors may cause a zonal vegetation to exist outside its distribution area proper.

Glenn-Lewin et al. (1992) note that instead of the traditional deterministic and holistic succession concept of Clements, a mechanistic approach is recognized today which emphasizes the study of the causes of immediate changes in vegetation. An effort is made to describe every change by means of a quantitative model describing birth rate, death rate and growth, which are influenced by varying environmental factors. There has been a shift from the equilibrium paradigm to a non-equilibrium paradigm. The importance of disturbances is emphasized and the climax, i.e. a long-term state of stability, is no longer seen as the final point of development.

According to Haila (1995), the 'superorganistic' view of the community succession was clearly dominant until the 1960's. He considered the following factors to contribute to the shift in paradigms: empirically backed criticism of the balance of nature within ecology, the realization that adaption on the population level is not likely to be in equilibrium with environmental change, the realization that chance events have had a decisive influence on the course of biological evolution on the Earth, and theoretical developments in the theory of non-equilibrium thermodynamics and the dynamics of complex systems.

Our view of the nature of disturbances has changed as well. These are no longer considered to be rare events but natural processes occurring on various scales in space and time (Pickett et al. 1989). Glenn-Lewin and van der Maarel (1992) considered the succession a phenomenon situated chronologically between long-term vegetation history and the short-term fluctuation. Its time span varies from decades to a few centuries. A primary succession concerns the development of vegetation on a newly exposed substrate and secondary succession sites where a fully developed vegetation changes considerably on account of a disturbance. These authors summarize that nature of the succession as follows: The succession is a gradient in vegetation, mainly in relation to time but partly in relation to space as well. Peet (1992) divided the forest vegetation succession into the following stages: establishment, thinning out, a transition phase during which the original crown cover begins to break up, and a steady state characterized by balance between a closed canopy and gaps.

It is customary to distinguish small and large cycles in the dynamics of the natural boreal conifer forests of Central Europe. In the former, the forest structure changes with age from a closed, very dense youth stage via an optimum corresponding to the final felling age and a phase of natural thinning, to a uneven-aged stage in which forest development proceeds with age beyond the stage of self-thinning or catastrophe as a product of succession and alternation of tree species (Schmidt-Vogt 1995). Parviainen and Seppänen (1994) emphasize that there is a clear difference between the natural succession in a boreal coniferous forest and that in a forest of the temperate zone. In the temperate zone the small cycle is dominant, and in a forest consisting of shade-tree species the change constitutes a mosaic cycle, while in the boreal forest, development is mainly governed by a large cycle, initiated by disturbances. The large-cycle succession is well known in Finland (Parviainen and Seppänen 1994), whereas the small cycle, taking place in forests that have reached the final felling phase, has been less extensively studied.

The work of Huse (1965) on the pine forests of the Paatsjoki valley is the only thorough study in which the small-cycle development of pine forests in the Inari region has been described. The percentages of the development stages by area, according to Huse, were as follows: youth stage Δ %, optimum stage about 40 %, old stage about 30 %, regeneration stage about 20 % and uneven-aged phase about 10 %. Huse considered regeneration a continuous process, the results of which appear when favoured by external conditions, e.g., the forest structure.

The succession in a tundra vegetation differs from that of the boreal zone, and the concept of climax becomes problematic. The tundra succession is characterized by slow development, short succession chains and a small number of possible chains. The southern tundra and forest tundra already show some boreal features in this respect (Chernov 1985). Bliss and Peterson (1992) emphasize that biomes subjected to powerful environmental stress factors, e.g. tundra and deserts, have a more diffuse or even non-existent succession as compared with the forests of the temperate zone, for instance. They regard the freezing of soil and vegetation in the tundra as significant with regard to the succession. According to Lamb and Edwards (1988), the arctic vegetation is constantly affected by stress-type disturbances, which cause reactions in individual plants rather than in plant communities. Under such conditions interactions between plant species are more diffuse than further south. Kryuchkov (1978), studying the long-term succession in the biogeozenoses (i.e. ecosystems) of timberline regions at the landscape level, shows how the development of permafrost and unfrozen ground, controlled by fluctuations in climate, affects the forest via paludification, growth of the moss layer, etc. Tyrtikov (1995) has emphazised the role of paludification in long term succession of ecosystems in flat areas of West-Siberia.

The distinction between primary and secondary succession is not as clear at the timberline as elsewhere, since the history of the timberline vegetation frequently displays features of both. A study by Scott et al. (1987) of the vegetational history of the Hudson Bay land-uplift coast may be mentioned as an example of a distinct primary succession. They found that open forest and forest tundra differ in their mode of development with regard to the generation of young trees, tree growth and crown shape. Factors effective in the primary succession over long periods were climatic fluctuation and the lichen cover, which controls the generation of young trees. Hustich (1957) regarded the primary succession of the vegetation of the Hudson Bay coast as practically identical to that of the land-uplift coast of the Gulf of Bothnia and certain parts of the White Sea coast.

Various views have been expressed regarding the secondary succession in timberline forests, and in general the distinction relative to typical boreal forests is considered to be a clear one. The difference may in principle be regarded as lying in the long establishment stage which frequently shows characteristics of a primary succession. If competition is slight, the natural thinning stage will be delayed or completely lacking. The transition stage and stable stage will merge together on account of the low degree of closure of the canopy. The progress of the stable stage will depend on the prerequisites for regeneration, and may vary considerably according to the conditions and the tree species involved. Extensive research has been carried out, especially in North America, regarding the basis for the modern concept of succession, including its application to timberline forests.

Relatively little research has been carried out into tree species dynamics in timberline regions. It is commonly believed in Finland that site quality is less important in the vicinity of the timberline than climate (see Lehto and Leikola 1987). For this reason the idea of climax tree species for a certain site is a more diffuse than in areas further south. *Betula pubescens*, apart from its mountain birch form, is considered a distinct pioneer species, whereas the relation between spruce and pine is different from that found in more southerly areas. The situation is also affected by the distribution history of the species, forest fires, edaphic factors and the reproductive properties of the tree species.

According to Peet (1992), it has been found in several studies in the Rocky Mountains that the forests of the upper and lower zones of the mountains do not follow the general four-stage pattern of succession. Billings (1969) describes a special succession in the 'ribbon forest' of the alpine timberline in the Rocky Mountains which is controlled by fires and the duration of the snow cover.

Bradshaw (1993) has studied the tree species dynamics and the effect of disturbances over a period of more than 2000 years at a site near the timberline in Norrbotten, northern Sweden. Pine had reached a dominant position three times on account of forest fires and storm damage, while the proportion of birch had decreased. Each pine population had died at an age of 100 - 300 years and regeneration had proved unsuccessful, probably due to the cold climate, so that birch had gained ground. During the last century an undergrowth of spruce had succeeded in regenerating gradually. Bradshaw arrived at the conclusion that the proportional distribution of tree species over a long period is determined by the total effect of climatic fluctuation and disturbances.

Veblen et al. (1994) made the observation in the subalpine belt of the Rocky Mountains that the vegetational history of the forest may be affected by the sum of numerous disturbances, including fires, avalanches and insect damage. Some disturbances are hard to prove afterwards, which makes it difficult to obtain an overall picture of the situation. Payette et al. (1985) found an old *Picea mariana* forest to be quite a stable form at the timberline of Canada, as it regenerates slowly in accordance with the succession, remaining unchanged provided that no forest fires occur. Viereck (1983) studied the post-fire development of forests dominated by *Picea mariana* in Alaska and northern Canada and found that in general the succession advances via an intermediary stage dominated by deciduous trees to a mossy spruce forest on mesic soils and directly to the lichen woodland stage on nutrient-poor soils.

The pine forests of eastern Inari may be mentioned as a Finnish example of the situation in timberline forests. Fires have not occurred there for a long time, the ground is covered by a thick layer of raw humus, and an abundant admixture of *Betula pubescens* of the mountain birch type frequently occurs. In practical terms, birch-dominated stands are excluded from felling plans because of the great risks attached to their regeneration. Birch is not a distinct pioneer species at such sites (cf.

Huse 1965). Sirén (1961) and Hustich (1966) regard the mountain birch stands mainly as 'pseudotundra', formed as a result of a post-fire succession. The regeneration of pine has failed and mountain birch has gained virtually a climax status.

The causes of the timberline pine zone, the regio subsylvatica, have been discussed since the time of Wahlenberg, and the question has still not been finally solved (see Kihlman 1890, Fries 1913, Enquist 1933, Mäkitalo et al. 1994, Oksanen 1995). Kujala (1929) considered the northern spruce limit to be caused primarily by the soil and the history of species distribution, and only secondarily by the climate.

Nekrasova (1961), in her consideration of the relations between spruce and pine on the Kola Peninsula, found that *Picea abies* differs in its site requirements from the eastern subspecies *Picea abies ssp. obovata* in that it competes with pine almost everywhere, including nutrient-poor sites. The only exception is the iron podzol soil type, on which spruce does not grow. Characteristic of the Kola Peninsula are the stable mixed stands of spruce and pine on nutrient-poor soils, which should be distinguished from stands in which a slow transition is taking place from pine to spruce forest. According to Nekrasova, the position of pine as the main timberline conifer in western Kola is due to the later arrival of spruce in the area and its minor chances of expanding on account of the nutrient-poor soil.

Marr (1948) expressed the view that the forest tundra of Labrador is a combination of plant communities at various stages of a succession in which forests of *Picea glauca* and *Picea mariana* represent the climax and the communities of the tundra vegetation are edaphic subclimax communities which will in time become forested. According to Hare (1950), the conifer-dominated forests of Labrador represent climax associations, which will replace the post-fire birch-aspen forests within a few decades.

Larsen (1980, 1989), having studied the succession in timberline forests, is critical of the European phytosociological approach with its frequently subjective sampling and complex definitions. The landscape approach has been used in North America to analyze the forest vegetation, meaning that the relations between plant communities, climate, topography and soil are studied on all scales of the landscape. Larsen (1980) found that the succession and its climax stage are insignificant factors under conditions in which only slight competition exists between species and it is environmental factors that directly decide the structure of the plant communities. Ecoclines and continua are determined by topography and soil properties, and all species are pioneers. The further north the location, the more frequent this situation is.

Vegetation continua have usually been studied by ordinate or gradient analysis. Larsen (1989) found the work of Johnson (1981) in the

Northwest Territory of Canada an important example. The latter had studied vegetation continua simultaneously in time and space, and his site analysis had revealed a landform-crown closure gradient and a nutrient content gradient. The fire frequency, on which species are distributed on the basis of how they react to fire on a temporal dimension, represents a dynamic element with a shorter periodicity, causing differences in relative abundance but not in species, whereas the site gradient represents the long-time dynamics, leading to the main changes in species. Johnson arrived at the fundamentally interesting result that the old *Picea mariana* forests with their thick ground vegetation of *Hylocomium* and *Pleurozium* mosses, which had earlier been considered representative of the climax phase, are only a normal element of the site gradient. He based this view on the short fire cycle and physiology of the mosses, which allows them to develop rapidly in a forest which generally has a closed canopy layer. Johnson further emphasized that under timberline conditions the forest will seem to remain fairly constant in composition in the short term (400-500 years), whereas the succession over a long period will be difficult to predict.

According to Pettapiece (1984) the first post-fire tree generation in subarctic forests grows better than the following ones, on account of the favourable effect on the soil and the adjacent air layer of the removal of the thick moss carpet (cf. Sirén 1955a). Strang (1973) reports observations made in spruce forests in the Mackenzie River valley, where fires have not occurred for about 150 years and the tree layer vegetation is markedly degenerate. In timberline forests where no fires have occurred for a long time, the proportion of *Picea mariana* increases due to vegetative regeneration, while *Picea glauca* and *Larix laricina* (Black and Bliss 1980) retreat.

Bonan et al. (1990) analyzed the effect of the warming of the climate on the *Picea mariana* and *Picea glauca* forests of the plains in the interior of Alaska by means of a simulation, which also provides a background for the understanding of the succession. The model they used comprised one part for environmental factors and one for the demography of tree populations. The following environmental factors were included: solar radiation, potential evapotranspiration, water content of the soil, and freezing-thawing effects in the soil. The demographic factors were: annual regeneration, growth and death. This model included numerous random factors, e.g. the annual fluctuation in temperature and precipitation, whereas death, regeneration and forest fires occur with a certain probability. The simulation pointed to the great significance of the humus and the ground layer vegetation and to the complexity of the history of boreal forests as a whole.

In their studies of the forest tundra vegetation, Russian researchers have paid special attention to the degree of closure of the stand, and thus the significance of crown closure and root competition for the ground vegetation (see Norin 1993). Their findings show that no tree species succession will occur in a situation of incomplete closure in areas of forest tundra and open taiga, but rather it is the degree of closure of the forest that will largely control the development of the rest of the vegetation. The microtopography of the soil also has a pronounced effect on the vegetation. According to Tolchelnikov (1970), a low level of available nutrients, cold soil and the influence of crown closure on the radiation balance are crucial factors regarding the succession. Tyulina (1936) considered the lack of *Larix gmelini* at the timberlines in the valleys of Anadyr to be a consequence of competition factors. The landscape approach is widely used for studying vegetation in Russia, alongside phytosociological analysis. Chernov (1985) considered a knowledge of the succession in the vegetation of northern areas to be of crucial importance for the utilization of organic natural resources.

Glawion (1986), studying the development of the subarctic birch forests of Iceland, which have been almost completely destroyed by man, found that the remaining birch stands are undergoing a secondary succession, resulting in open stony ground due to overexploitation, fires and grazing. If measures are eventually taken to protect the forest, the secondary succession may turn into a progressive development, so that after stages dominated by shrubs and dwarf shrubs, secondary birch-dominant forests may again develop.

It seems that the existence and significance of the succession also depends on how it is defined and over what time span the examination is made. It is clear, however, that findings concerning the succession in average boreal forests may not be directly applicable to timberline forests. The random variation in generative regeneration due to temperature causes special features of its own, which together with occasional disturbances form a model of tree species dynamics with emphasizes randomness. Thus the forest tundra with its incomplete crown closure will in particular differ crucially from the closed forests. On account of climatic fluctuation, the area of fairly regular tree species dynamics and that of markedly random dynamics will vary constantly in extent and location within the timberline region.

Betula pubescens provides a good example of differences between the timberline region and the boreal forest in the history of a tree species. Mountain birch is a species in the active phase of phylogeny and its relation to conifers in their marginal area of regeneration is completely different from that of a pubescent birch proper to conifers further south. It is an interesting question from a forestry viewpoint how far south the pubescent birch displays mountain birch characteristics to a significant extent. According to Hämet-Ahti (1987), forms that are intermediate between *Betula pubescens* ssp. *pubescens* and ssp. *czerepanowii* are common in the conifer-dominated forests of the plains of Northern Finland.

According to Shugart (1984), two permanent vegetation types may exist in internally unbalanced ecosystems which include two species that differ in their characteristics. He refers to research carried out in mountains and northern regions, showing that such situations are most probable in the transition areas between vegetation zones (cf. Bradshaw 1994). These landscapes, which consist of patches at several permanent stages, do not vary around one assumedly permanent stage on account of disturbances, and it may be very difficult to change them by silvicultural methods, for example. This general conclusion fits in well with features observed in the relations between pine and birch in particular in the timberline regions of Fennoscandia. Some pine sites in the vicinity of the climatic timberline are such that the development of pine or birch-dominated forest after a disturbance will depend on the climatic phase prevailing at the time. Birch is capable of invading a site after a disturbance during a climatic phase that prevents the generative reproduction of pine, and the more distinctly the birch present consists of mountain birch, the more permanent or stable the birch-dominated stage will be.

A birch-dominated forest with some pine does not become pine-dominated by the processes of normal tree species dynamics under these conditions, but it may do so after a disturbance occurring during a climatic phase when pine is producing germinating seed. The most probable types of disturbance are forest fires and *Oporinia* damage. Grazing by reindeer affects forest development in two ways: grazing that breaks the lichen cover and uses birch to a moderate degree favours pine, whereas overgrazing increases damage to young pines. These sites possessing two alternative tree species constitute the most favourable parts of the present mountain birch zone and the northernmost part of the pine zone (Figure 37). The fact that it is possible to change a birch forest into a pine forest by silvicultural methods shows that birch-dominated timberline forests can be potentially pine- dominated. No actual research has been carried out into how the proportions of the tree species are affected by *Oporinia* damage in forests containing a significant proportion of pine, but practical experiences and observations in Inari and in the Pasvik valley in Norway indicate that this disturbance may markedly favour a trend towards pine dominance. According to an estimate by Tømmervik and Johansen (1992), based on the findings of Kullman (1991c) on the fells of Västerbotten in Sweden, *Oporinia* damage in combination with warming of the climate may have the effect of stabilizing the pine and spruce treelines.

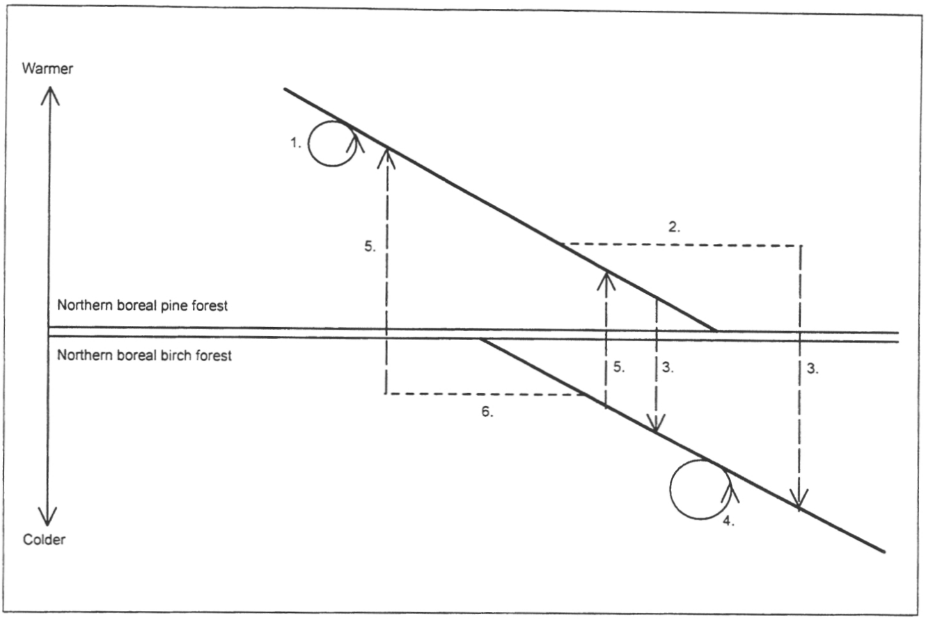

Figure 37. Two states of equilibrium and deviations from them. Central phenomena of the pine and mountain birch timberline in northern Fennoscandia.

1. Regeneration of pine possible. Normal tree species dynamics between pine and birch. Tree species and climate in equilibrium.
2. Gradual degeneration of pines with long delay. Pine is not in equilibrium with the climate.
3. As a result of a disturbance (forest fire, storm, felling) the pine forest changes rapidly into birch forest, as the cold climatic phase does not permit regeneration. Rapid shift to the second state of equilibrium.
4. Gradual birch forest regeneration by sprouting.
5. As a result of disturbance, the birch forest gives way to pine forest, as a warm climatic phase permits seed maturation and stocking with seedlings becomes possible. This change may also be achieved by silvicultural intervention.
6. The birch forest is preserved despite the warm climatic phase since regeneration of pine is not possible without disturbances. A birch forest that regenerates vegetatively is very stable.

5.5 Climatic fluctuation

5.5.1. Measured temperature fluctuations

Although regular temperature observations have been made in Helsinki since 1828, observations from a number of points in Finland did not become available until the Meteorological Institute was founded in the 1880's (Heino 1978). A great deal of research has been carried out into temperature fluctuations in the course of the present century.

Wallén (1962) found a distinct rise in winter temperatures to have taken place in Fennoscandia since the 1850's, whereas the change in summer temperatures was a more complex one. These decreased roughly during the period 1850-1915, which combined with the increase in winter temperatures meant an increase in maritimity in Fennoscandia. After 1915 the summers became warmer for approximately the next 20 years, i.e. the climate became more continental. This warming was most pronounced in the north. Wallén estimated that the warming had actually come to an end before 1940, but it was too soon in the early 1960's to draw conclusions regarding the duration and significance of this change. According to Wallén (1986), the climate of Northern Finland became cooler at all seasons from the 1950's to the 1970's, and especially during the 1960's. Although temperature patterns show no distinct trend, a general feature of the last few decades has been a cooling relative to the early 20th century.

According to Hansen (1974), an increase in temperature has been observable in Norway since about 1860, the effect being greatest in winter and smallest in summer, with the most pronounced changes recorded in the northern and interior parts of the country. The greatest increase occurred in the 1930's, whereas the temperature even declined slightly in the 1940's. Although the changes were small, Hansen considered them significant under the conditions prevailing in northern Norway. According to Kryuchkov (1978) it is commonly believed in Russia that the warming of the climate ceased in the 1950's and that it then started to cool. The warming in the Kola Peninsula region was most pronounced in winter during the 1920's, and the summers also became slightly warmer in the 1930's.

Heino (1978, 1994), in his examinations of climatic changes in Finland over the last hundred years, found that the worldwide temperature rise from the 19th century to the mid-20th century and the temperature decline since then are clearly observable in Finland. The annual mean temperature rose 1.5°C, and the rise in winter temperatures in Northern Finland was especially distinct, whereas the summer temperatures varied less. The changes in temperature were most pronounced in the interior of Northern Finland (Heino 1994). Also, the continentality gradient has increased during this century: the maritime areas becoming more distinctly maritime and the continental ones more continental than before.

Koutaniemi (1990), in an assessment of trends in temperature and precipitation in Finland during the period 1751-1984 in which he also makes use of data from some foreign observation stations, regards the general pattern in temperatures as having been the following:

1. The time before the 1870's is characterized by exceptional cold. This period formed part of the Little Ice Age, which seems to have ended in the late 19th century. The years of famine in Finland during the 1860's fall within this period.

2. After the Little Ice Age, temperatures rose fairly regularly for about 60 years, culminating in the 1930's.

3. Temperature variations since the 1930's show a periodicity of 10- 15 years, but without any observable trend towards colder or warmer conditions.

Koutaniemi concludes that the climate in Finland has become considerably warmer relative to conditions in the last century but has cooled in Northern Finland in particular during the last thirty years (Figure 38). Simultaneously the mid-points of the winter and summer have moved earlier. Koutaniemi found that these results fit in with earlier observations and with reports from elsewhere. The most surprising thing is that the greenhouse effect cannot been demonstrated; in fact the statistics rather tend to indicate the reverse.

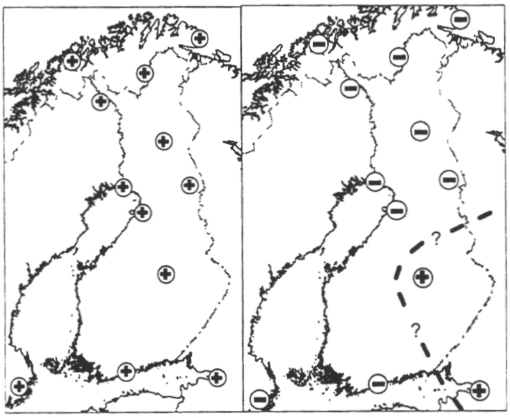

Figure 38. General trends in temperature before the 1940´s (left) and after that time (right) (Koutaniemi 1990).

Solantie (1992), studying temperature changes in Finland between the 'old' normal period, 1931-1960, to the 'new' one, 1961-1990, found that the latter period was a maximum of 0.1° colder. The coldest temperatures in relative terms were recorded in Lapland and in the timberline region, where the annual mean temperature decreased by 0.6-0.8°. The most distinct decrease in the effective temperature sum occurred in the middle boreal zone, for although a marked decrease was also noted in the north boreal zone, it was of the same magnitude as the dispersal in the figures, apparently attributable to the increase in discharges of cold air.

Employing data from the Swedish Meteorological Institute, Eriksson (1988) found the cooling of the climate that started in the 1940's to have continued for nearly 50 years. The mean July-August temperature in Sweden decreased by 0.18-1.6° from the period 1931-1940 to 1978-1987, and the cooling in the timberline region was as much as 1.2-1.6°. Eriksson notes, however, still more distinct decreases in temperature have been found at many observation stations elsewhere in the northern hemisphere. On the basis of temperature observations for the inland part of Norrbotten in 1933-1988, Lindgren et al. (1989) conclude that the late 1980's was a time of declining mean temperatures for the growing season. Flohn (1985) attributes the cooling that occurred over the entire northern hemisphere during the period 1945-1970 at least in part to volcanic activity.

5.5.2 Proxy data on temperature fluctuations

Eronen (1990) maintains that it has been possible to obtain a fairly clear general picture of the climatic history of the postglacial period, i.e. the Holocene (10 000 B.P. to the present) based on the history of the vegetation, studied mainly by pollen analyses of horizons usually dated by the radiocarbon method.

Useful results have also been yielded by dendrochronological research (e.g. Sirén 1961), and intensive use has been made of this approach recently in connection with the Finnish Research Project on Climatic Change. Eronen and Zetterberg (1992) found that northern pines are highly suitable for dendrochronology. The aim now is to compile a chronology based on annual rings going back up to 7000 years by means of Nordic collaboration (Zetterberg and Eronen 1994). This 'master chronology' for Finnish Lapland extends to approximately 4900 B.C., while the absolute dating interval current covers the period from the present back to 165 B.C. (Zetterberg and Eronen 1995).

The proportions of various isotopes of carbon, hydrogen and oxygen in annual tree rings can be determined by isotope analyses, and the results so far obtained indicate that a marked change took place in the behaviour of the climatic system of the northern regions around 3000 B.C. The alternating temperature fluctuations became more pronounced and irregularly alternating cooler and warmer periods lasting for several decades at a time began to occur. The analysis of the fluctuation in summer temperatures in northern Fennoscandia since the year 500 performed by Briffa et al. (1990) employing dendrochronological methods points to significant annual, decennial and centennial fluctuations, leading them to conclude that the Little Ice Age was a fairly short period covering approximately the years 1570-1650. On the basis of density analyses of the summer wood of conifers, Schweingruber et al. (1991) have compiled time series for temperatures for the 17th century and for the period from the 1750's onwards applying to western Europe and western North America. Again using annual ring data, Briffa et al. (1992) present conclusions regarding variations in summer temperature since the year 500, and show that cold intervals relative to the normal period 1951-1970 occurred in AD 500-700, 790-870, 1110-1150, 1190-1360 and 1570-1750. Temperature maxima occurred during the following decades: 750, 930, 990, 1060, 1160, 1410, 1430, 1760 and 1820.

5.5.3 Prediction of climatic change

According to Budyko (1991), a general global warming trend related to the increase in atmospheric carbon dioxide was observable as early as the 1970's. It is difficult to predict the regional or local implications of this, however. Two types of method are used for this purpose: mainly climatic modelling in the western countries and mainly paleoanalogical methods in Russia. A general outline of the prediction methods employed is given by Flohn (1985). The paleoanalogical approaches make use of ice drilling etc., and are based on the assumption that warming during earlier periods was likewise caused by an increase in greenhouse gases in the atmosphere. According to Shukla (1991), the natural variability in regional climates is so great that the uncertainty attached to climatic models will remain large unless it is possible to simulate this natural variation sufficiently well in them. In addition, he emphasizes that interaction between the atmosphere, the oceans, the biosphere and the glaciers has played a central role in all climatic fluctuations that have occurred during the last hundred years. Wigley and Raper (1991) observed that the mean temperature of the Earth has risen by 0.5°C during the last hundred years, although the cause is not known. Many factors in the climatic system and outside it may have contributed to this warming. Sulphate aerosols are mentioned as a possible factor slowing down the warming caused by the increase in atmospheric carbon dioxide.

The climatic change is also being studied in Finland, e.g. in the research project referred to above, interim reports on which were published in 1992 and 1994 (Kanninen and Anttila 1992, Kanninen and Heikinheimo 1994). In this connection Fortelius et al. (1992) estimate the climatic change in Finland on the basis of physico-mathematical climate models and conclude that regional climatic predictions are highly uncertain, partly because it is not known how the sea currents will change as the climate becomes warmer. As their best guess, they present the view that the greenhouse effect will raise the mean temperature in Finland by approximately one degree by the year 2010, two degrees by 2030 and three degrees by the end of the century. More detailed predictions of the warming in various parts of Finland cannot be given at present. Heino (1994) correspondingly arrives at the conclusion that the climate of Finland has remained quite stable during this century and the measured changes are only a part of normal climatic fluctuation. The predicted change due to the greenhouse effect cannot as yet be measured.

Russian climatologists have presented a forecast of the warming to be expected over the entire area of the former Soviet Union, based on an extensive body of data (Zavelskaya et al. 1993). This takes into account changes in the temperature sum, length of the growing season and precipitation in individual major regions. The greatest temperature rise is predicted for the Arctic Ocean coast, and especially for the Chukotsky Peninsula. A pronounced warming is also to be expected on the eastern Kola Peninsula and on the Yamal Peninsula (Figure 39).

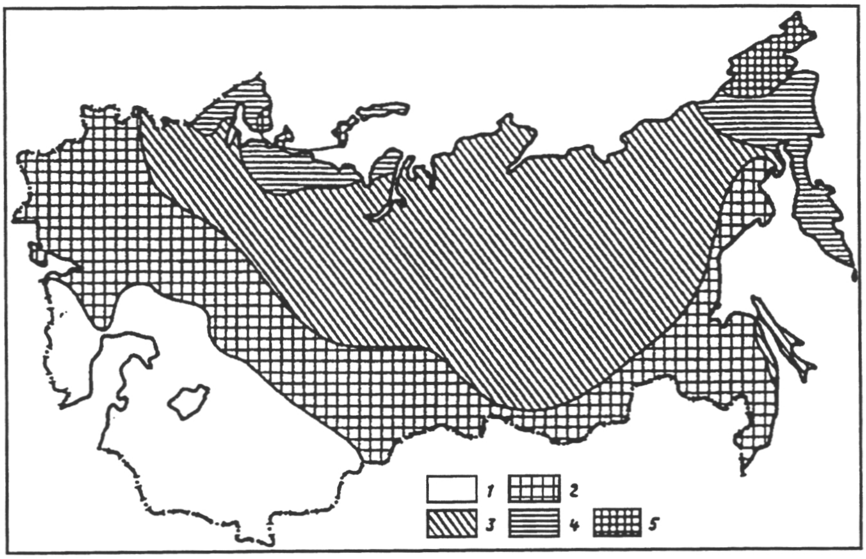

Figure 39. Change in the length of the growing season by the year 2005 (Zavelskaya et al. 1993). Increases in the numbers of days a mean temperature over +10° C: 1. *0*, 2. *0-10*, 3. *10-20*, 4. *20-30*, 5. *>30*

5.6. Changes in the timberline caused by climatic fluctuations

5.6.1. Response of the vegetation to climatic fluctuations

It is often difficult to distinguish the changes caused by cyclic fluctuations in climate of different periodicities within the general postglacial history of the distribution of tree species, although the further one goes back in history, the more clearly these fluctuations leave their mark on the distribution patterns. In fact the more recent, more accurately dated and described periods can most easily be looked on as exceptions from the general trend. Climatically induced changes in timberlines have been examined on a wide variety of time scales. Frequently the overall framework is that of the whole Holocene, the analysis being weighted according to the extent and age of the material available, while another type of investigation is represented by descriptions of short, precisely determined periods closer to the present day, the exact relation of which to the long-term scheme may remain an open question. In addition to the time scale, the geographical extent of the investigation may vary greatly, from an analysis of a single mountain valley to a description of the situation over a whole continent. Prentice (1992), for example, distinguishes global, regional, landscape and patch-level reactions of the vegetation to climatic changes, although patch-level changes are largely connected with the vegetation succession and tell us relatively little about the effects of climate. Correspondingly, a forest ecosystem at the landscape level is quite well buffered against climatic changes at the decade level but reacts with a certain delay to changes at the millennium level.

Wimsatt (1982) arrived at the conclusion that many ecologists regard response times in a hierarchical system as being markedly longer at higher levels in the hierarchy than at lower ones. A response time describes the way in which processes at a given level are in equilibrium with the environment, and thus a higher hierarchical level will provide information on events connected with long-term fluctuations. Woodward (1987), examining the responses of plants to climatic changes on a general level, notes that this is a complex hierarchical system that extends from the cellular level via the individual to the population level, a system in which reaction times become more protracted further up in the hierarchy. In the case of extensions in the geographical distributions of species, the response time must in principle be at least the time required to complete one full life cycle, whereas that for a reduction in distribution will be substantially longer and will be dependent on mortality in the population concerned. Thus Woodward (1987) estimates that only climatic cycles of over 15 years' duration are relevant to the spread of slow-growing tree species that appear late in the succession, and only cycles of over 164 years to their retreat stages.

Davis (1986) claims that climatic change is one of the major factors bringing about a state of imbalance in plant communities, and that the reaction of a community to such a change consists of a combination of the differing reactions of individual species. It is typical of marginal populations of species with a long life-span that they react to climatic deteriorations only with a considerable delay. Davis goes on to note that a change brought about by warming of the climate will become visible more quickly at the timberline than immediately within the closed-crown forest, where the situation is greatly affected by competition between old trees. The change may take about 100 years to manifest itself in the latter case, although the plant community can be said to be in a state of disequilibrium all that time. Thus Davis comes to the conclusion that any explanation of a flora and its species abundances must take account of the effects of climatic changes.

The theory was put forward by Smith (1965) that a simple climatic change can exercise a complex effect on the vegetation, the reactions of the latter being regulated by a number of critical thresholds and by a certain inertia that prevails in vegetational change as a whole. If there are a number of factors involved, the threshold for each one may vary greatly. The temperature sum required for seed maturation can be regarded as one such critical threshold in the case of Scots pine. In his evaluation of Smith's views, Bradshaw (1994) concludes that variations in the critical thresholds for individual species between different parts of their range of distribution can lead to further complexity in the reaction of the vegetation to climatic change. He emphasized the importance of disturbances as one reason for pronounced changes, but did not regard the delay or inertia factors as decisive.

Recent Russian research has drawn attention to the significance of hysteresis in the determination of vegetation boundaries and their reactions to climatic fluctuations. Bogatyrev (1991) observed from his empirical material that mathematical models for the tundra-taiga transition zone may be constructed on two alternative premises: either that a change in biomass can be explained by the temperature factor, or largely on account of the forest microclimatic, the ecotone will include an area of hysteresis in which the increase in biomass cannot be explained by the temperature factor. In their study of biomass and potential evapotranspiration, Vedyushkin et al. (1995) observed that there can be large hysteresis areas at the boundaries of vegetation zones, especially where the boundary is formed by shade tree species. Where the gradual transition zones are dominated by light-demanding species, changes in environmental factors tend to be reflected directly in the vegetation, whereas under hysteresis conditions the vegetation boundary is not immediately dependent on environmental factors.

The most common climatic factor examined in this connection is temperature, so that Bortenschlager (1992), for instance, regards it as a generally accepted fact that growing season temperatures in the European Alps varied 1 - 1.5°C on either side of the mean during postglacial times, causing changes of up to 200 m in the altitude of the timberline. Puzachenko (1985), on the other hand, emphasizes that combinations of climatic factors affecting timberlines have to be taken into account, which in the case of regions with a maritime climate implies mainly the inclusion of relative air humidity alongside temperature. He goes as far as to claim, in fact, that the timberline in a maritime area reflects chiefly variations in relative humidity whereas that in a continental area will reflect mainly the effect of temperature.

Ritchie (1986) proposes the following scheme of factors affecting vegetation with respect to the time dimension:

- Direct fluctuation: time span less than 20 years, e.g. effects of heavy rain sand storms

- Indirect fluctuation: time span less than 20 years, e.g. effects of volcanic eruptions
- Trend-like fluctuation: time span 20-1000 years, e.g. effects of 20th century climatic warming

- Change: time span over 1000 years, e.g. change from a glaciation to an interglacial

He also mentions many factors that may speed up, retard, prevent or alter the reaction of the vegetation to climatic fluctuations, most prominent among which are anthropogenic factors, variations in topography and soils, properties of individual species and hysteresis, by which he means the influence of the earlier history of the plant community on its reaction in a given situation. Brubaker (1986) is of the opinion that the reactions of tree populations to climatic changes are affected principally by the life span and growth rhythm of the species, seed production and dissemination, phenotypic plasticity, genetic variation, competition factors and disturbances (mainly forest fires), and notes that such reactions can occur with delays of up to a hundred years. The dynamics of such changes are species-specific and the response time can differ according to whether the population is in an increasing or declining phase, on account of the differences in sensitivity between young and old trees. Payette and Gagnon (1985) note that the effects of climatic fluctuations on forests at the timberline are modulated to a great extent by the combined impact of climate and forest fires, i.e. changes in disturbance dynamics. Thus Payette et al. (1985) conclude that an old spruce forest at the timberline will be in a state of dynamic equilibrium with the climate provided that it is unaffected by external disturbances, while Sirois and Payette (1991) point out that the combined effects of climate and fire should be considered when predicting the impact of climatic change on timberline forests.

Hustich (1978) notes that the reaction of trees to climate may be exaggerated, or, as is usually the case, it may occur with a certain 'lag effect', in addition to which the outcome is affected by species-specific ecological properties. In his global assessment of such effects, Holtmeier (1985) concludes that regression does not take place on a broad front but is a gradual process that is dependent on local conditions and trees' individual tolerance levels. Old trees and forests may exhibit considerable tolerance of changes and may remain alive for centuries even though they are no longer able to reproduce, e.g. *Pinus aristata* and *Pinus albicaulis* in the Rocky Mountains. In the case of old forests and ones that are subjected to pronounced stress, passive protection mechanisms gain in importance as elements tending to slow down any regressive trend. This is a matter of the chemical properties of ligneous material (Loehle 1988).

The development that takes place in response to favourable climatic periods generally proceeds rapidly and can be affected by small-scale site differences (Holtmeier 1985, cf. Brubaker 1986). The future growth of seedlings will naturally depend on the duration of the climatic change, but saplings growing at the timberline have to survive many setbacks, e.g. frost drought, and it is a long time before a change in the timberline can be said to be permanent. Thus Kullman (1987) notes that it is still too early to say whether or not the pines that seeded themselves in the Scandes in 1950-1970 can be regarded as constituting an established age class. Numerous corresponding experiences could be quoted in connection with reforestation experiments at high altitudes. One good example of a progressive trend is the advance in the timberline brought about by the warming of the climate in the first half of the present century.

Aario (1941b) put forward the interesting thought in connection with his research in the Petsamo region that short cooler and warmer periods which deviate from the long-term climatic trend could give rise to a situation in which progressive and recessive features were to be seen in nature simultaneously. Davis (1986) estimates that species that have reacted slowly to the cooling of the climate which began in the 1950's may still be advancing towards the north, whereas those that have reacted promptly are already retreating and advancing southwards.

Hustich (1944) mentions that one may easily overestimate the importance of the immediate past for changes in the timberline by treating a tendency which is no more than a short deviation from the long-term pattern as a trend in its own right. Likewise, Gorchakovski and Shiyatov (1978) suggest that short-term climatic fluctuations may not cause any appreciable changes in the Alpine timberline and that changes can be described best by deducing the long-term cycles; or conversely, short-term tree-line changes cannot be used to form far-reaching conclusions regarding long-term trends in the timberline (Holtmeier 1974). Shiyatov (1967), in his treatment of the relation between climatic fluctuations and the age structure of the *Larix sibirica* forests forming the timberline in the Northern Urals, concludes that a short-term warming of 20-30 years, for example, will not be sufficient to create a new, established generation of trees, but that a period of at least 50-60 years is needed for this. Puzachenko (1985) claims that a period of 100-200 years is necessary for the creation of new forest vegetation communities and that a change in vegetation zone boundaries requires a periodicity of the order of 1000 years.

Holtmeier (1985) notes that long-term climatic fluctuations together with the present-day climate determine the variable width of the timberline ecotone, the physiognomy and age structure of the tree layer and the structure of the ground vegetation, while Kullman (1993a) puts forward the hypothesis that the responses of at least the mountain birch treeline to climatic changes throughout the Holocene have been largely a matter of variations in the shape and vitality of individuals, and that these effects have manifested themselves at the population level with a very long delay. Similarly, Payette et al. (1985) conclude that the timberline spruce forests of Quebec have reacted to the climatic amelioration by developing from a krummholz to a stem-form morphology, although with a delay of several tens of years in places. Kullman (1993b) deduced that the pine treeline in the southern Scandes is determined by the combined effects of climate, age of the trees and disturbances, and that any lowering in the treeline can be expected only as a consequence of a long-term climatic deterioration. The results of Kullman (1983) led Davis (1986) to conclude that pines are more numerous near the treeline in the southern Scandes than could be expected on the grounds of an equilibrium between the species and climate, and to attribute this to a long time-lag with respect to the cooling of the climate in the 18th and 19th centuries.

The examination of climatic changes over different time scales requires some decision as to what climatic periods are regarded as sufficiently significant and clearly defined that they will serve as a basis for this. Prentice (1992) distinguishes orbital, millennial, decennial and annual fluctuations in the dynamics of climate change and vegetation, while Kullman (1990a) discusses the alpine timberlines of Scandinavia on the followong time-scales: a long-term time scale covering the whole of the Holocene, the Little Ice Age, the subsequent warming and the cooling of the present-day climate. This forms a suitable basis for examination in spite of the fact that varying interpretations have been put forward regarding the timing and duration of the Little Ice Age (see Koutaniemi 1990, Briffa et al. 1992).

The results and opinions set out above fit in well with the general theory of the dynamics of ecotone changes in various space-time relationships. Gosz (1991) sums this up by stating that climatic change is a broad-scale feature which has a long temporal behaviour pattern. This implies that it is only through long-term, large-scale studies of ecotones that it is possible to analyze climatic changes, since their deduction from individual, local fine-scale investigations are apt to result in pseudoprediction. The effects of local factors can admittedly be eliminated by using long-term results for a number of fine-scale sites spread over a wide geographical area, but it is essential for the study of the dynamics of change in ecotones and the assessment of the results that the time-space relationships should be correct.

5.6.2 The whole Holocene as a time scale

Finnish Lapland and adjacent areas. The long-term history of the distribution of tree species in Finnish Lapland and adjacent areas is discussed in section 5.3.2.

The Scandes. The main outlines of the long-term history of the alpine timberline in the Scandes, as described by Kullman (1990a), are as follows:

1. Pine spread to the area immediately after the retreat of the continental ice sheet and formed the timberline. There is no evidence of the presence of a subalpine birch zone until 6000 B.C. The history may be somewhat different in the maritime areas further west, however. The pine limit was some 150-200 m higher than the present-day timberline.

2. The pine limit in the southern Scandes reached its highest level prior to 6000 B.C., after which pine retreated in the course of the subsequent millennia and subalpine deciduous forests of birch and alder spread in its place, although alder relatively soon retreated to a lower level.

3. The pine timberline dropped to close to its present level from 3300 B.C. onwards on account of a deterioration in the climate. The history of the subalpine birch forests later in the Holocene is still unclear, but spruce is known to have spread into Sweden from the east and north-east over the last 3000 years.

Kullman (1992) observes that the decline in the limit of pine in the Scandes from the maximum height that it reached around 8000 B.C. took place at a fairly steady rate of approx. 25 m per 1000 years. Pine was replaced by birch, but its treeline began to descend from around 4000 B.C. onwards. Kullman regards these findings as lending support to the general theory of the effect of variations in the orbits of the earth and sun on climate and thereby on the vegetation.

The timberline in northern Russia. The last glaciation affected timberlines in different ways in different parts of northern Russia. In the west it destroyed the preglacial vegetation almost entirely, with the exception of refugia in the Khibiny Mountains, the Northern Urals and Novaya Zemlya. From the Taimyr eastwards the ice sheet was discontinuous and tundra ecosystems of the present kind became established there. Thus a differentiation arose between the ecosystems of the western and eastern parts of northern Russia at a relatively early juncture (Tikhomirov 1961).

Afforestation of the land that emerged from beneath the ice in the Holocene began as early as 12 000 B.C., when birch and spruce spread to the area. The cooling of the climate around 8000 B.C. transformed the taiga in the western parts of the area into a forest tundra, but the forest advanced into the region again between 6000 and 4600 B.C. (Sirois 1992). According to the findings of Tikhomirov (1963) on the Yamal Peninsula, *Betula alba*, *Larix sibirica* and *Picea obovata* occurred 2-4 degrees further north during the postglacial climatic optimum than they do nowadays, and the trend was approximately the same in other areas, too. The retreat of the timberlines in response to cooling of the climate began about 2000 years ago (Tikhomirov 1961), and as noted by Tikhomirov (1963), the extent of the forests during the Holocene climatic optimum is well indicated by the composition of the dwarf shrub vegetation in the present-day tundra, which features taiga species such as *Betula nana, Empetrum nigrum, Ledum palustre* and *Linnea borealis* (cf. Larsen 1989). Solonevich (1940) regards the retreat of pine and advance of spruce that commenced on the Kola Peninsula at the beginning of the Subatlantic period as having continued until the present century. A detailed description of current and historical timberlines on the White Sea coast and in the Pechora region is provided by Andreyev (1956).

The northern timberline in North America. Although the timberline areas of North America are geographically relatively homogenous, clear differences exist between the eastern and western parts of the continent in the postglacial vegetation history and in the timing of the retreat of the ice sheet (Sirois 1992). The ice had melted around the mouth of the Mackenzie River by 15 000 B.C. and the scrub tundra was invaded by *Picea* species around 10 000-9000 B.C. Further east, however, remains of the ice sheet were still to be found in Quebec and Labrador until around 6500 B.C., after which spruce spread to the area under gradually deteriorating climatic conditions (Sirois 1992). Larsen (1989) notes that the location of the timberline has varied during the Holocene according to climatic fluctuations, and suggests that the summer temperatures in central Northern Canada were higher than average in the period 5500-4000 B.C., cooler than average in 4000-3000 B.C., higher again in 3000-2000 B.C. and cooler from 2000 B.C. onwards.

5.6.3. The Little Ice Age

The Little Ice Age has been one of the most significant of the climatic fluctuations of the present millennium, and has been the topic of considerable amounts of research. This climatic deterioration had major repercussions for agriculture, settlement and navigation, and for the whole development of society in some areas (see Flohn 1985). As noted by Grove (1990) in his extensive work on the Little Ice Age, this concept is usually taken to refer to the sequence of a few hundred years between the warm periods of the Middle Ages and the early 20th century during which the glaciers increased in size in many places. Grove describes the significant effects that this cold period had on the natural environment and on human activity, based on the large amounts of historical data available with regard to Europe in particular, and above all the Alps, Iceland and Scandinavia.

Fennoscandia. Existing historical documents and lichen measurements provide a fairly accurate picture of the Little Ice Age in Scandinavia (Karlén 1988). The glaciers of Norway increased in size steadily up to around 1750, after which their gradual retreat was punctuated by occasional short periods of growth, around 1780, 1810, 1820, 1840, 1840, 1890, 1910 and 1930. Kullman (1990a) defines the Little Ice Age as a period of global cooling of the climate covering the interval 1550-1880, during which cold summers and other extreme climatic conditions were common. It can be deduced from proxy data that the climate of North-West Europe during that period was 1-2 degrees colder than for a reference period in the 20th century, and Kullman demonstrates on the basis of hiatuses in the age structure of the forests that regeneration failed to occur in the alpine and northern areas of Scandinavia at some points in time and old pine forests perished. The state of health of the northern forests by the end of the Little Ice Age in the 19th century can best be described as very poor (Kullman 1990b).

The Little Ice Age has not been picked out as a regressive period in the forest history of Finland in the same way as in Scandinavia, although a period of unfavourable pine regeneration and radial growth has been detected in the 19th century (Mikola 1952, Sirén 1961). Correspondingly, the pessimistic views of future prospects for the timberline areas put forward in the first half of the present century are evidently attributable to the fact that the effects of the long cool period were still visible but no information was available on climatic fluctuations (Montell 1904, Renvall 1912b, 1919, Hagem 1917, Juul 1925).

As noted by Kullman, evidence of the effects of the climatic deterioration on timberline forests can be found in photographs taken at the turn of the present century and in travelogues from that time. In the case of Finland, direct comparisons can be made between such photographs, e.g. of the gold panning areas beside the River Ivalojoki, and the present-day situations. The reports of early forest surveyors concerning the timberline areas point systematically in the same direction. Malmborg (1896), for instance, described the state of the forests to the north-east of Lake Inari in the following manner: "It may be noted that the northern pine limit is receding southwards, to judge from the traces of a recently extinct pine forests found on the fell slopes. It should also be noted that entire pine stands, in which all the trees without exception have dried up, without this being caused by fire or by man, are found in valleys of the mighty Vätsäri fell. The above would indicate a deterioration in the climate." Kranck (1907-1909) analyzed dying pines at the timberline and noted that for the most part their deaths had not been caused by forest fires and that the dead trees were taller and of better shape than the stunted trees around them that had remained alive. He thus came to the conclusion that this could be explained only by a change in climate, and regarded drought as the fundamental reason for the deaths. The report of the Forest Protection Zone Commission (Komiteanmietintö 1910) put forward the firm opinion that the limit of birch forest, and even more obviously that of pine forest, was receding, and that the reason probably lay in a cooling of the climate. This relatively well documented situation at the timberline in the early years of the present century is highly illustrative and provides a realistic basis for comparison when considering the effects of possible future cold periods on timberline forests and a good starting point for considering the care that should be taken when evaluating the management of the forests in the protection zone.

Russia. The results of the dendrochronological investigations of Chernavskaya (1985) concerning the occurrence of *Larix gmelini* in Ary-Mas and material covering the whole timberline zone in northern Russia point to a clear decrease in radial growth during the Little Ice Age, with minimum values recorded in the early 17th and early 19th centuries. It is calculated that mean temperatures in northern Eurasia in the early 17th century were about one degree lower than at present. Shiyatov (1967) obtained results in the northern Urals which showed a general warming of the climate over the last 450 years, although with intervening cold periods, e.g. in the late 17th and early 18th centuries and in the late 19th and early 20th centuries. No forest regeneration took place at the timberline during these colder intervals and there were even some forest deaths, promoted further by the increased relative humidity in the late 17th century, which moved the optimum growth conditions for larch to drier areas with a thinner winter snow cover. The shift meant that the last cooling of the climate was still more damaging to the forests than the previous ones.

North America. Larsen (1989) and Sirois (1992) quote the reports of the explorer Hearne, who indicates that the timberline west of Hudson Bay still lay some 100-200 km further north in the 18th century than nowadays. They regard this as a clear example of the effect of the Little Ice Age. Elliot-Fisk (1983) mentions that dendrochronological investigations point to poorer than average growth in the intervals 1680-1720 and 1770-1880. Although Sirois (1992) notes that the Little Ice Age had only a minor effect on the timberline east of Hudson Bay, Lavoie & Payette (1994) explain that the forests of *Picea mariana* at the timberline in Quebec had degenerated to a krummholz form in the mid-19th century.

5.6.4 Climatic warming after the Little Ice Age

Fennoscandia. Kullman (1990a) describes a distinct warming of the climate in the Northern Hemisphere from the 1880's onwards, to reach a peak in the 1930's (cf. Heino 1978, Koutaniemi 1990). The first person in Scandinavia to draw attention to the effects of this warming on forest regeneration at the timberline, and to the abundance of young pines and their propitious development right up to the treeline was Hustich (1940), who later went on to discuss this trend in greater depth (Hustich 1948, 1958). A pine advance in the Petsamo area was observed by Aario (1940).

All the tree species reacted to this warming of the climate in the Scandes, and their treelines rose by an average of 40 m, and by as much as 100 m in some cases. This rise did not take place everywhere, however (Kullman 1990a). The birch treeline was also observed to have gained in altitude by some 40 m in eastern Norway (Aas 1969), while the inventory map of young pine forests in the Muotkatunturi area of Inari in 1958, published by Sirén (1970), shows new forests to be developing over extensive areas. When considering the same data at an earlier stage, Sirén (1960) notes that "the existence of young forests beyond the timberline and our knowledge of the periods of forest fires mentioned above should suffice to demonstrate conclusively that the climatic conditions of the past centuries cannot be regarded as the main reason for the retreat of the timberline imagined earlier to have been taking place". Having recently carried out a new inventory of the same area, Sirén (1994) notes that the treeline has advanced about 3 km in 50 years. Similarly, Sonninen (1993) comes to the conclusion that the treeline zone on the fell of Pyhätunturi has become a timberline zone as a consequence of the warm period in the 1920's and 1930's, while Kullman (1987) regards climatic warming as the main stimulus for the establishment of the young forests that had been generated earlier in the zone below the treeline, since this favourable period has ensured that the northern forests have remained healthy and viable right up to the present day (Kullman 1990b).

Although no detailed survey has been made of the structure of the pine forests in Finland in the zone immediately south of the timberline, age structure data from the forest inventories and information on human influence provide some grounds for the hypothesis that the generally old, sparse pine forests of the areas close to the timberline have assumed a normal density in the course of the present century. The starting point for such a comparison could well be inventories and observations made just before or after the turn of the century, in which the lack of young trees and saplings is a systematic feature. Renvall (1919) reported that no regeneration of pine had taken place in the timberline areas of Utsjoki and Inari since the good seed year of 1850, a firm indication of this being the total lack of tree growth in areas affected by forest fires since that date. Similarly, Moring (1897) mentions in the results of his transect inventory of the forests in eastern Inari that the tree stands become sparser towards the north and that there is no forest under 80 years of age. Further comparative material is provided by the map appended to the report of the Forest Protection Commission drawn up by Heikinheimo (Komiteanmietintö 1910), which points to an extensive zone with scattered pine forest.

Provided the effects of felling can be distinguished, later data on the age structure of the timberline forests can also be used to draw conclusions regarding developments during the present century. It was observed in the 1963-1964 forest survey of the Utsjoki district that forests of age 1-80 years accounted for only 3.7% of the area of forest land, but that a further 13.4% consisted of undergrowth, mainly in the north of the district (Metsähallitus 1964). The Seventh National Forest Inventory (Mattila and Kujala 1980) divided Northern Lapland into the zone of commercial forests and the protected forest zone, and indicated that 23.0% of the forest land of the former and as much as 39.9% of the latter consisted of young stands. Felling and reforestation had taken place over considerable areas of the zone of commercial forests since the 1950's, while the volume of felling in the protected zone had been much less and activity had been confined largely to the 1970's. The Finnish Forest Research Institute set up a network of permanent experimental plots in the protected zone in 1978-1980, and measurements were repeated at these in 1988-1990 (Timonen et al. 1993). The research material consisted of data on 113 selected pine-dominated sites which were in a natural or unmanaged state, 49.8% of these being young stands and 65.0% of age 1-90 years.

The plan drawn up by the Finnish Forest and Park Service for the state forests of the Enontekiö district (Metsähallitus 1995b) places the proportion of stands aged 1-80 years 40 % in the forest area outside forestry, approximately 16 000 ha. Most of the forest land of this kind is to be found close to the timberline in the area north of the road from Palojoensuu to Nunnanen. No forestry has taken place in this area and little wood has been cut for domestic use. The collective forest of Utsjoki, amounting to some 8000 ha of forest land, consists of plots in the Muddusjärvi and Syysjärvi areas, both immediately adjacent to the limit of continuous pine forest. The first plan for this collective forest was compiled in 1973 (Lapin piirimetsälautakunta 1973). No significant felling had taken place in the area prior to that time. Young stands, partly with hold-overs were stated to occupy 44% of the forest land. Similarly, Sirén (1994) points out that the roadside forests on the way to Karigasniemi provide a good example of the way in which the treeline zone of isolated pines of the 1950's has grown into an area of continuous forest. The management plan for the Vätsäri wilderness area describes near the timberline an open and uneven-aged forest zone in which the old forest has been filled in by trees that have developed during the present century (Tynys 1996; Figure 40). This extreme northern part of the pine zone can be regarded as an area which is labile in its development and dependent on the most minor of climatic fluctuations. Likewise Mikkola and Sepponen (1986) came to the conclusion that the mountain birch forests of the Könkämäeno valley near Kilpisjärvi are unstable communities liable to react to climatic variations in a highly sensitive manner.

Even allowing for the uncertainties involved in the classification of undergrowth and stands of uneven-aged structure, the above observations show that significant amounts of young forest stands have grown up close to the timberline during the present century which are not connected with felling. Similarly their existence over such wide areas cannot be explained by forest fires. Thus in addition to bringing about treeline changes, the warmer climatic period in the first half of the present century also had a more extensive and profound effect on the timberline forests.

Some of these young forests are now beginning to offer opportunities for forestry, the most illustrative example being the collective forest of Utsjoki, although the same situation also prevails in the northern part of the timberline pine forests of the Forest and Park Service. It is important, however, not to be tempted into excessively optimistic conclusions regarding the long-term development of these forests on the grounds of the volume and growth of the current young stands (fig. 41-42 Appendix 1).

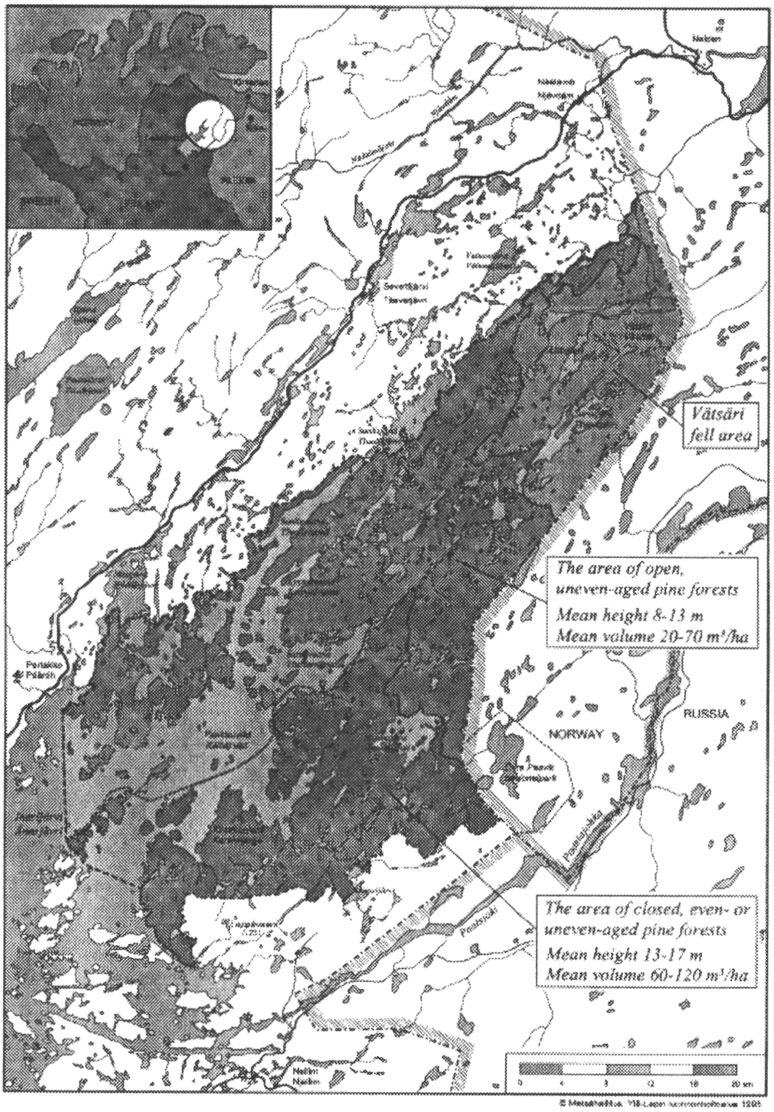

Figure 40. Landscape ecology zones of the Vätsäri wilderness area and their forest pattern, after Tynys (1995). The area of scattered pine forests south of the present timberline has filled in by natural regeneration during the 20th century.

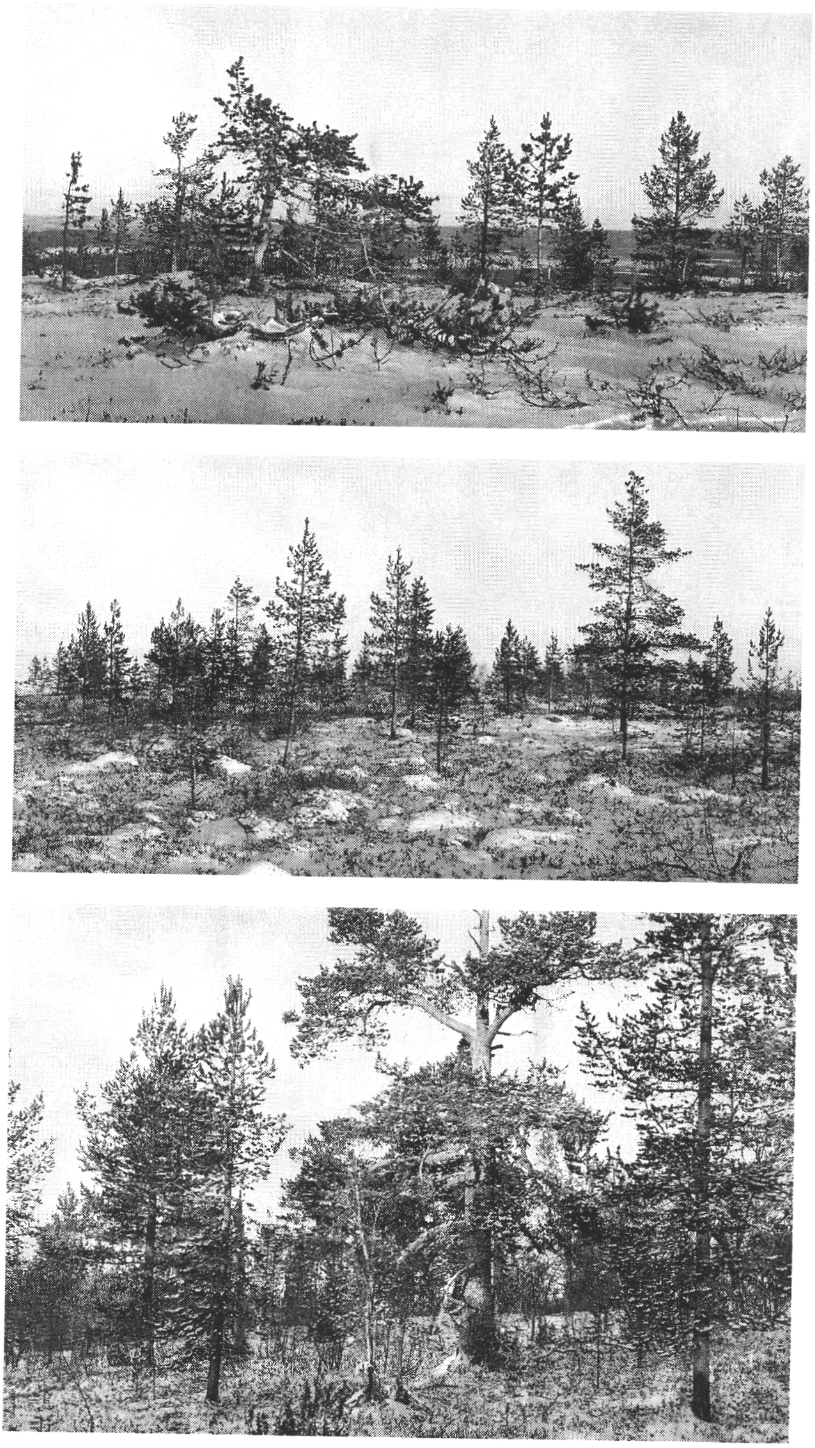

Figure 43. The forest of the low fell Naapää on southern side of the lake Inari tells of the developement during this century. Upper photo: The top of fell 385 m a.s.l. Young stem formed pine have grown among the old stunted pines. In the middle: Young pine forest dominates on the level 375 m a.s.l. Bottom: The old treeline of pine has filled in timberline, 340 a.s.l. Photo: Pertti Veijola 1995.

Russia. Tikhomirov (1963) mentions that many phytogeographers have continued to believe that the timberline is retreating southwards and downwards, even though in practice an advance towards the north is taking place as a consequence of climatic amelioration. Berg (1931), for example, citing Renvall's observation that good pine seed years in the area north of Lake Inari occur only once a century, estimated that the climate was deteriorating and the tundra advancing southwards, while Solonevich (1940) was of the opinion that pine was receding on the Kola Peninsula and reported that there were few young pines in the timberline zone.

Probably the first scholar in the world to note an advance of the timberline was Zhuravski (1915), who based his observation on seven years of investigations in the Pechora region and the tundra of Bolshezemelskoi. His main conclusions were that, with the northerly retreat of the Arctic Ocean, the timberline was also moving towards the north, that natural regeneration was detectable, that the climate was becoming warmer and that good prospects existed for settlement in northern regions.

Tyulina (1936) similarly noted a forest advance in connection with a basic survey of the forests of the Anadyr region performed in 1931 and 1932, and came to the conclusion that in view of fluctuations in the climate, the timberline had run further south in the recent past and was now advancing northwards. Tyulina was aware of the more or less contemporaneous observations of Griggs on forest advances in Alaska, and regarded these results as confirming the notion put forward by V.N.Sukatsev that cold and warm climatic phases drift in a wave-like manner from east to west. P′yavchenko (1956) had detected a forest advance in the Pechora region in the early 1950's, and Andreyev (1954, 1956) recounted parallel findings in the Nenetsky area, where he had carried out a new inventory of isolated patches of forest surveyed previously in the 19th century. He had also found areas within the northernmost taiga forest which could be regarded as relicts of tundra, and concluded that the forest had advanced to surround these. He estimated the rate of this change at approx. 200 m per year over the last 500 years, although it had not been so rapid at the early stages of climatic warming (Andreyev 1956). The total distance involved had been some 50-75 km in the Pechora region. Kryuchkov (1978) concluded in turn that no northward movement of the treeline had taken place on the Kola Peninsula in spite of the warmer conditions, because periods conducive to frost drought had also become more frequent.

Tikhomirov (1953) mentioned that research carried out under his direction had led to the observation of forest advances in a number of mountain areas, including the Khibiny Mountains, and Kozubov and Shaidurov (1965) found that the pine treeline in this latter range had been rising since the 1920's, as evidenced by the existence of young, straightstemmed pines in the midst of older, contorted ones. Gorchakovski and Shiyatov (1978) report that the upward movement of the timberline in the Khibiny Mountains began more than 200 years ago and that the *Betula tortuosa* treeline had risen more markedly over the last 30-40 years. They regard this as part of a general advance in alpine timberlines in the boreal zone. Shiyatov (1967) observed three generations of *Larix sibirica* at the timberline in the Urals, each connected with a warm climatic period: old (1630-1690), middle-aged (1780-1850) and young (from 1920 onwards). These periods were also ones in which radial growth was most pronounced. Puzachenko (1985) found larch to have prospered in the Putorana Mountains approximately in the period 1770-1800 and again from the 1920's and 1930's onwards. All told, the forest tundra zone had moved upwards by some 50-100 metres within 200 years.

In his summary of the views expressed in Russia on this topic, Kryuchkov (1978) notes that differences of opinion prevailed among researchers for a fairly long time as to whether the forests of all the subarctic areas of Eurasia were advancing or retreating, and he emphasizes that climatically different areas need to be examined separately in this respect. Estimates regarding the advance of the forests in Russia have been used as a basis for assessing the possibilities for silviculture and agriculture (Tikhomirov 1953, Andreyev 1954).

North America. Griggs (1937) was the first to point to an advancing trend in the forests of North America, based on observations on Kodiak Island, Alaska, where he estimated that *Picea sitchensis* was advancing at a rate of about a mile a century. He noted in particular the sharply defined nature of the timberline on the island, and the good growth potential and seed production capacity of the timberline stands (Griggs 1946). These stands were some 50 years old, and quite normal mature forest was to be found only 3 miles further south. The change in the timberline is also confirmed by historical data. At the same time Griggs mentioned that the timberline in the Rocky Mountains had remained stationary for a long time and that that on Mount Washington in the northern Appalachians was evidently receding.

Viereck (1979) concluded that the timberline in Alaska had remained stable for centuries in many areas, but that it had begun to advance noticeably over the last 40 years in central and western Alaska and for somewhat longer on Kodiak Island. Marr (1948) was of the opinion that the forests of Labrador were spreading northwards as suitable loose deposits became available in which it could grow, and Payette & Filion (1984) noted an advance of *Picea glauca* at the timberline in Quebec, especially during the interval 1920-1965. The main effect to be observed was nevertheless the increased density of the forest stands. Regeneration of the coniferous forests of central and western Canada improved during the period 1880-1940 in connection with the warming of the climate, and the same was observed in the east of the country in 1900-1970 (Elliot-

Fisk 1983). Payette et al. (1989), in their study of the history of *Picea mariana* at the northern timberline in Canada over the 1000 years, claim that the warming of the climate during the present century has not compensated for the effects of the Little Ice Age, nor is any positive development observable in the timberline stands. Lavoie & Payette (1994) conclude that the *Picea mariana* timberline has advanced some 4 km since the late 19th century, as the krummholz stands have now adopted an arboreal form as a consequence of the warmer winters. The forest advance is in any case not regarded as such a comprehensive phenomenon in North America as in Russia, and obvious discrepancies exist between different parts of the continent.

In his summary of the amelioration in tree growth at both northern and alpine timberlines in Europe and North America, based on over 40 studies, Innes (1991) describes this effect as beginning in the most favourable climatic regions. Its existence is supported by many descriptions of timberline advances over the last hundred years. The author's conclusion regarding the timing of the improvement in growth is particularly interesting, and is consistent with the views recounted above that the earliest observations of timberline advances concern areas of Russia where climatic conditions are poorer than in Fennoscandia (e.g. Zhuravski 1915). Of the Russian research, Innes refers only to the work of Gorchakovski and Shiyatov (1978). The following summary of Holocene changes in northern timberlines (Figure 44) was constructed by Sirois (1992).

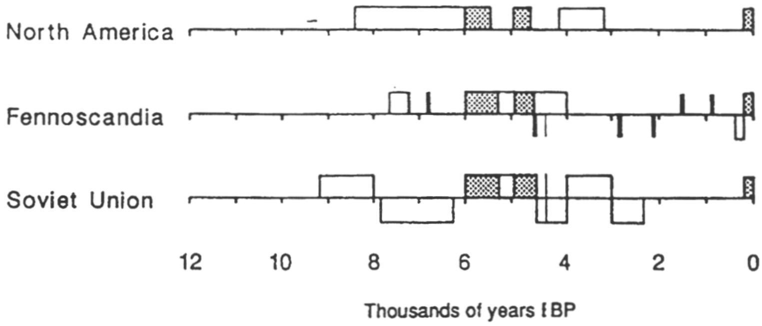

Figure 44. Diagrammatic representation of Holocene fluctuations in the timberline in the circumpolar forest tundra zone (Sirois 1992). Deviations above the line indicate advances and deviation below it regressions. Parallel trends in the three regions are shaded.

5.6.5 The current cooling of the climate and the greenhouse effect

Eriksson (1988) announced that the climate in the North Atlantic had been deteriorating for the last 50 years, while Glawion (1986) estimated that the drop of about 0.8°C in mean temperatures in Iceland since 1965 had reduced the potential forest area of that country by approximately 2500 km². Solantie (1992) observed a cooling of the climate in Finland upon comparing climatic data for 1931-1960 with corresponding data for 1961-1990. Kullman (1990a, b) likewise noted that the effects of a deterioration in the climate of Scandinavia are to be seen to some extent in the timberline birch and spruce forests of the Scandes but that the pine treeline has risen relative to the situation in the 1970's in spite of the cold summers. Kullman (1991a) reports results for the Tärna area which point to a retreat of spruce and birch on account of the late melting of the snow and lower soil temperatures. On the other hand, a certain inertia can be seen in the reaction of pine, which is still growing well in spite of the cooler conditions. Kullman (1993a) notes that the birch treeline has not declined in these mountains even though the climatic deterioration has been going on for some 50 years, affecting its growth and reproduction capacity. He had already estimated, in fact (Kullman 1990a), that regeneration by seeding has probably been virtually nil in all the tree species at the treelines in the Scandes for the last twenty or thirty years. He claims that insufficient attention has been paid to the declining condition of the old forests caused by the deterioration in the climate, or else it has been attributed to air pollution. In his opinion the timberline regressions documented earlier in the Holocene took place by the same mechanism.

The results of Tømmervik and Johansen (1992b) in Troms suggest that the treeline for mountain birch on nutrient-poor growing sites has remained stationary or regressed slightly over the last 30 years, whereas it has risen by as much as 35 m at better sites. They therefore regard birch forests occupying poor sites as more susceptible to climatic fluctuations than those growing at favourable sites, the prospering of which must have been partly promoted by the cessation of grazing. Changes in humidity are also thought to be implicated in these effects. Holtmeier (1993) concluded that the main reason for the rise of treeline in Alps during last decades has been the cessation grazing and not the amelioration of climate.

There is no information to suggest that the cooling of the climate has lowered the timberline in Finland, and although the cold summers of the 1960's are generally regarded as being clearly reflected in forest planting results in Lapland (see Leikola 1979), no corresponding problems have been encountered in naturally regenerating young forests. Eronen (1981) conjectures that the natural distribution area of pine in Northern Lapland seems to be extending northwards at present, but adds that it will be a long time before we can be certain that this is the case. Similarly, Holtmeier (1974) emphasizes that no far-reaching conclusions can yet be built up on the fact that the treeline appears to be advancing.

Sirén (1993b) observes that pine obviously occupied new territory in the Muotkatunturi area of Inari during the period 1951-1990, with new pine stands of an average density of 17 stems per hectare having become established on open, birch-dominated fell terrain at an altitude of 360-400 m. Likewise, the tree line has advanced northwards by up to 3 km on average over the last 50 years (Sirén 1994). Vormisto (1992), in her investigation into natural regeneration of pine, spruce and birch in the timberline zone based on timberline monitoring carried out by the Finnish Forest Research Institute in which inventories were made in 1989 of experimental plots established on many fells in 1983-1984, notes that young pines, spruces and birches had begun to grow in these areas over the last 20 years and that the proportion of pine and birch seedlings of less than 10 centimetres was high at the treeline. Engelmark and Zackrisson (1985) quote an example of regeneration at the pine-dominated timberline in the area of Lapland inland from Piteå as a consequence of a forest fire in 1711 and mention that the majority of the young pines originate from the period 1920-1960, most of them being above the timberline, whereas the young spruces had seeded earlier, at a time when pine had not been able to regenerate at all. This advance of pine at a time of cooler climatic conditions cannot be regarded solely as a matter of inertia, as generative reproduction has taken place as well.

In Canada, Elliot (1979) attributed the lack of reproduction by seeding to the cooling of the climate that began in the 1940's, while more recently, Landhäusser and Wein (1993) predicted on the basis of their analysis of the development of the vegetation in an area devastated by fire in 1968 that the treeline would move further north in connection with the warming of the climate, chiefly as a result of efficient reproduction by *Betula papyrifera* and *Populus balsamifera*. They also put forward the hypothesis that fires of this kind are themselves apt to promote an advance in the treeline. Bryant and Reichardt (1992) considered that the *Betula* and *Salix* species, with their capacity for invading new areas and their resistance to disturbances, would profit most from an advance of the forest towards the tundra. They also predicted that the cover percentages of the grasses and sedges would decrease, causing difficulties for animal species grazing in the tundra and thereby affecting the livelihood of the aboriginal people of the arctic regions.

No evidence has been put forward of any detrimental effect of climatic deterioration on timberlines in Russia over recent decades. Gorchakovski and Shiyatov (1978) mention that although the treeline has continued to advance, the cooling of the climate is likely to cause it to decrease in altitude in many alpine timberline zones, and likewise Andreyev et al. (1987) note that *Larix gmelini* is continuing to advance at the northern timberline in Yakutia. Orlova (1972) reports on the occurrence of viable pine saplings 1 - 1.5 m in height in the forest tundra and even the tundra area between Uraguba and Titovka to the west of the Kola fjord and concludes that pine would be capable of growing further north than it does at present in the western part of the Murmansk region. Likewise extensive stands of healthily developing young pines were to be seen beside the Murmansk-Petsamo highway in the area between the Kola fjord and Pervomaisky in autumn 1995, but very few old pines.

Zavelskaya et al. (1993) put forward very far-reaching estimates of the probable warming of the climate and its consequences, including a movement of the timberline some 200 km further north at a rate of 80-500 m a year. The changes would also affect the species composition of the forests, in addition to which the lower rainfall and attendant increased risk of fire would favour an increase in the proportions of pine and larch. Spruce and pine can be expected to improve their position relative to larch on account of the reduction in permafrost depth, but larch will be able to compete better than at present in felled areas.

Puzachenko (1985) criticized the predictions of a rapid change in connection with the greenhouse effect, stating that relatively rapid progression would be possible only in mountain areas with a maritime climate in the presence of variable edaphic and orographic conditions and a reliable availability of seed. On the other hand, he believed that the warming effect would lead to rapid changes in the brush tundra north of the timberline, where the vegetation is able to react to climatic fluctuations more rapidly, and estimated that if the warming trend continues the northern treeline could advance by as much as 100-200 kilometres in 1000 years, even though the forest as such could not be expected to advance any more quickly than the rate at which natural afforestation occurs in large-scale forest fire areas in the northern boreal zone, for instance. Tyrtikov (1995) have stressed the negative effects of paludification on the northern timberline in Asia.

The major international research project on climatic change, the IPCC, came to the conclusion that the greenhouse effect is already observable at the global level and that mean temperatures can be predicted to rise globally by about one degree by the year 2025 (Houghton et al. 1990). As pointed out by Jantunen and Nevanlinna (1990), however, the world's research community appears to be divided into two camps with respect to opinions on the greenhouse effect: those who believe that we already have sufficient evidence of the effect of the greenhouse gases on temperature, and those for whom this whole climatic change is as yet an unsubstantiated theory. Kauppi and Posch (1985) conclude that the greatest absolute increase in vegetation growth as a result of the greenhouse effect is to be expected in southern areas with a maritime climate, whereas the relative increase would become greater towards the northern maritime regions. Hari et al. (1992), in turn, interpret the preliminary calculations based on growth and production models as suggesting that the broadleafed trees will improve their competitive position relative to the conifers as the climate becomes warmer, and that the productivity of forest ecosystems will increase. In Northern Finland in particular, this increase in productivity can be expected to be accompanied by an invasion of the currently almost treeless areas lying beyond the timberline by productive forest, even though Karjalainen et al. (1991) emphasize that there will also be risk factors attached to this change in forest area and forest yield in Finland. Overpeck et al. (1990) also point to possible increases in disturbances in forest ecosystems as the climate warms up.

All in all the assessments of the possible effects have up to now been relatively general and preliminary in character as regards the variations in the predicted rise in temperature, cf. on the one hand Fortelius et al. (1992) and on the other hand Briffa et al. (1990), for example, who conclude that no evidence of warmer summers will be detectable in Fennoscandia until some time after the year 2030. Varjo (1986) predicts that yields of grain crops in Finland will increase significantly in the future in response to climatic warming.

Innes (1991) points out that it is necessary when considering the effects of climatic warming caused by increased concentrations of greenhouse gases to remember that, at least in some areas, tree growth will also be promoted by the fertilizing effects of nitrogen deposition and increased carbon dioxide concentrations. Similarly, Ross (1992) observes that little is known of the changes in precipitation that are likely to follow from warming of the climate. If precipitation decreases, the risk of forest fires will become greater. This is already the most pronounced stochastic disturbance factor in regions with a continental climate, and both the frequency of fires and their extent are known to be greater in dry areas. As Ross puts it, the vegetational changes brought about by climatic warming will be easier to observe in the vegetational succession following fires than in the original plant communities. The simulations carried out by Bonan et al. (1990) lead them to deduce that the effects of warming of the climate in Alaska will not be direct ones as much as indirect, operating through mechanisms connected with the increase in potential evapotranspiration. It is also pointed out by Kullman (1990b) that the process of predicting the future warming of the climate as a result of greenhouse effect may have incidentally diverted attention from the true state of the climate at the present time (cf. Heino 1994). Kullman (1991b) is of the opinion that results obtained in Swedish Lapland do not support the hypothesis that the elevated atmospheric carbon dioxide concentrations have improved forest growth at the timberline.

5.7 Conclusions

The factors affecting the dynamics of the timberline are the distribution history of the tree species concerned, the vegetation succession, climatic fluctuations and human activity. Different ideas have been put forward on the nature of the vegetation succession in timberline forests, but it is evident that the same species dynamics as will be found in normal boreal forests cannot be assumed to prevail in these areas. Forest tundra biotopes in particular are not subject to the same succession as closed-crown forest, as the success of the trees is determined directly by primary growth factors. Also, the ground vegetation develops in a different way from that of either a taiga or tundra biotope on account of the permanently sparse tree layer. The relation between conifers and mountain birch in the species dynamics of treeline forests also differs from that between conifers and the pubescent birch in boreal forests. The mountain birch is quite obviously not a pioneer species that will give way to others as the succession proceeds, but rather its relation with pine is best described by a model of two parallel states of equilibrium regulated by climatic fluctuations and external disturbances.

It is often difficult to distinguish the effects of climatic fluctuations from amongst the overall vegetation dynamics, and it is particularly important when analysing changes to define clearly the time scale over which they are being examined. There is substantial agreement over the general features of the Holocene distribution history of the tree species in Fennoscandia, although differing opinions exist on the timing of the Little Ice Age, approx. 1550-1880, and its effects on timberlines. The advance of timberlines in the first half of the present century has been accepted as a circumpolar phenomenon which was observable first in Russia (Zhuravski 1915) and later in Finland, only in the 1940's (Aario 1940, Hustich 1940). One consequence of this trend is the common existence of young pines at the northern timberline in Finland, although no definite predictions can be made as to what future they may have.

Seeding and the growth of young forests has been observed in Finland in areas south of the treeline, and the areas of scattered pine forests, and to some extent those of scattered isolated pines, have gained sparse forests of varying structure which can be regarded as forming a labile forest zone strictly regulated by fluctuations in climate. Little attention has been paid to this change so far, even though it is clearly detectable in forest inventories and other surveys. The filling in of timberline pine forests to form a closed-crown forest zone during the warmer climatic phase in the present century has led to a situation in which the abundance of young trees has made the forests close to the timberline more viable than many denser commercial forests located further south, where regeneration takes place very slowly under present-day climatic conditions. These young forests can be expected to continue to grow favourably even if the climate becomes cooler, as vegetative development is not so critically dependent on temperature as generative reproduction. The most serious threat to them would be the action of frost drought on poorly hardened shoots resulting from cold growing seasons.

The detrimental effects of the period of cooler summers that began in the 1940's have already been detected at the timberline in the Scandes and in North America, but not in either Russia or Finland. Nevertheless the rarity of good seed years and the incidence of frost drought following the coldest growing seasons provide illustrative examples of the effects of cold climatic periods.

Variable notions exist of the timetable of the greenhouse effect and its influence on growing season temperatures. Although the general warming trend is regarded as more or less a certainty, regional and seasonal predictions are still somewhat indeterminate. The current cooler period prevailing in the timberline zone and evaluations of the effects of this should not be allowed to be overshadowed by the extensive body of research devoted to the global warming trend. The simulations available for the effects of warming on forests (see Karjalainen et al. 1991, Hari et al. 1992) are of a general character and do not take account of the particular circumstances prevailing at the timberline in Fennoscandia. Holtmeier (1995) came to the conclusion that timberline advance in connection of global warming will not run parallel to an altitudinal and northward shift of any isotherme considered to be essential to tree growth. He stressed the importance of site history and other regional and local factors.

If the well-founded argument of Kryuchkov (1978, 1987) and Puzachenko (1985) that the northern timberline in Fennoscandia is not primarily regulated by thermal factors is correct, evaluations of the effects of climatic change should place more emphasis on changes in precipitation, relative humidity and winds. If the rise in mean annual temperatures implies a rise in winter temperatures and an increased probability of spells of warm weather, the effect on conifers in particular is likely to be a detrimental one, as the danger of frost drought will increase. Although warming of the growing season will increase the yields of germinating pine seed, no rapid northward progression of pine can be expected, as the mountain birch zone to the north constitutes a permanent ecosystem with which pine would be unable to compete in the absence of serious external disturbances. On the other hand, any northward advance of the mountain birch forests in Finland would be effectively prevented by the pronounced effects of reindeer grazing.

In connection with the dynamics of timberlines, one is also obliged to consider the inertia and time-lag factors associated with the reaction of trees to environmental changes. Little attention has been paid to these mechanisms in Finland, where there has been a tendency to assume a direct reaction to climatic effects, even though the view of Holtmeier (1985) that old timberline forests in particular tend to react to deteriorations in growing conditions in a detailed, individual manner and with a long delay would seem to be logical and well justified. Similarly it may be assumed that reactions to even a short period of change in a favourable direction will be more rapid, as it will be mediated by their reproductive mechanism, although there are evidently clear distinctions between species in this respect. In addition, the behaviour of shade trees at the boundaries of vegetation zones is affected by the hysteresis factor arising from the forest microclimate, which contributes to the fact that the timberline is not determined directly by temperature conditions (Bogatyrev 1991, Vedyushkin et al. 1995).

One should be wary of reaching precipitous conclusions regarding possible changes in the timberline on the grounds of the rise of young forests during favourable periods (Shiyatov 1967, Holtmeier 1974, 1985, Kullman 1983). Hustich (1966) noted that we are liable to make excessively far-reaching forecasts on the basis of even quite short periods of favourable conditions, and attention has also been drawn to the significance of rapid changes of the hazard type for timberlines (Hustich 1966, Seppälä and Rastas 1980, Kullman 1989). It is difficult to assess the effects of rapid changes a long time after the event.

6 Timberline forests

6.1 Proximity of the timberline

Timberline forests are looked on as possessing certain properties that need to be taken into account when considering their utilization. Those designated as protected forests require particular care to be exercised with regard to all management procedures, since their primary purpose is to ensure the permanence of the timberline. Their designation as such has usually taken place by formal administrative decisions made in accordance with official regulations, a process in which actual ecological information defining the proximity of the timberline serves merely a background function. On the other hand, proximity to the timberline cannot be restricted only to administratively defined protected zones but should be open to examination on a broader basis. It is in any case a far more widely used concept, applying to the discussion of many elements of the natural environment, economic activity and culture in northern and mountain regions, and is as such used relatively freely, without any attempt at a more precise definition.

The discussion of the timberline as an ecotone in Chapter 2 concluded with the notion that in the narrow sense, this zone extends from the treeline to the current physiognomic forest limit. The northern timberline ecotone is usually interpreted as a forest tundra that is regarded as part of the boreal zone or tundra, although it can also be taken as forming a vegetation zone in its own right. The emphasis here is on the forests of the southern part of the broadly defined timberline ecotone, i.e. lying close to its southern or lower zone boundary, which can be regarded as coinciding with the notion of the economic timberline, the boundary of the area within which regular regeneration occurs and normal forestry practices can be observed. Proximity to the timberline also has aspects which impinge upon cultural anthropology and geography, and definitions have been provided starting out from phytogeography, geography, forest science or practical forestry.

6.2 Phytogeography

6.2.1 The boreal zone

The dependence of the world's vegetation on climate may be appreciated from the similarity between the systems of climate zones and vegetation zones. As explained by Ahti et al. (1968), most phytogeographical zonations are either edaphic-topographical, bioclimatic or floristic, of which the first-mentioned are most suitable for relatively small areas and the second for global systems. In practice, most classifications make use of varying combinations of climatic, edaphic, floristic, ecological and phytosociological criteria (Ahti et al. 1968). The general bioclimatic zonations are usually based on variations with respect to three gradients: temperature, continentality/maritimity and aridity/humidity. The chief units in such systems are 'zones', which characteristically run parallel to the lines of latitude and are most closely linked with temperature factors, while the corresponding concept in terms of altitude is the 'belt'. 'Sectors' may then be defined in a direction parallel to the lines of longitude, and represent above all degrees of continentality/maritimity, while 'provinces', which can be either latitudinal or longitudinal in orientation, are associated with the degree of humidity. The general term 'region' can be used for any area defined in this system (Tuhkanen 1984).

The northernmost and uppermost zone in the international classification system for European forests in a natural state, which seeks to combine the views of different schools on this topic, consists of the main group of subarctic and montane-subalpine forests and brush (Neuhäusl 1990). Finland forms a part of the boreal vegetation zone, which covers a strip over 1000 kilometres broad spreading over the northern areas of Eurasia and North America. North of this is the largely treeless arctic zone, the altitudinal correlate of which, the oroarctic (alpine) zone extends to the fells of northern Finland. The boreal zone is commonly subdivided into four parts: the hemiboreal, south boreal, middle boreal and north boreal subzones (Hämet-Ahti 1988). Walter and Breckle (1986) refer to this zone in Eurasia as the Eurosiberian boreal coniferous forest zone, in which the Scandes and the Khibiny Mountains stand out as distinct orobiomes. The coniferous forest zone is divided in terms of continentality/maritimity into the following subzonobiomes, or sectors:

1. An obviously maritime western sector with an abundance of birch.

2. A mildly continental sector with *Picea abies*, extending as far as the River Dvina.
3. A continental sector, the 'dark taiga' continuing as far as the River Yenisei.

4. A highly continental sector, the 'light taiga' of eastern Siberia.

5. An extremely continental sector around the Rivers Lena and Yana.

6. The markedly maritime Kamchatka sector, with birch and alder.

In the Russian subclassification, which deviates somewhat from the subzones of Ahti et al. (1968) and Hämet-Ahti (1988), sectors 2, 3 and 4 are distributed over the northern, middle and southern taiga. The generally accepted northern boundary of the boreal zone and southern boundary of the arctic zone is the climatic treeline at an average growing site under 'placor' conditions (see Bliss and Matveyeva 1992).

Neither Ahti et al. (1968) or Haapasaari (1988) regards the tree layer as decisive for defining the zones, and Mikkola and Sepponen (1986) also note in the case of the timberline birch forests of the Kilpisjärvi area that the limit of birch forest as such forms a relatively unstable zone that is highly sensitive to changes in the macroclimate by comparison with the vertical belts observable in the surface vegetation. The definition of the maritime sectors located on the edges of the continents in the boreal zone has generally proved something of a problem, which is further compounded by considerable variations in topography which make the relations between the units extremely complex. By comparison with the situation in the flat areas characteristic of the continental sectors, the zones are compressed together, as it were, and take on various special features brought about by the maritimity factor itself. Other areas of this kind apart from northern Fennoscandia are Alaska, Labrador and Anadyr (Hustich 1979). We will now take a closer look at the northern part of the boreal zone in Fennoscandia from both a western and a Russian viewpoint.

6.2.2 Regions of northern Fennoscandia

Western viewpoint. Varying notions have been expressed on the phytogeographical regions of Scandinavia and Finland in the area close to the timberline. The early proposal by Wahlenberg (1812) has continued to be reflected in the systems put forward up to the present, and his main principles still hold good (Rune 1965). Kihlman (1890) concluded his timberline research with the view that the Lapland forest region can be divided into two parts: a coniferous zone and a birch zone, where the boundary of the coniferous forests runs in principle at the limit of generative reproduction of spruce, since this species is climatically more resistant than pine. The reason for the occurrence of pine further north than spruce is that the latter has been banished from the most northerly sites for the time being on account of forest fires. Kihlman regarded the birch zone as probably an extreme part of the coniferous zone climatically, an area where spruce could still have grown but to which it has not been able to spread because of a lack of seed production.

Ahti et al. (1968) assign all the more or less flat areas of Lapland north of a line Kolari-Kittilä-Kemijärvi to the north boreal zone, together with Kuusamo and northern Kainuu in the east. In the north the same zone comprises the mountain birch forests on the fells and the treeless areas on the coast of the Arctic Ocean, likewise the forests of the Kola Peninsula and wide areas of the forests to the east of the Scandes in Sweden. This system covering the whole of North-West Europe allows assessment of conditions in the proximity of the timberline largely in terms of a division of the north boreal zone into sectors. The work of Ahti et al. (1968) and that done by Haapasaari (1988) in filling in some of the details possesses an interesting point of contact with the relatively treeless zone of Kryuchkov (1978), which contains many of the same areas as the treeless parts of the north boreal zone in their classification. Oksanen and Virtanen (1995), in their adjustment of the definition of the vegetation zones in northern Fennoscandia, define the boundary between the north boreal and hemiarctic zones in terms of climatic indicators and features of the ground vegetation. This interpretation also seems logical as far as the arboreal vegetation is concerned, since the north boreal zone contains not only pine forests but also the pine - birch transition zone and the closed mountain birch forests.

The forest tundra as defined by Hustich (1966, 1979) comprises the area between the treeline and the economic timberline, and Hustich (1979) defined the subarctic region as coincident with the forest tundra. Since the southern boundary of the subarctic region on the map presented by Hustich (1960) is approximately the limit of pine forest in Finland, we can conclude that Hustich places the economic timberline remarkably far north, or else the definitions are not consistent. Corresponding definitions are nevertheless accepted by Kallio et al. (1969) (Figure 45). Kalliola (1973) observed that the fell region of Lapland can be regarded as part of the circumpolar subarctic zone, an interpretation which clearly designates the mountain birch forests and isolated pines as subarctic, and thus as timberline forests. Kryuchkov (1976) defined the southern limit of the northern taiga as the southern boundary of the subarctic zone and recommended that timber cutting for industrial purposes should not extend north of that line. The question is complicated further by other definitions of the subarctic zone which describe it as extending very much further south (e.g. Löve 1970, Varjo 1986). Blüthgen (1970) was of the opinion that regarding the timberline as the southern boundary of the subarctic was not a satisfactory solution and emphasized the importance of the economic forest limit. Thus he preferred to draw the southern boundary of the subarctic as the point where a satisfactory seed yield is obtained at 5-10-year intervals. Thus the subarctic as indicated on Blüthgen's map includes Forest Lapland, the forests of northern Norrbotten and the whole of the forest region on the Kola Peninsula, designated as the southern paraboreal region. This can in principle be regarded as valid as a definition of timberline forests.

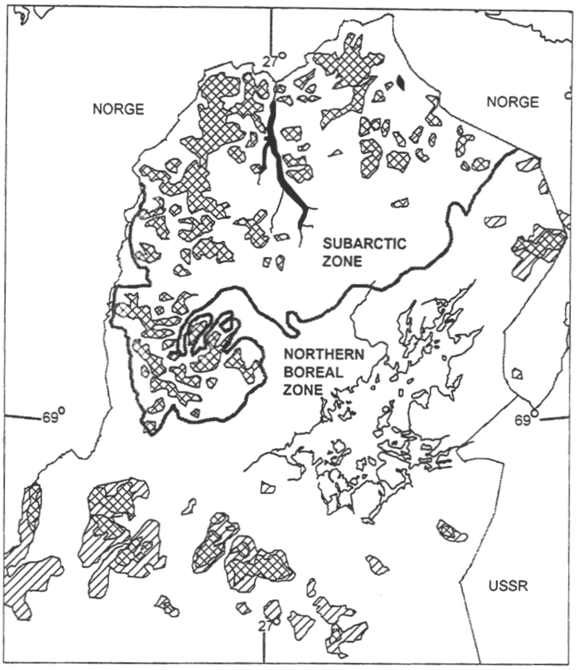

Figure 45. Vegetation zones of the Inari district of Lapland (Kallio et al. 1969). Subarctic zone: dense shading = alpine zone, black = separate pine forests. North boreal zone: dense shading = alpine zone, hatching = subarctic zone.

Kalela (e.g. 1961), concentrating on regional differences in the forest vegetation on the basis of the theory of forest site types and starting out from the situation in Southern Finland, distinguishes as his main zones the Finnish archipelago, the Finnish coniferous forest zone (subzones Southern Finland, Ostrobothnia, Perä-Pohjola and Forest Lapland) and the birch zone of Northern Finland (subzones the continental fell region of Lapland and the maritime fjord region). In the terms of Ahti et al. (1968), Southern Finland, Ostrobothnia, Perä-Pohjola and Forest Lapland are parts of the boreal zone and the fell and fjord regions of Lapland belong to the forest tundra. This system weighted in favour of the ground vegetation has been used extensively in forestry contexts and has provided the framework for a more general division of Finland into phytogeographical regions, as set out by Kalliola (1973). The latter author also likens the highest hill sites in Kainuu to conditions in Perä-Pohjola and those in Perä-Pohjola to those in Forest Lapland, even to those of the subalpine or alpine zones to some extent. The main distinctions between the Forest Lapland and Perä-Pohjola in the opinion of Kalela (1961) were the absence of spruce from the former and its domination by pine, the sparseness of the forests, the common occurrence of nutrient-poor soils, the appearance of dwarf shrubs characteristic of mires at sites of all types, the rarity of southern floristic elements and the spread of subalpine species.

In the system of forest growth regions put forward by Koivisto (1971), the Northern Lapland region, which stands out clearly from that of Perä-Pohjola, is practically identical to Kalela's Forest Lapland. Eurola (1978) came to the conclusion that the latter region possessed mild indicators of forest tundra features and could perhaps be regarded as a westerly equivalent of the southern forest tundra in which the absence of permafrost in the mineral soil meant that the forests were denser, grew better and were more extensive than in the forest tundra of Russia. Correspondingly, he conjectured that the Fell Lapland could perhaps be looked on as a western equivalent of the northern forest tundra subzone. The southern boundary of Forest Lapland can arguably be regarded as the limit of the timberline forests, even though the conditions for forest regeneration were not considered when defining the region. Kujala (1964) defined his Lapland region on floristic grounds in a manner which approximately coincides with the area north of the boundary of Kalela's Forest Lapland, and then divided this into a northern and a southern part. If one wished to define the timberline forests more precisely, a suitable limit would be the southern boundary of this Northern Lapland region of Kujala, in which case the zone would incorporate also the northern edges of the administrative districts of Muonio, Kittilä and Sodankylä and a strip of Eastern Lapland from northern Salla to the fells of Saariselkä. Solantie (1980) places the northern boundary of the Perä-Pohjola region in his system of climatic regions at approximately the same level, regarding the Inari basin and the Teno valley as belonging climatically to the same region and differing radically from the surrounding, higher areas of the fell region of Lapland and Saariselkä.

In his system of vegetational zones for northern Europe, Sjörs (1967) distinguishes the Scandes and their continuations as forming alpine zones, below which one finds the subalpine birch zone, which may be regarded as the northernmost part of the boreal zone. This birch zone reverts to forest tundra further east, where it clearly occupies a position north of the pine timberline. The uppermost subzone of the coniferous forests in the Scandes is the 'fjällbarrskog', a term adopted earlier by Du Rietz (e.g. 1964). Sjörs appended to this the extensive north boreal subzone definable in Finland and Russia. The above-mentioned subdivisions of the boreal zone may together be considered subarctic. Sjörs notes that typical features of the 'fjällbarrskog' subzone are a pronounced admixture of birch and poor regeneration on account of the rarity of seed years. Coniferous forests on dry sites are very sparse in this zone and grow slowly, while the mesic sites characteristically possess a thick humus layer which is detrimental to growth. Sjörs (1967) reckoned that poor chances of natural regeneration constituted the main reason for the failure of the closed coniferous forests to extend any further. The birch zone, forest tundra and coniferous fell forest (fjällbarrskog) can justifiably be regarded as timberline forests, whereas the north boreal subzone, which Sjörs associates with his 'fjällbarrskog' region, is a more extensive notion. Sjörs (1963) had drawn attention previously to the sparseness of the forests as an important phytogeographical criterion. Rune (1965) comments that much research has been devoted in Sweden to the upper boundaries of vegetation zones, to the exclusion of their lower boundaries, and maintains that the only available boundary for the fell region in the east is a geological one, in that the limit of the Caledonides and their bedrock region also serves as a clear vegetational boundary.

The set of phytogeographical regions for northern Fennoscandia proposed by Eurola and Vorren (1980) on the basis of the mire vegetation pays particular attention to maritime areas. They consider the conifers and mountain birch to be such continental species that their growth and reproduction will decrease under obviously maritime conditions, so that they are of little value as phytogeographical marker species where maritime areas are concerned. They distinguish a narrow band of hemiarctic vegetation mainly identifiable on the Varanger Peninsula as representing a transition zone between the tundra and the taiga, and regard the north boreal zone as covering approximately Forest Lapland together with the majority of the Kola Peninsula. This definition also serves fairly well to delimit the timberline forests. The problematic isolated forest areas on the coast of Troms and Finnmark, regarded as middle boreal by Ahti et al. (1968), are assigned by Eurola and Vorren to the southern part of the north boreal zone.

It is particularly important to form a correct impression of the phytogeographical status of the isolated forests to be found north of the continuous timberline on the Norwegian coast, because these form the northernmost location in the world where forestry takes place. Also, any conclusion reached regarding them will be of help in classifying the timberline pine forests of Finland. Ilvessalo (1970) considered that there were many pine stands on the Norwegian side of the border in Fjord Lapland that had a timber production capacity comparable with that of the EMT pine forests of Inari or even Perä-Pohjola. On the same basis Vorren (1993) presents a system of regions for the whole of Scandinavia and Finland that deviates from that described earlier in that the Inari basin and the Paatsjoki valley are strangely assigned to the southern subzone of the north boreal zone. He also recognizes a separate series of alpine zones in the Scandes in which the subalpine birch zone is followed downwards by a pre-alpine orozone of pine and broadleafed mixed forest. Moen (1987), on the other hand, is of the opinion that there is no essential difference between horizontal zones and vertical belts where a limited geographical area is concerned, and regards the isolated patches of forest on the coast of Troms and Finnmark as belonging to the middle boreal zone and the mountain birches of northern Norway and the pine area in the Paatsjoki valley as part of the northern boreal zone, which borders directly on a treeless alpine zone.

The Nordic Council of Ministers (Nordiska Ministerrådet 1984) commissioned the construction of a scheme of physical regions for Scandinavia and Finland in which attention would be paid to other factors as well as vegetation. This joint project involving experts from all the countries concerned arrived on the basis of earlier surveys at a system of 75 regions, in which the treeless areas north of Lake Torne were regarded as arctic-alpine and those to the south of this lake as alpine. The forests of the following northern regions may be considered timberline forests: the submaritime birch-pine forests of northern Norway and the birch-pine forests of Southern Varanger, both belonging to the arctic-alpine zone, and the continental forest and open fell summit area of northern Norway and the fell region of Lapland and the Inari-Paatsjoki area, both in the north boreal zone. Also, part of the extensive northern coniferous forest area of Lapland consists of timberline forests. The pine and birch occurrences on the coast between Kirkenes and Lyngen are assigned to the arctic-alpine zone, and those found further west to the north boreal. The outer coast and islands of Troms are defined as falling into the middle boreal zone. Oksanen and Virtanen (1995) similarly place the outer coast of Troms in the middle boreal zone. They then describe a continuous north boreal zone extending as far as the Alta fjord, while the pine occurrences in the valleys to the east of this constitute north boreal enclaves within the hemiarctic zone.

Also connected with the definition of regions to describe the physical geography of the Nordic Countries, another joint project has been carried out to define a set of vegetation types, which includes alpine vegetation and forest vegetation (Pålsson 1994). In addition to the various mountain birch site types distinguished in terms of nutrient status, a relatively commonly defined type of timberline pine forest is the *Barbilophozia* variant of the dry heath forest. There is no particular spruce forest type found predominantly at the timberline.

Russian viewpoint. Russia also possesses long traditions in the field of phytogeographical classifications for northern areas, and a wide variety of concepts are in use. In the case of the Kola Peninsula the very thorough investigation of Tsinserling (1932) has provided a firm basis for future surveys. The Russian classifications assign particular weight to questions of landscape ecology, especially as criteria for distinctions at the lower levels in the hierarchy (Billwitz 1973). The most recent vegetation map of European Russia (Lavrenko and Isachenko 1979) presents a zonal scheme for the vegetation of the Kola region in which the northernmost zone is a strip of southern brush tundra, south of which one finds a zone of forest tundra belonging to the taiga. The whole coniferous forest zone of the Kola Peninsula is part of the northern taiga, while the highest mountain and fell areas are described in terms of altitudinal zones. The tundra of this region is designated as forming the Kola subprovince of the European-Western Siberian province of the circumpolar tundra zone, while the forest tundra and northern taiga form part of the Kola-Pechora subprovince within the Northern Europe coniferous forest province of the Eurasian coniferous forest zone. The forests are further divided into various spruce and pine-dominated groups according to their variations in species composition and ground vegetation.

As noted by Kurnayev (1973), the phytogeographical classification of forest vegetation differs from general phytogeography in that more attention is paid to the forest and its growth potential than to the vegetation as a whole. In his own classification of the forest vegetation of the Soviet Union, Kurnayev (1973) places both the Kola tundra and the forest tundra in the Norwegian coast and Kola Peninsula tundra province of the Eurasian tundra zone, this being distinguished from other tundra regions on the grounds of the better conditions for tree growth. Correspondingly, the coniferous forests of the Kola region, together with the forests to the south of the White Sea, belong to the eastern Russian plain province of the Eurasian forest zone, forming a separate Kola Peninsula northern taiga district (okrug). The zonal forests in this area are in principle composed of spruce, but intrazonal pine forests are also to be found in connection with specific bedrock areas. The presence of *Betula pubescens* in the upper and more northerly parts of the forest zone is a special feature of the region.

Vatkovski and Kuznetsova (1983) explored the possibilities for using satellite images of the Kola Peninsula for phytogeographical survey purposes and presented a set of regions based on optical effects, noting that the boundary between the northern taiga and forest tundra could be defined fairly reliably from satellite data, whereas that between the forest tundra and tundra was much less certain. Ramenskaya (1972), in her more detailed examination of the timberline areas of Petsamo, concludes that the tundra of the Petsamo uplands occurs only as an orozone, while the narrow treeless zone along the coast is due to the rocky substrate and winds. The real forest tundra is encountered only to the east of the Petsamo River. The ground vegetation also differs markedly from that of the easternmost parts of the Kola Peninsula.

Ramenskaya (1975) then went on to produce a phytogeographical and landscape-based classification of Karelia and the Murmansk area. She defines the forests of the Murmansk area as a more open (redkostoinye) variant of the northern taiga and those of the northern areas of Karelia as a light (osvetlennye) variant. More recently, Yurkovskaya and Payanska-Gvozdeva (1993), following a comparison of phytogeographical regions recognized in the area close to the Finnish border according to Russian and western classifications, have set out a new zonation for the region on the Russian side of the border, which they then compare with western information (Figure 46). This makes use of the division proposed by Ramenskaya (1975) in the case of the northern subzones. The northernmost part of the northern taiga is surprisingly extensive in this scheme and comprises a wide scale of forests as far as their growth potential in concerned, but the open forests and forest tundra can be regarded as representing timberline forests. Ahti et al. (1968) were of the opinion that their north boreal zone corresponded to the northern half of the Russians' northern taiga, and regarded the open forest (redkostoinye lesa) lying between the Russians' forest tundra and taiga as coming close to their north boreal zone.

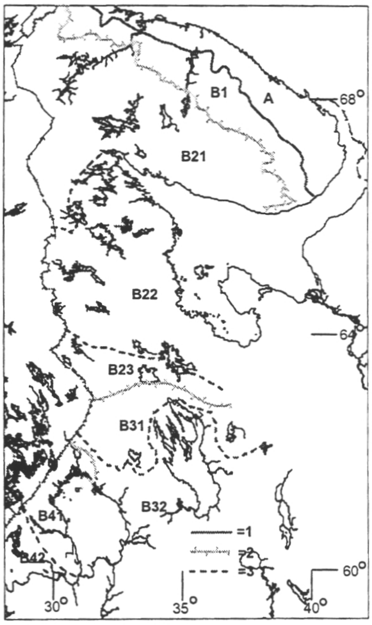

Figure 46. Zonation of the vegetation in eastern Fennoscandia (Yurkovskaya and Payanska-Gvozdeva 1993). 1. zone boundary, 2. subzone boundary, 3. lower-level boundary. Zones: A = tundra, B= boreal coniferous forest. Subzones: B1 = southern forest tundra, B2 = northern taiga, B3 = middle taiga, B4 = southern taiga. Lower-level divisions: B21 = northern part of the northern taiga (open forest), B22 = central part of the northern taiga (light forest), B23 = southern buffer zone of the northern taiga, B31 = northern part of the middle taiga, B32 = southern part of the middle taiga, B41 = northern part of the southern taiga, B42 = southern part of the southern taiga.

Payanska-Gvozdeva (1990), in her research into the northern taiga vegetation of the southern Kola Peninsula, presents a more precise phytogeographical scheme for that area (Figure 47). This complements the earlier system of landscape/phytogeographical regions for the Kola Peninsula and Karelia proposed by Ramenskaya and Shubin (1975). It can be deduced from these maps and their explanations that the phytogeographical districts (okrugi) of Umba and Kandalaksha possess the best conditions for forestry, while those of Ponoi and Western Teri may be regarded as lying on the timberline, likewise that of Khibiny-Lovozero. The district of Kola-Tuloma, only part of which appears on the map, has many open fells and adjacent forests, the largest continuous area of forest being that of Lotta-Tuloma, which Ramenskaya and Shubin (1975) recognize as a separate district. This area is to a great extent linked to the pine-dominated forests defined by the Nordic Council of Ministers (Nordiska Ministerrådet 1984) as the Inari-Paatsjoki region. In the opinion of Ahti et al. (1968), the north-eastern part of Inari appeared to belong to the same sector as north-western Kola, the difference with respect to western Inari lying in the higher proportion of pine forests with a ground layer of mosses. The results of the Finnish forest inventories point in the same direction.

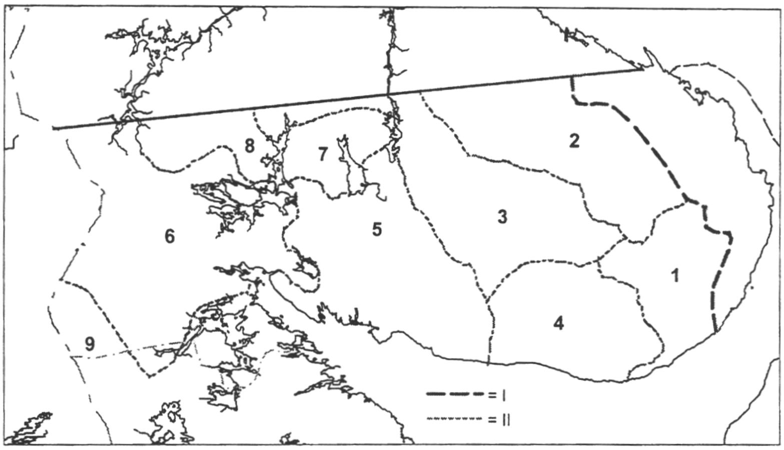

Figure 47. Phytogeographical regions of the southern Kola Peninsula (Payanska-Gvozdeva 1990). I = boundary of the Kola-Karelia subprovince of the Northern Europe coniferous forest province. Districts in the southern forest tundra: 1. Voroninska Ponoi, 2. Pnoi-Teri. Districts in the northern taiga: 3. Ponoi, 4. Western Teri, 5. Umba, 6. Kandalaksha, 7. Khibiny-Loovozero, 8. Kola-Tuloma, 9. North-western Karelia.

6.2.3 Open forests

Most of the above systems of phytogeographical regions have 'open' or 'sparse' forests as one of the northernmost categories (Kalela 1961, Sjörs 1963, Ahti et al. 1968, Kurnayev 1973, Ramenskaya 1975). No corresponding orozone is normally recognized between the subalpine zone and the forest zones in mountain areas (Löve 1970), but Walter and Breckle (1986) do note that their "Krummholz" and "dichter Hochwald" zones in the northern Alps are separated by a narrow, more or less subalpine zone of open forest, "lichter Wald".

Gjaerevoll (1992) observes that the boreal forest becomes gradually more open towards the north, grading into forest tundra. It is this forest tundra that should really be referred to as taiga, which literally means "land dotted with small posts", but the word was applied to the boreal forests as a whole. Hustich (1949) divided the boreal zone south of the forest tundra in Labrador into a taiga zone in the north and a spruce forest zone in the south, with the taiga characterized by spruce forests with a ground layer of lichens. Polunin (1960) notes that the concept of taiga should be reserved for the northernmost, sparse, park-like boreal forests, while Sirois (1992) uses it of the northernmost part of the boreal zone but regards this at the same time as a part of the transition zone between forest and tundra lying to the south of the forest tundra. The northernmost, open lichen forests of the boreal zone are commonly referred to in North America as the "woodland subzone", "open coniferous forest", "open woodland (parkland)", "open lichen woodland" or "lichen woodland". Hare (1950) took the boundary between the open and closed-crown forests to mark the northern limit of felling and looked on this as one of the most significant economic boundaries on the whole continent.

Hustich (1979) mentioned that the Russians used the term "redkoles" as an equivalent of "open woodland", while Tikhomirov (1970) claims that "redkolesya" may be translated as "parklands". In fact the practice within the Russian literature varies somewhat, but "redkoles" is mostly used to refer to the southern part of the forest tundra (see Norin 1961), while the most common term for the northernmost part of the boreal zone is "redkostoinaya taiga", which Kurnayev (1973) defines as a region in which a zonal pattern of open coniferous forests occurs on nutrient-poor sites and in places where the ground vegetation possesses tundra features. Abaimov and Bondarev (1995) proposed that for unifying the terminology, forests with crown closure 0.1-0.3 should be called the northern open forests, ”severnye redkoles′ya” and areas with crown closure 0.1-0.05 natural openings, ”biologicheskie redini”. Kryuchkov (1978) regarded the open forests as forming the southernmost zone of the subarctic, and was of the opinion that their southern boundary ran at the point where the density of the tree stand began to regulate entirely the conditions for the ground vegetation. This marks at the same time the limit of distribution of the hypoarctic shrubs and dwarf shrubs and a change in soil conditions, e.g. the point beyond which patterned ground ceases to occur.

Although the open forest zone is regarded as a circumpolar phenomenon (Tikhomirov 1970, Sirois 1992) (Figure 48), Kurnayev (1973) described the "redkostoinaya taiga" as occurring as an independent zone only in the Pechora-Mezen region east of the White Sea and eastwards from there. Yurkovskaya and Payanska-Gvozdeva (1993), however, use the same concept to describe the forests of the Kola Peninsula, and Ahti et al. (1968), observing that the slightly continental pine-dominated forest sector of their north boreal subzone corresponds roughly to Forest Lapland in the system of Kalela (1961) and the 'regio subsylvatica' of Wahlenberg (1812), where the typical feature is the occurrence of a predominantly lichen ground vegetation on till, state that to the best of their knowledge the same feature is to be found elsewhere in Fennoscandia only in the basins of the Rivers Varsuga and Ponoi on the Kola Peninsula. The occurrence of nutrient-poor site types on till is to be seen in the results of the forest inventory of Inari, where till soils account for 96% of the area but in terms of site types the relatively dry heaths reach 65% and dry heaths 33% (Metsähallitus 1985). The status and characteristics of the open forests as part of the subarctic zone (sensu Kryuchkov 1978) are illustrated in Figure 49.

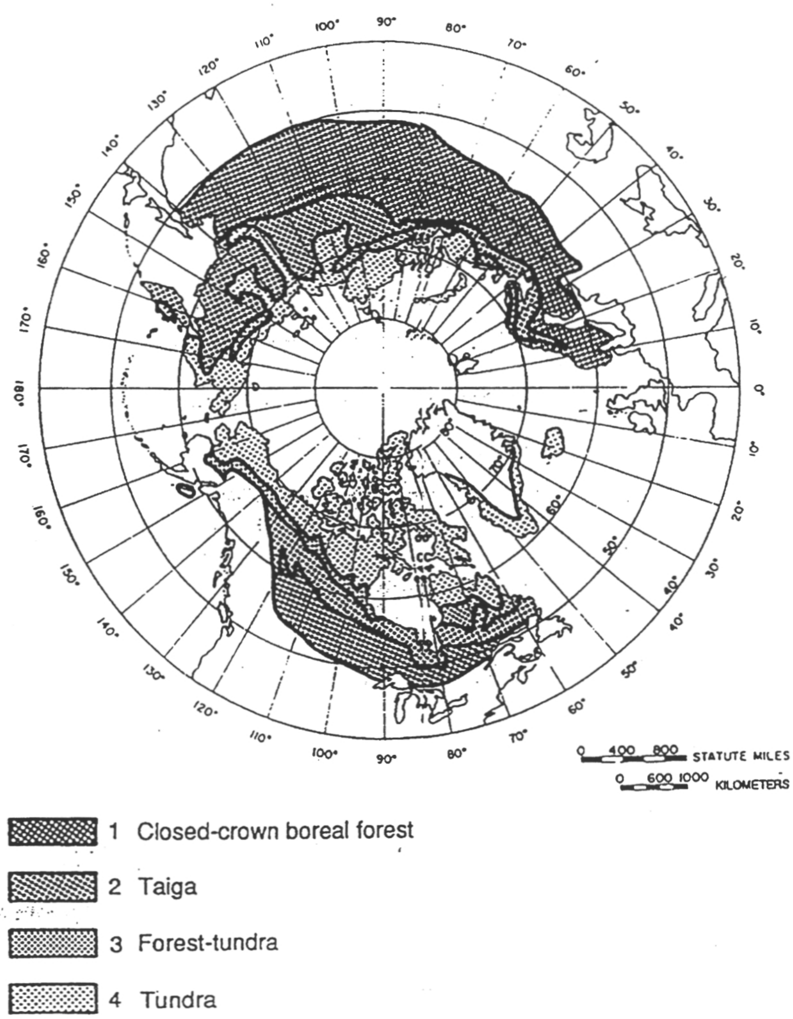

Figure 48. Schematic map of the northern vegetation zones (Siroi 1992). 1. = closed-crown boreal forests, 2. = taiga, in the sense of open forests, 3. forest tundra, 4. = tundra. The forest tundra and taiga belong to the transitional zone between the boreal forest and tundra proper.

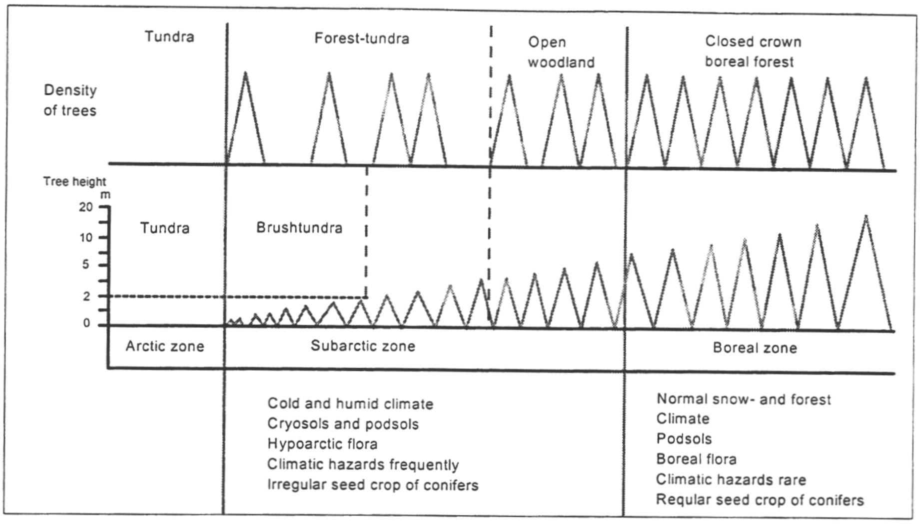

Figure 49. Typology of timberline forests in terms of formal features, after Mattsson (1987), and characteristics of the subarctic zone.

When discussing the distribution of dry heaths in Lapland and the reasons for this, Sarvas (1952) notes that these are a circumpolar phenomenon and concludes that the reasons do not lie in the abundance of coarse soils, nor in the scarcity of mineral nutrients, soil acidity or climatic humidity factors. He ends up by doubting whether the northern nutrient-poor forest types are ecologically comparable to those found further south, in that the lichens and xeromorphic dwarf shrubs are not xerophilous under the conditions prevailing in Lapland. This leads him to raise the idea of the tropophytic nature of both the conifers and the ground vegetation, i.e. their ability to adapt to dry conditions in winter and moist conditions in summer.

Hustich (1951) is of the opinion that the occurrence of the "lichen woodlands" in Labrador is not governed by humidity but rather by temperature, and considers that forests of this kind are likely to revert to open lichen heaths as a consequence of fire or felling. Ahti (1961), for his part, regards the majority of Northern Finland as belonging to the "open boreal woodland" subzone, which includes Perä-Pohjola, Forest Lapland and the more continental part of the mountain birch zone. He attributes these forests to climatic effects, whereas the dry heaths of Southern Finland are edaphic in origin. Ahti and Oksanen (1990) propose that the vegetation of the lichen pine forests is regulated by soil factors, climate and the vegetational succession, and divide the lichen forests of Finland into two groups: from hemiboreal to middle boreal on the one hand and northern boreal on the other, where the latter are richer in species and occur on a greater variety of soils that their more southerly counterparts.

Hare (1950) looks on the "lichen woodlands" as representing a last stage in the vegetational succession on dry sites, while Rowe (1984) believes that they could be a manifestation of environmental stress. This theory is supported by other features of this vegetation type, e.g. its impoverished ground vegetation (cf. Larsen 1989) and the occurrence of mycorrhizal root systems in the dwarf shrubs. Weighing up the various explanations put forward for the open character of the forests, Rowe concludes that the reasons are many, starting out from a low level of solar radiation, the cold, nutrient-poor soils, and a possible alleopathic effect of the lichens on the young trees. Another factor that may be implicated is repeated forest fires, which would prevent the succession from proceeding to a closed-crown forest, i.e. this is a permanent subclimax biotope brought about by the effects of fire. On the other hand, observations exist of well-established open forests that have not been affected by fire. Rowe also notes that dryness of the soil may be regarded as the main reason behind the occurrence of such forests in a European context, and is himself of the opinion that drying of the surface soil in the layer immediately below the lichens may be of particular significance, as the root systems of the characteristic plants are predominantly superficial. Even though the lower strata of the soil may contain adequate moisture, even sporadic drying close to the surface may exercise a significant effect on the vegetation. In Finland, Viro (1962) has shown moisture conditions to be a decisive growth factor in the dry heath forests of Northern Lapland. On the other hand, Tolchelnikov (1970) regards the temperature balance in the soil, which is regulated by the degree of crown coverage, as the main reason for the development of open forests in connection with the forest tundra of Western Siberia.

Taken all in all, the open forests and their ecology reflect well the special characteristics of timberline forests. A suitable definition for this type in Finland can be found in the zone recognized by Ahti et al. (1968) which corresponds roughly to Forest Lapland, even though spruce-dominated lichen forests are nearly absent from this. The particular ecological features of open forests also have their analogies in land use planning when considering the potential for forestry relative to other forms of land use and when planning management procedures, e.g. the stem densities to be aimed at or methods of site preparation or afforestation. Fennoscandia is the only part of the world where significant forestry takes places in the open forest zone, so that it is essential that its special characteristics should be known and taken into consideration (fig. 50-52 Appendix 1).

6.3 Forestry

Finland. Discussions were entered into fairly early regarding the differences between timberline forests and those growing under normal conditions, since the people responsible for the very first inventories of such forests had drawn attention to the problems involved. Moring (1897), for example, recommended that the forests of eastern Inari should be divided into three zones in a north-south direction, as they differed in certain fundamental properties as they approached the timberline, notably in density, tree height and the incidence of natural regeneration. Likewise, Malmborg (1896), in his survey of the forests of Vätsäri, wrote 'It would be best, no doubt, to establish protected zones ten to twenty kilometres wide in the northernmost forests of our country'.

The State Forest Committee (Komiteanmietintö 1900) proposed that the northernmost fell areas should be declared a protected zone and suggested that a commission be appointed to arrange for this. The resulting Protective Forests Commission (Komiteanmietintö 1910) carried out a detailed survey of the state of the timberline area and drew up a formal proposal for the creation of a protective zone, the main principle being that "All the northern forest, tree and fell zones located north of the point at which pine or spruce achieves more or less regular development should be regarded as protective forest zones." The proposal was discussed separately as a question of administration and as a question of forestry practices. The special status of the Utsjoki forest district, for example, was recognized at an early stage, since its task was primarily the protection of the timberline forests and the ensuring of a supply of wood for the local inhabitants (Metsähallitus 1941).

In addition to the protective forest zone, however, the question of proximity to the timberline was also examined in relation to altitude, and the directive for the management of protective forests (Oinonen et al. 1960) contains arguments for a height of 250-300 m a.s.l. as the limit above which one should speak of highland forests. The National Board of Forestry had in fact adopted the 250 m contour as the altitudinal limit for felling and other forestry measures. In his examination of the influence of altitude on the viability of forestry, Roiko-Jokela (1980) set the mean level for the boundary between forest land and low productivity land at 325 m. He also went on to evolve criteria for determining the upper altitudinal limit for felling and other forestry measures.

The Forest Research Institute (Metsäntutkimuslaitos 1971) drew attention to the importance of the temperature sum and reported that discussions had been held with the National Board of Forestry on the possibility of dividing Lapland into three zones on these grounds:

Economic forests I: temperature sum over 800 d.d.
Economic forests II: temperature sum 700 - 800 d.d.
Highland forests: temperature sum less than 700 d.d.

Figure 53. The normal rules of thinning cannot be applied in the open forests. In the openings are often found patches without ground vegetation. Inari, Saariselkä 270 m a.s.l.

Poso and Kujala (1973) found an obvious correlation between altitude and temperature and noted the effect of these on the trees, while Kuusela (1977) demonstrated a clear association between growth and temperature sum on the basis of the results of the 6th National Forest Inventory. Thus the temperature sum was later included in the directives, alongside altitude (see Metsähallitus 1991). The Lapland Regional Planning Association (Lapin seutukaavaliitto 1980) drew up a set of forestry zones for the Lapland area, again largely on the grounds of temperature sum, as follows:

I Intensive timber production zone. Temperature sum over 900°C d.d.
II Normal forestry zone. Temperature sum 900-800°C d.d.
III Intermediate zone. Temperature sum 800-750°C d.d.
IV Extensive forestry zone. Temperature sum 750-700°C d.d.
V Protected and highland forests. Temperature sum less than 700°C d.d.

The highest forests later came to be referred to simply as high areas. On the other hand, Valkonen (1992a, b) concluded a thorough survey of the definition of these areas, their ecology and forest regeneration in them by coming to the opinion that so far no ecological factor or combination of factors has been discovered which will delimit these areas unambiguously. Thus the current limit for forestry measures is largely based on economic considerations and practical experience. A theoretical framework for research into forest regeneration in high areas has been proposed by Ritari and Timonen (1992), who also present figures for the distribution of forest areas into altitudinal and temperature zones.

The concept of high areas applies mainly to the fell areas, which can be variable in their characteristics. In the light of the analysis of fell areas by Kalliola (1961a), the high areas in the forestry sense can be grouped as follows (Figure 54):

Hemiarctic timberline areas (fell areas 4 and 2b)

The high areas of Enontekiö and those extending from western Inari to Näätämö are immediately adjacent to the northern hemiarctic-alpine timberline. Delimitation of the zone in the hemiarctic timberline area between Kaamanen and Näätämö is based on the low temperature sum rather than on altitude.

Forest tundra uplands (terrain between areas 4, 2a and 3 and the eastern part of area 1)

The extensive upland bounded by Nunnanen, Pulju, Pokka, Appistunturi, the fells of the Lemmenjoki area and the Norwegian border is one of the most clearly defined forest tundra regions in Finland, containing a significant proportion of coniferous forests as well. The corresponding unit in the eastern protected forest zone is the Värriö-Tuntsa upland. Both have typical mixed forests of birch and conifers, and also occasional spruce stands.

Coniferous forests on fells (forests in areas 2a, 3 and 1 located close to fells)

The forests located close to the fells of Muotkatunturi, the Pallas-Ylläs chain, Saariselkä and others in Central Lapland form clearly defined altitudinal zones. The forests on the smaller fells and hills further south are not so obviously of a timberline character.

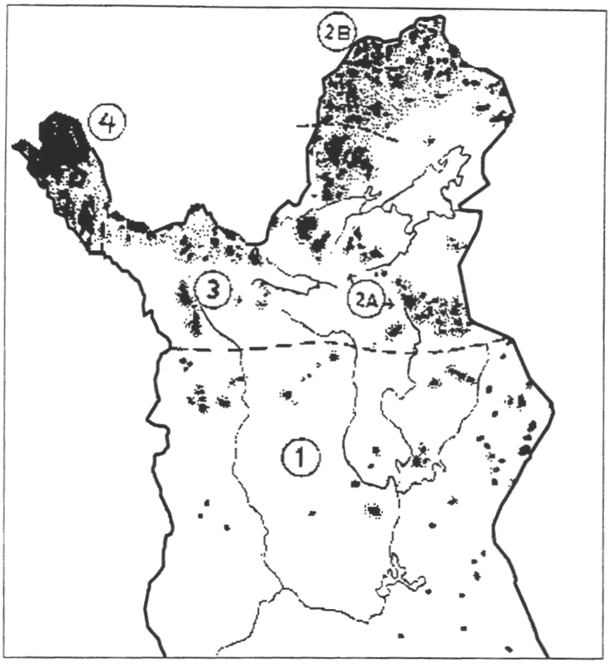

Figure 54. The fell areas of Finland (Kalliola 1961). 1. Souther Lapland, 2a. Southern granulite fells, 2b. Northern granulite fells, 3. Pallas-Ounastunturi, 4. Kilpisjärvi region. Black = alpine orozone, shaded area = subalpine orozone.

The high areas have begun to be equated more and more with the protected forest zones, and where questions of management are concerned, increasing attention is being paid to uses other than timber production (see Ympäristöministeriö 1994). It is possible in a broad sense to regard the protected zone, the high areas and the economic forests of Inari as together constituting the timberline forests of Finland (Figure 55). These are areas that contribute little to the country's timber production but can be of great local significance for forestry in a region where almost a half of the satisfactorily growing forest land is beyond the reach of normal forestry as it belongs to these various protected zones. With the recent reorganization of the state forests, the majority of the state forests located near the timberline form part of the Northern Lapland District for Wilderness Management, the main duties of which are the conservation, management and utilization of state-owned land and water resources and reconciliation of the pressures that may exist between these modes of land use. Due attention is also being paid to the significance of the home territories of the Sàmi (Metsähallitus 1994a).

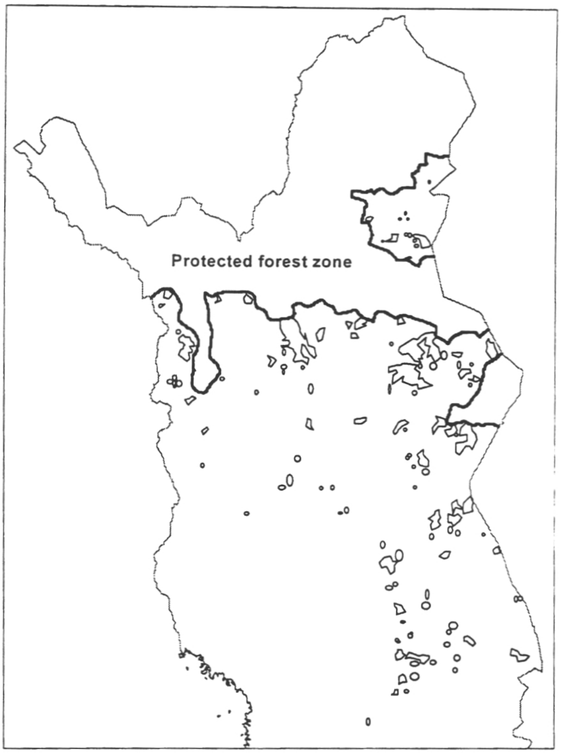

Figure 55. Forests in high areas below the protected zone and outside conservation areas (Ympäristöministeriö 1994). The Inari commercial forestry region is enclosed entirely within the protected zone.

Russia. The timberline forests are referred to in the Russia forestry literature as "forests close to the tundra (predtundrovye lesa)", and they are regarded as including enclaves of forest within the tundra, the forest tundra and the more open forests of the northern part of the northern taiga, i.e. the "redkostoinaya taiga". The majority of these forests were set aside as "protected forests bordering on the tundra (pritundrovye zashchitnye lesa)" under an administrative decision of 1956 (Chertovskoi et al. 1987). These forests, which belong to category I in the Russia classification, are intended to serve a protective function. Although established some time ago, their management became the topic of a scientific conference for the first time only in 1983. The conference concluded that a separate system of forestry should be developed for these areas, research into their protective effects should be intensified, adjustments should be made to their southern boundary and a division into regions should be attempted. Proposals have also been put forward for a significant extension of the protected forests bordering on the tundra in the Murmansk region (Kryuchkov et al. 1988, Tsvetkov 1995) in the

Arkhangelsk region (Tsvetkov et al. 1995) and in Middle-Siberia (Abaimov and Bondarev 1995).

The main practical problems mentioned are commercial fellings, uncontrolled grazing of reindeer, forest fires and air pollution (Semyonov 1984). The development of a protective form of forestry for the timberline forests has become a matter of urgency in Russia (see Semyonov 1993) and lively discussions have been held on protection in relation to the opening up of forestry in the north to the principles of a market economy (see Kazakov 1993). The following data on the forests of Russia bordering on the tundra are taken from Chertovskoi et al. (1987). These areas comprise a total of about 45 million hectares, of which 47% are forest. About one fourth of the area is located in European Russia. All in all, they are very much in a natural state, and old forests account for some 80%. Only about 0.1% of the forest area has been clear-felled and about 1% has been destroyed by fire, but almost 9% of the total area is affected by erosion and thermokarst formation. The total volume of the growing stock is approx. 1400 mill. m^3, of which 95% consists of conifers. No division of the forests bordering on the tundra into regions has ever been made, but they are usually examined in terms of the major forest vegetation regions, i.e. Kola, Eastern Europe, Western Siberia, Central Siberia, Eastern Siberia and the North-East. This division is also recognized in the forest management instructions, and more detailed figures for timber reserves are available for these regions.

Semyonov and Tsvetkov (1990) proposed a system of regions for the forests bordering on the tundra in the European part of Russia (Figure 56), i.e. those belonging to three forest vegetation regions: the Kola arctic-alpine region, the plains of Eastern Europe and the Urals alpine region. Growing conditions become markedly more severe towards the east, as temperatures become lower, continentality increases and permafrost becomes more common. The forests of the Kola Peninsula form a subregion, or "podoblast", of their own, which can be further divided into a north-eastern and a south-eastern forest vegetation district, or "okrug". The relations between the species are 47% birch, 31% pine and 22% spruce in the north-eastern district and 35% spruce, 34% birch and 31% pine in the south-eastern district. These figures reflect the increase in the proportion of spruce in the forests towards the east. The incidence of mires is high in both districts and the nutrient status of the forest land is poor.

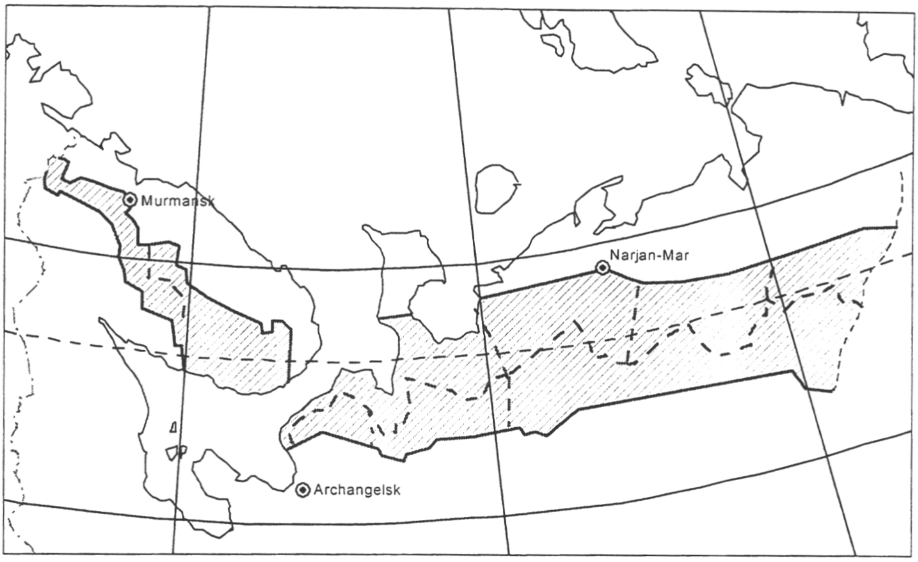

Figure 56. The forests close to tundra in the European part of Russia (Semyonov and Tsvetkov 1987). - = the border of the forests close to tundra, - - - = the border of the forest vegetation regions.

Sweden. The coniferous forest lying below the mountain birch zone and officially classified as low-productivity forest land is referred to in Swedish as "fjällbarrskog". This forms a zone of varying width containing large amounts of mountain birch located between the mountain birch zone proper and the productive forest land. The birch zone, "fjällbarrskog" and the upper part of the productive forest land are together regarded as forming the forest bordering on the fells, or "fjällnära skog" (Skogsstyrelsen 1989), the lower boundary of which is the "skogsodlingsgräns", or limit of silviculture, defined for state forests in 1952, as a temporary investment limit above which no felling or planting of forest was to be carried out (Höjer 1954). The definition of this limit was made in connection with an extensive programme for the improvement of underproductive forests in Sweden, which was also governed by the notion that felling operations should not be attempted in excessive remote places and by general considerations of nature conservation in addition to the obvious forest regeneration problems (Höjer 1954, Linder 1987). The term cultivation limit, "odlingsgräns" as such was defined in the 19th century to prevent pioneer settlement from spreading into the mountain area, and was not directly connected with forestry (Gustavsson 1989), but the form "skogodlingsgräns", limit of silviculture, was later adopted under the forest management act to be binding upon all landowners, whereupon the forest bordering on the fells was taken to mean that part of the poorly regenerating forest, "svårföryngrad skog", that lies above the limit of silviculture in the definition employed in the national forest inventory (Skogsstyrelsen

1989). This poorly regenerating forest represents the least favourable zone in the Swedish climatic classification of forests (Lundmark 1990), and has an annual effective temperature sum of less than 750 d.d. The forests bordering on fells in Sweden amount to a total of 1.6 million hectares of productive forest land, or 7% of the country's forests in that category (Kardell and Ekstrand 1990).

Once the concept of a limit of silviculture had been abandoned in 1982, lively discussions arose in Sweden on land use and forestry in the zone adjacent to the fells, and the opinion expressed by the government led the national forest administration and the local forestry boards to initiate a more precise survey of these forests for the purpose of defining the limit above which felling would not be feasible because of regeneration difficulties. The main indices to be taken into account were northerly latitude, altitude of the terrain and exposure of the slope. The eventual limit corresponds to the same temperature sum on average, but local exceptions are common (Lundin 1994).

Norway. The corresponding concept of "fjellskog" is also used in Norway, the distinctive features of such forest being defined by Mork (1968) as poor regeneration of pine and birch as a consequence of the harsh climate. The altitudinal location of this zone is usually 30-40% of the height of the timberline itself, but Mork emphasizes that its position cannot be defined schematically on the grounds of height alone, but attention also has to be paid to latitude, distance from the coast, the position of the timberline and the local microclimate. The report of the Committee on the Multiple Use of Forests (NOU 1989) defines the "fjellskog" as an area in which temperatures and winds in particular place restrictions on seed production, maturation and germination and forest regeneration and growth. It has been calculated that over 20 000 km² of productive forest land are located within 150 m vertical distance of the coniferous forest limit in Norway, accounting for 20% of such land in the whole country, 15% of the volume of growing stock and 10% of the total annual increment (Landbruksdepartementet and Det norske Skogselskap 1993). Kielland-Lund (1981) presents the following data on the altitude of the lower boundary of the "fjellskog" zone: Østlandsfylker 600 m, Telemark and Agder 450 m, Trøndlag and Helgeland 300 m and Troms and Finnmark 0 m. This implies that all the forests in the far north of Norway are classified as bordering on fells, even if some of them are also close to sea level. As these figures clearly indicate, timberline forests are of greater importance to Norway than to any other of the countries examined here.

6.4 Geography

Geographers have been interested in timberline areas largely from the viewpoint of phytogeography. Kalliola (1969) regarded the northern limit of the coniferous forest zone as a good example of a boundary that was of both phytogeographical and geographical significance, whereas the boundary of the oak forest zone that ran along the south coast of Finland was a purely phytogeographical concept. The most recent synthetic works to be published in Finland on timberline questions have been mainly produced by geographers, e.g. Hustich (1966), Heikkinen (1984) and Tuhkanen (1993a, b), and some general surveys in the field of physical geography that set out from the notion of landscape contain analyses of the characteristics of timberline areas.

Tundra forest. The Russian Parmuzin (1979) presented a synthesis arising from a long-term research project which involves the establishment of a zone definable in terms of physical geography that is known as the tundra forest, 'tundrales´ye'. This is a circumpolar zone which comprises both the forest tundra and the open taiga forest and stands out from both the tundra and the taiga on the grounds of climate, soils, vegetation, fauna and the exploitation of natural resources. Natural conditions in this zone alter somewhat from west to east in Eurasia, chiefly with respect to increased continentality and the involvement of permafrost. Parmuzin divided the tundra forest of Russia into six regions: western European, eastern European, western Siberian, central Siberian, eastern Siberian and eastern coastal. The western European region consists solely of the Kola province, which accounts for the whole peninsula except for the coastal tundra. This is the least continental of all the regions, and thus the least typical of the tundra forest. The forest tundra zone in this area is some 20-50 km across, and isolated patches of permafrost exist in the north, mostly only in the form of palsas. The remainder of the peninsula is open forest, where the only differentiation is attributable to an altitudinal zonation and to variations in soils and ground vegetation derivable from moisture conditions and the nature of the bedrock. The moisture conditions are themselves largely related to the topography.

The subarctic and the cold, damp zone. Kryuchkov (1978) recognizes a subarctic region as a separate unit comprising the typical tundra, the forest tundra and the northern open taiga, maintaining that these zones have so many features in common with respect to climate, soils, vegetation and fauna that the region can be regarded as a geographical entity. In this view the timberline as such is not a decisive, ecologically distinctive boundary, and the open northern taiga is clearly associated with the timberline ecotone. As proposed earlier by Targulyan

(1967), the tundra, forest tundra and a large part of the northern taiga make up a cold, damp zone that stands out sharply from the taiga proper in terms of temperature and humidity. He emphasized in particular the way in which the cold, damp soil conditions were reflected in the history of the vegetation.

The mountain birch formation. Blüthgen (1960) set the Scandinavian mountain birch zone aside as a landscape formation in its own right, a "Landschaftsformation" on geographical grounds, since it has distinct physical, biological, occupational and cultural characteristics of its own. He noted that a geographical synthesis shows that the mountain birch zone is not just a phytogeographical association complex but can also be divided into geographical facies on the basis of all their geographical properties, of which Blüthgen distinguished 11. The northern part of the Finnish mountain birch zone belongs to a subarctic valley and upland facies and the southern part to a subarctic marginal facies. By comparison with the Russian interpretations, one may very well ask whether it is justified to recognize the birch zone alone as a geographical region, and whether it would not have been more natural to include the timberline areas on a broader scale.

The Sàmi territory. As Rikkinen (1990) puts it, the principal aim of regional geography is to describe and explain regions as syntheses of all the factors that have contributed to them. His system of regions for Finland based on the spatial interaction between man and nature, in which nature assumes the dominant role in the more northerly regions, has as the northernmost region of all the Sàmi territory, with the watershed area of Maanselkä as its southern boundary. The southern part of this region corresponds to what we have referred to above as Forest Lapland, and the northern part to the fell region. The Sàmi and their way of life based on the sustainable exploitation of natural resources features prominently in the description of human activities in this region, even though it is mentioned that the majority of the population are Finns and that tourism, farming and forestry are also practised. Rikkinen's definition reflects the importance of the very special quality of the natural environment in timberline areas and emphasizes the significant role of indigenous peoples and their traditional occupations. Similarly the forest vegetation zones of Kalela (1961) proved useful for the purposes of defining a set of geographical regions. Sources of livelihood and related questions are discussed in more detail in connection with the utilization of timberline forests.

6.5 Conclusions

The location and extent of the timberline forests can be determined from a phytogeographical, geographical or forestry perspective. Many ideas have been put forward on the division of northern Fennoscandia into phytogeographical regions, but the widely accepted general scheme of Ahti et al. (1968) for the subdivsion of the boreal zone provides a good starting point for the discussion of timberline forests even though it does not lay down precise boundaries. The latest interpretation of the position of the northern boundary of the north boreal zone based on climatic and ground vegetation criteria, that of Oksanen and Virtanen (1995), fits in well with known forestal indicators.

Of the subarctic approaches (e.g. those of Hustich 1966, Kallio et al. 1969 and others), the definition by Blüthgen (1970) of the southern paraboreal region of the terrestrial subarctic provides in principle a correct delimitation of the timberline forests. The southern boundary of the subarctic region as laid down by Kryuchkov (1978) is approximately the same, but he places more emphasis on the special ecological characteristics of the open forests.

The character and ecology of the open timberline forests are questions that have been considered relatively little in Fennoscandia, other than in Russia, by comparison with the attention paid to them in North America. The zone concerned in Finland is approximately that referred to as Forest Lapland (Ahti et al. 1968). These open forests constitute the more southerly part of the forest tundra ecotone, i.e. of the transition zone between the tundra and the boreal forests. The successful practising of sustainable forestry under such specialized conditions calls for a profound awareness of these circumstances. The forestry sector in all the countries of Fennoscandia has clear definitions available of what is meant by proximity to the timberline: the "predtundrovye zashchitnye lesa" in Russia, the "fjällnära skogar" in Sweden and the "fjellskog" in Norway. In the case of Finland it would be reasonable to regard the economic forests of Inari and the high areas as timberline forests as well as the protected forests, as all of these stand out from the true commercial forests on both thermal and phytogeographical criteria.

More use should be made of the results of phytogeographical and other ecological research when seeking support for practical measures to be taken regarding utilization of the timberline forests. The theory of open forests should be invoked to analyze in detail the conditions that exist for forestry in small areas of the timberline forests. In the meantime it must be accepted that the significance of these forests for purposes other than forestry has increased, and they are now easily identifiable as a distinct geographical region from the overall viewpoint of the relationship between man and nature (Blüthgen 1960, Parmuzin 1979, Rikkinen 1990). The subarctic region as defined by Kryuchkov (1978) stresses the ecological characteristics possessed in common by the northernmost taiga, the forest tundra and the tundra proper.

The geographical perspective can help us to form an image of the timberline areas as a whole and provide criteria for the management of the diversified exploitation of their resources. The timberline areas of Fennoscandia form the core location of the Sàmi culture and traditional means of livelihood based on a close relationship with nature, and are thus areas in which sufficient emphasis should be placed on protection of the indigenous culture and ways of living when considering the use and conservation of natural resources, as allowed for under international agreements. "The northern edge of the pine forests forms an extremely important demarcation line used according to local custom to divide the "forested lands" from the "fell lands", since the Finnish pioneers do not look on the mountain birches as forming a forest" (Rosberg et al. 1931). For the Sàmi, on the other hand, the timberline areas are not a periphery far removed from the centre but the very centre of the world (Magga 1993).

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Total of 665 references

Seloste

Fennoskandian pohjoinen metsänraja ja metsänrajametsät

Laadullisen tutkimuksen lähestymistapaa käyttäen ja monitieteisestä näkökulmasta on tutkittu Fennoskandian pohjoisen metsänrajan ekologiaa sekä sen asemaa maapallon muiden metsänrajojen joukossa. Lisäksi on selvitetty metsänrajan läheisten metsien rajaamisen perusteita ja vaihtoehtoisia ratkaisuja.

Ekotoniperiaate todettiin hyvin sopivaksi myös Fennoskandian metsänrajojen tarkasteluun. Suomen havumetsien pohjoisesta metsänrajasta esitetään uusi tulkinta. Metsänraja on hemiarktinen välillä Karesuvanto - Skietsim, vertikaalinen Muotkatunturien ympärillä ja hemiarktinen edelleen välillä Kaamasmukka - Näätämö. Pohjoisten jokilaaksojen männiköt ovat ekstrazonaalisia esiintymiä.

Suomen havumetsien metsänrajaa ei voida pitää yleisenä hiilitaseteorian selittämänä "nälkärajana", jonka sijaintia voitaisiin kuvata lämpösummalla. Männyn vertikaalinen metsänraja on yleensä ilmastollinen raja mutta hemiarktista metsänrajaa säätelevät männyn lisääntyminen, männyn ja tunturikoivun välinen häiriöistä riippuvainen puulajidynamikka sekä ihmisen vaikutus. Paras yleinen metsänrajan selitys on suhteellisen ja absoluuttisen metsättömyyden teoria.

Metsänrajaekotonin dynamiikka eroaa selvästi boreaalisista metsistä, koska vajaan sulkeutuneisuuden takia kilpailun vaikutus on vähäisempi. Suomen pohjoisella havumetsänrajalla on kaksi mahdollista tasapainotilaa: mäntyvaltainen ja koivuvaltainen metsä. Häiriöt ja ilmastonvaihtelu ratkaisevat tuloksen. Tunturikoivuvaltainen kasvullisesti uudistuva metsä on pysyvä verrattuna boreaalisiin hieskoivikoihin.

Ilmastonvaihtelun vaikutus männyn puurajaan ei ole suora vaan monet tekijät voivat vaikuttaa esim. lämpenemisen aiheuttamaan reagointiin. Suvullisen lisääntymisen ja kasvun reagoinnin ero on selvä. Tämän vuosisadan alkupuolen lämpimän ilmastovaiheen tuloksena puurajalle on syntynyt männyn taimia, joiden pitkän aikavälin kehityksestä ei vielä voida tehdä luotettavia arvioita. Lämpenemisen tärkein vaikutus on puurajan eteläpuolisen alueen tihentyminen erirakenteiseksi metsäksi.

Harventuneet metsät ovat osa subarktista aluetta, missä monet ekologiset tekijät poikkeavat varsinaisista boreaalisista metsistä. Metsänrajametsät ovat myös maantieteellisin perustein oma kokonaisuutensa, jonka hyödyntämisessä luonnonsuojelun ja alkuperäiskansojen kulttuurien turvaamisen tarpeet ylittävät puuntuotannon merkityksen.

Appendix 1: Photographs

Figure 2. In the southern part of Chunatundra in Laplandski zapovednik spruce forms the coniferous treeline. Stunted spruce 440 m a.s.l. on the fell Yel'nun. Photo: Pertti Veijola 1994.

Figure 3. On the fell Yel'nun the species line of Scots pine is located higher than the species line of spruce. Stunted pine 470 a.s.l. Photo: Pertti Veijola 1994.

Figure 4. Windformed spruce close to the maritime timberline on the coast of the White Sea near Varsuga. Photo: Pertti Veijola 1994.

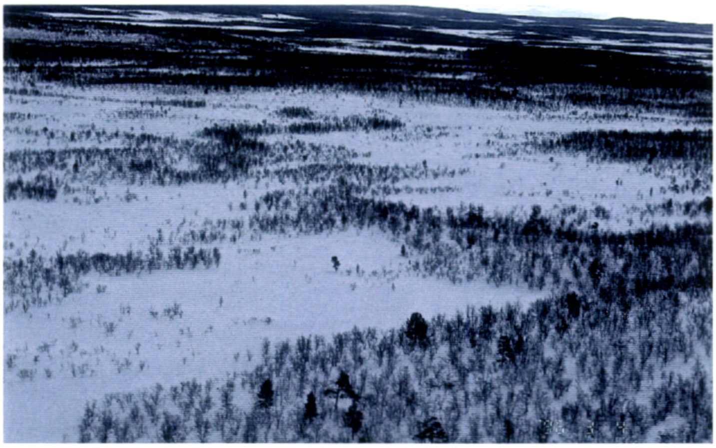

Figure 9. The northern hemiarctic treeline and timberline in Enontekiö south from the lake Pöyrisjärvi. Photo: Arvo Olli 1994.

Figure 10. The vertical timberline of pine on the slope of the fell Hammastunturi in Inari. Photo: Matti Mela 1993.

Figure 11. An extrazonal pine occurrence in the river valley of Kevojoki in Utsjoki. Photo: Matti Mela 1993.

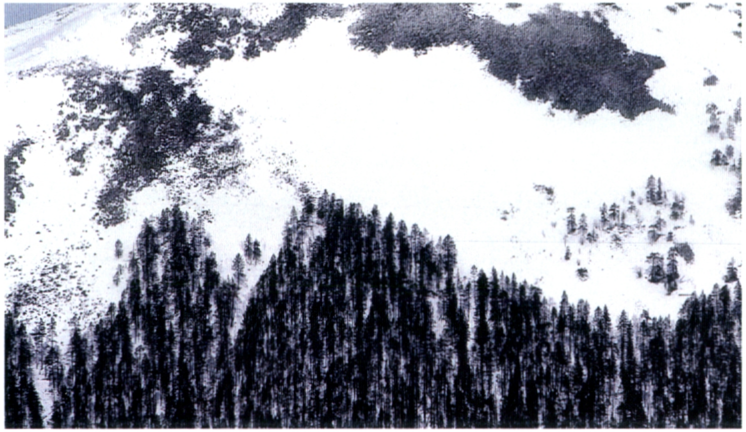

Figure 24. The stony bedrock and the steepness of the slope are reasons of the timberline on the fell Kellostapuli in the Ylläs area. Photo Matti Mela 1991.

Figure 25. The *Oporinia*-damage has changed the fell birch forest into open heath in the northeastern Inari. Photo: Matti Mela 1994.

Figure 27. This old forest fire area, 360 m a.s.l., in the Hammastunturi area in Inari is a good example of the long lasting natural regeneration of timberline forests after a disturbance. Photo: Tapio Tynys 1991.

Figure 28. In the northeastern Inari by the side the old trail to Norway the timberline forests were burnt and cut on large areas in the beginning of this century but the natural regenaration has been successful. Photo: Sampo Parkkonen 1991.

Figure 32. Frost drought on the tree species line on the fell Yel'nun in Chuna tundra. Top: Pine 460 m a.s.l. In the middle: Juniper 460 m a.s.l. Bottom: Spruce 450 m a.s.l. Photo: Pertti Veijola 1994.

Figure 36. An extrazonal pine occurrence in the valley of Utsjoki. On the western slope in the background is the treeline of pine and in the foreground on the eastern slope is a well growing pine stand, seed in the 1930's. Examples of this type demonstrate that the reasons of timberline should not be evaluated only on the basis of the existing forest in areas where the human impact has been heavy. Photo: Matti Mela 1994.

Figure 41. A pine stand in the northeastern Inari near the northern limit of the closed crown forests. Photo: Tapio Tynys 1992.

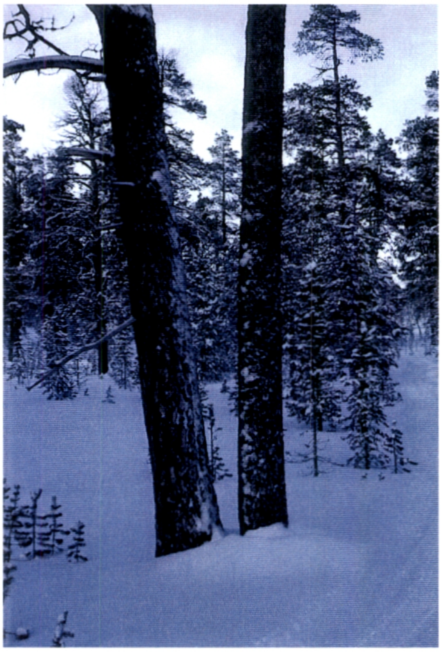

Figure 42. A pine stand in the northeastern Inari in the area of open uneven-aged forests. Photo: Tapio Tynys 1995.

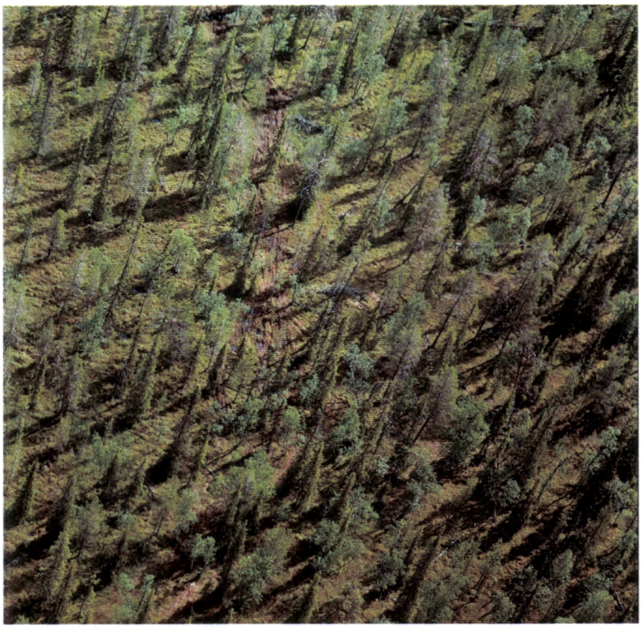

Figure 50. Spruce dominated open forest in the southern part of Inari. Photo: Ariel Ilmakuva Oy 1994.

Figure 51. A typical pine forest of Inari in the Paadarskaidi area belongs to the open forests. Photo: Matti Mela 1993.

Figure 52. There are found only partly regenerated heaths in the timberline forests. Picture is from Kittilä, Pulju area. Photo: Matti Mela 1992.

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