Jyrki Autio

ENVIRONMENTAL FACTORS CONTROLLING THE POSITION OF THE ACTUAL TIMBERLINE AND TREELINE ON THE FELLS OF FINNISH LAPLAND
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Academic Dissertation to be presented with the assent of the Faculty of Science, University of Oulu, for public discussion in Raahensali (Auditorium L10), Linnanmaa, on February 25th, 2006, at 12 noon

OULUN YLIOPISTO, OULU 2006
Abstract

Air and soil temperatures, snow cover, serious snow load damage to coniferous trees, wind, topography and edaphic factors on the fells situated between 67°N and 68°N in Finnish Lapland are described and their influence on the location of the actual timberline and treeline is discussed. In addition the relation between annual climate conditions and pollen deposition in the timberline ecotone is analysed and the results of seedling density monitoring in the same environment are presented. The potential for the actual timberline and treeline to advance to a higher elevation is also discussed. The field studies were carried out on the fells of Aakenustunturi, Yllästunturi and Pyhäirtunturi.

The average altitude of the actual timberline varies from 370 metres to 402 metres a.s.l. The actual timberline is hardly ever composed of a single tree species but featured alternating occurrences of Norway spruce (Picea abies), Scots pine (Pinus sylvestris) and mountain birch (Betula pubescens ssp. czerpanovii). The mean tetratherms on the southern and northern slopes (+10.3°C and +10.1°C, respectively), the mean maximum tetratherm on the southern slope (+15.1°C) and the corresponding measures for the treeline (460 m a.s.l.), the minimum tetratherm (+6.3°C), mean July temperature (+12.6°C), biotemperature (+3.3°C) and minimum effective temperature sum (455 d.d.), coincide closest with the results of earlier studies. The maximum altitudes of the actual timberline are dictated by many climatic factors on southern and western slopes with a gentle inclination, and the forest cover gradually becomes thinner, in which case the actual timberline does not form any easily distinguishable line. The lowest altitudes of the actual timberline are the results of an extremely high proportion of block fields, slope steepness and snow patches on the northern and eastern slopes. On the precipitous and rocky slopes trees have difficulties in taking root and in obtaining nutrients and water, while as a consequence of snow patches the growing season may be too short for tree growth at all, and if trees exist there they are suffering from low soil temperature and parasitic snow fungi. Serious snow load damage to trees evidently hampers any advance in the actual timberline, as do avalanches and mires.

The location of the treeline is the result of a combination of a great number of unfavourable conditions for tree regeneration, seedling establishment and tree growth, such as inadequate snow protection, extreme soil temperatures, almost total destruction of trees by the snow load, wind pressure, an often inadequate effective temperature sum and length of the growing season, night frost in early summer, and poor, dry soil suffering from excessive evaporation.

Actual timberline responses to predicted climate warming will differ greatly from site to site in relation to the local topography, edaphic features and associated ecological limitations. Any advance in the treeline to a higher elevation is likely to be slower and at least less certain than that in the actual timberline. In addition, advances in the actual timberline and treeline may even be prevented by phenomena occurring along with climate change. A potential key factor in this is serious snow load damage to the trees.

Keywords: actual timberline and treeline advance, climate warming, edaphic feature, thermoclimatic indicators, timberline and treeline ecotone, topography
Acknowledgements

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Oulu, 7 January 2006
A day of mild, southerly wind

Jyrki Autio
List of original papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals:


Responsibilities of the authors

Paper I. The material was gathered and processed by Jyrki Autio, and the paper was written jointly by Jyrki Autio and Olavi Heikkinen. Jyrki Autio was responsible for the publication process, as with the other papers.

Paper II. Jyrki Autio was responsible for the field survey, except for the pollen deposition measurements, which were planned by Sheila Hicks. The pollen samples were analysed by Raija-Liisa Huttunen. Jyrki Autio carried out most of the data analyses and all the statistical analyses. Sheila Hicks was responsible for the description of the pollen deposition background and for the part of the manuscript dealing with it. Jyrki Autio wrote remainder of the manuscript. The interpretation was the work of both authors.

Paper III. Jyrki Autio was responsible for this paper alone.

Paper IV. Jyrki Autio carried out the field survey, data analyses, writing and interpretation. Alfred Colpaert defined the elevations of the actual timberlines by the GIS technique.
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1 Introduction

The timberline is a traditional and still fascinating object of phytogeographical research (Tuhkanen 1999). The uppermost limit of continuous or almost continuous forest, i.e., the actual timberline, is the most conspicuous phytogeographical boundary in mountain areas almost everywhere in the world (Holtmeier 2003). It is a socioeconomically important transition zone, being the one in which the largest winter resorts in Finland are situated. It is also an ecologically significant transition zone, in which the tree-ring width (Hustich 1948, Mikola 1952), density, growth and the altitudinal limit of young seedlings (Kellomäki et al. 1997, Juntunen et al. 2002) react quite quickly to climate change. The current interest in studying the timberline has been prompted by widespread predictions of future climate change and its impact on the environment, including the altitudinal location of timberlines (Kullman 2000, Juntunen et al. 2002, Holtmeier 2003, Kultti 2004).

The effects of earlier climate changes on the advance of the timberlines horizontally or vertically have nevertheless been found to have taken place slowly (Payette & Fillion 1984), even over decades or centuries (Holtmeier 2003). Holocene changes in timberlines and treelines in circumpolar and mountain areas in Europe have been studied using evidence from pollen (Hyvärinen 1975, Seppä 1996) and plant macrofossils, including tree-ring widths (Eronen, 1979, Eronen & Zetterberg 1996, Barnekow 1999, Kultti 2004).

Forest cover may gradually become thinner with increasing altitude, in a manner similar to the case of continuum theory (Whittaker 1956, Walter 1964), so that it is difficult to distinguish the vegetation types from each other (Fig. 1, line B). In this case, the actual timberline does not form any easily distinguishable or delineable line that can be perceived in the terrain or on aerial photographs. On the other hand, it may be abrupt, bordering on a treeless or almost treeless area in the landscape. This is similar to line D in the continuum theory, as shown in Figure 1, where the vegetation types form a distinguishable flat growth zone. Sometimes an actual timberline suggestive of the case line C in Figure 1 is to be found in Finnish Lapland. It is always possible to define the uppermost limit of continuous forest, in contrast to the total continuum of the continuum theory (Fig. 1, line A).

The timberline has fascinated researchers for about 200 years. The earliest reports, in which the focus was on observing its altitudinal position, appeared about 200 years ago (Zschokke 1805, cit. Holtmeier 2003). Early timberline research was reviewed by Däni-
ker (1923), who first studied this phenomenon with special regard to ecological conditions and who was the first to use ecological research methods (Tranquillini 1979, Tasanen & Veijola 1994, Holtmeier 2003), although some studies on ecological conditions at the timberline were carried out also before Däniker (1923), such as the monograph of Kihlman (1890) on the northern tree line on the Kola Peninsula. Those studies were based on careful observations and considerations, but not on experimental ecological measurements. Proposals have been appearing in the scientific literature for more than a hundred years concerning the climatic parameters and indices that best denote the location of the timberline and treeline (Tuhkanen 1984, 1999). Supan (1884) and later Köppen (1919) emphasized at an early stage the conspicuous coincidence of the polar treeline and timberline with the 10°C isotherm for the warmest month of the year, which is the oldest and best-known climatic indicator for these limits.

![Fig. 1. Schematic diagram of floristic change in a plant association with a gradually changing climate, according to Walter (1964).](image)

The timberline and treeline are influenced by many abiotic (climatic, edaphic and topographic), biotic (parasitic snow fungi, insect pests, other animals) and anthropogenic factors (felling, grazing, air pollution, fire), which are often interrelated in a complex way (Holtmeier 2003). There is a firmly established conception among timberline researchers, however, that climate is the main factor primarily controlling the general position of timberlines and treelines in polar and mountain regions (Hustich 1948, Tranquillini 1979, Wardle 1993), just as it acts as the main factor governing the distribution of vegetation on the Earth as a whole (Tuhkanen 1984). Air temperature has generally been considered the main climatic factor determining both the altitudinal and northern timberline and treeline (Tranquillini 1979, Larsen 1989, Dahl 1998, Tuhkanen 1999). The impact of thermal fac-

Sometimes the timberline is unable to reach its climatic limit, in which case its location may be regulated more obviously by locally varying orographic (Hustich 1937, Piirila 1967, Holtmeier 1974, 2003, Tranquillini 1979, Autio 1995a, 1995b, Holtmeier et al. 2003) and topographic (Perttu 1972, Arno 1984, Mayer & Ott 1991, Autio 1995a, 1995b, Kjällgren & Kullman 2002, Holtmeier 2003) factors than by climatic factors. Also, soil temperature has proved to be just as important as air temperature as a controlling factor (Holtmeier 2003), and anthropogenic and biotic factors have been shown to lower the altitudinal position of the timberline (Holtmeier 1974, 2003, Veijola 1998).

Despite the long tradition of timberline research, there is still no uniform theory that accounts for it exhaustively, and there is still an evident need to investigate the timberline and treeline, especially with respect to its local levels (horizontal distribution 100 m – 1 km) and regional levels (horizontal distribution 1 – 100 km) (Holtmeier 2000, 2003, Kjällgren & Kullman 2002). In the case of Central Finnish Lapland, for example, the area between the parallels 67°N and 68°N, no highly accurate local or regional picture is available on the relation between climatic, orographic or topographic factors in determining the location of timberline and treeline. The purpose of the present work is to remedy this insufficiency.

1.1 Timberline and treeline definitions and terminology

An operational definition of timberline and treeline is often needed (Tuukkanen 1993). Most definitions of the timberline refer to a certain minimum forest cover and those of the treeline to a minimum tree height (Holtmeier 2003). The critical minimum cover may range from 30 to 40% (Holtmeier 1974, Ellenberg 1986, Påhlsson 1995) and the mini-
mum tree height may range from two to three metres (Wardle 1974, Kullman 1979, 1990, Holtmeier 2003).

The terms related to the timberline, i.e., the transitional zone between forested and treeless areas, are numerous and rather ambiguous (Hustich 1966, 1979, Heikkinen 1984, 2005, Tuhkanen 1993, 1999, Autio 1995b, Heikkinen et al. 2002, Holtmeier 2003), on account of the great ecological, physiognomic and taxonomic variety of mountain timberlines (Tuhkanen 1993, Holtmeier 2003) and multidisciplinary and multilingual nature of the subject matter (Tasanen & Veijola 1995). Some terms refer to the location of the timberline (upper, lower timberline), others are related to factors controlling it (climatic, orographic, anthropogenic timberline) and others refer to both location and causes (alpine, northern, continental, maritime timberline). Proposals for the standardization of the nomenclature have been made (Löve 1970, Hustich 1979), but the generally accepted nomenclature is far from complete (Hustich 1966; Atkinson 1981, Payette 1983, Kullman 1990, Tuhkanen 1993, Holtmeier 2003). It seems that there are almost as many definitions as there have been researchers working with timberlines, and it is certainly the case that traditions regarding timberline terminology differ from one country to another (Tuhkanen 1999). It is nevertheless obvious that an abundant terminology and range of concepts is needed so that the phenomenon can be discussed accurately.

One of the most widely used sets of timberline terminology is that suggested by Hustich (1966, Fig. 2), more detailed descriptions of which are presented in paper III. This has been used later by many others to define the physiognomic forest line (Heikkinen 1984, Tuhkanen 1993, Autio 1995b, Heikkinen et al. 2002) or the physiognomic timberline (Veijola 1998) as that represented by the limit of continuous or nearly continuous forest cover bordering on a treeless or almost treeless fell summit. Since this line is more or less clearly distinguishable in the landscape, it is also known as the empirical (Dahl 1998) or actual timberline (Lauer & Klaus 1975, Dahl 1998, Veijola 1998, Holtmeier 2000, 2003). As far as the altitudinal limit of forest is concerned, the concepts of upper timberline and alpine timberline are used, too (Tuhkanen 1999, Holtmeier 2003, Heikkinen 2005), although these are not very coherent concepts in the case of Finland, which has no lower timberlines, for example, to the counterpart of the upper timberline. This may the case in spite of the fact that the upper timberline may be a consequence of the same effect that brings about the lower timberline, e.g., a cold air lake (Whiteman 2000) and forms the front for the actual timberline (III). For this reason altitudinal timberline (see Kullman 1990, Barnekow 1999) would be a more neutral and applicable term than upper timberline. The word alpine is closely associated with the Alps and high-mountain regions, and is therefore not entirely accurate for describing the low, rounded fells of Northern Finland (Heikkinen 2005). Since the term alpine should, according to Holtmeier (1974), be defined as applying only to the Alps, maybe fell timberline would be more logical to use in Fennoscandia. There are several reasons why it was decided here to use the term actual timberline to describe the limit of continuous or nearly continuous forest cover bordering on a treeless or almost treeless fell summit. Firstly, actual timberline is more common and customary than physiognomic or empirical timberline. Secondly, the word actual (Hustich 1979) literally means the present limit of continuous forest, which reflects the importance of prevailing environmental conditions such as climate together with the site history (Holtmeier 1997, 2002), thus alluding to the changing nature of the timberline in time and space, i.e., it is dynamic. Thirdly actual also means distinct; the actual timberline
is a more and less conspicuous phenomenon in the visible landscape, either abrupt or gradual. Fourthly, it doesn’t refer to any particular controlling factor; on the contrary, the actual timberline is a result of many unfavourable factors, as is a typical feature in mountain areas. In contrast to the present author, Holtmeier (2003) uses the term actual timberline to refer to a limit resulting from factors other than climate. Actual timberline will nevertheless be used here as a generic term for more or less continuous forests bordering on treeless or almost treeless fell summits whatever their causes.

The transitional zone between the economic timberline and the tree-species line is called the timberline ecotone (Fig. 2) (Heikkinen et al. 2002, III, IV). When the historical aspect, the changing nature of the actual timberline in time and space, is included, this ecotone could be extended as far as the historical timberline. The transitional zone between the actual timberline and the treeline, characterized by isolated trees and small stands, even forest patches, is called the treeline ecotone (Holtmeier et al. 2003). The treeline itself is the extreme boundary where trees still achieve arboreal form and size (2 m) (Hustich 1966, Tuhkanen 1993). Since the area between the remote individual trees is completely treeless, it may be said that the treeline ecotone is relatively treeless and an open fell summit is completely treeless (see Krujkov 1993, cit. Tasanen & Veijola 1995), with only crippled growth forms of tree species existing, e.g., mat forms.

Fig. 2. Different treelines and timberlines: ideas and concepts mainly according to Hustich (1966), Tuhkanen (1993), Veijola (1998) and Heikkinen and others (2002).
1.2 Aims of the research

The main questions considered in the present research are:
1. What are the altitudinal positions of the actual timberline and treeline? (IV)
2. What are the special characteristics of the local climate in the timberline ecotone? (I, II, III)
3. What factors control the position and formation of the actual timberline? (III, IV)
4. What factors control the position of the treeline? (III, IV)
5. What is the relationship between local climate conditions and pollen deposition at the timberline ecotone? (II)
6. What is the potential for actual timberline and treeline advance? (III, IV)
2 Material and methods

2.1 The area studied

The field studies were carried out on the fells of Aakenustunturi, Yllästunturi and Pyhä-
tunturi, situated between 67°N and 68°N in Finnish Lapland (Fig. 3). The area lies within
the northern boreal vegetation zone in the system of phytogeographical zones (Ahti et al.
1968) and sectors for north-west Europe, lying in sector OC, which is indifferent in terms
of the climate of northern Finland and the fell climate are presented in paper I and
detailed climate characterizations of Aakenustunturi in papers II and III.

The fells belongs to one of the most ancient residual mountains in the world, some of
its rocks being around 2000 million years old (Manner & Tervo 1988). Most of the rock is
quartzite (Mielikäinen 1979, Rastas 1984), with a high resistance to chemical weather-
ing. Angular quartzite blocks have been pried apart by water that freezes in the cracks at
their joints, forming wide fields of frost-shattered boulders. The round summits of the
fells display patterned ground and block streams formed on a till containing local quartz-
ite (Autio & Kinnunen 1992, McCarroll et al. 1996). The fells are characterized by geo-
morphological landforms such as lateral meltwater channels and glaciofluvial overflow
channels (IV). Orographic and topographic influence on the position of the actual timber-
line is discussed in paper IV. Human activity is confined to occasional visitors on Aake-
nustunturi and in the areas of Yllästunturi and Pyhäätunturi that are not reserved for down-
hill skiing. Ylläs, the westernmost summit of Yllästunturi, and Pyhäkero, the easternmost
summit of Pyhäätunturi, are important winter resorts, with downhill skiing slopes that are
visible in all directions over an area of dozens of kilometres in summertime (Ukkola
Fig. 3. Location of Aakenustunturi, Yllästunturi, Pyhätunturi and Muonio, together with the major vegetation zones of Fennoscandia: OA – oroarctic, NB – northern boreal, and MB – middle boreal (Ahti et al. 1968).

2.2 Field studies

Summary of the data used in the present work is described in Table 1.
Table 1. Summary of the data used in the present work.

<table>
<thead>
<tr>
<th>Data type</th>
<th>Observation period</th>
<th>Observation site</th>
<th>Data analyser</th>
<th>Used technique/instrument/data source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Air temperature at a 2.0 m above the ground</td>
<td>Eight growing seasons (1994–2001) and continuously 1.3.1996–28.2.1998</td>
<td>4 sites on Aakenustunturi</td>
<td>Jyrki Autio</td>
<td>Data logger, model KM1420</td>
</tr>
<tr>
<td>Air temperature at a 0.1 m and 0.3 m above the ground</td>
<td>Summer 1997</td>
<td>3 sites on Aakenustunturi</td>
<td>Jyrki Autio</td>
<td>Data logger, model KM1420</td>
</tr>
<tr>
<td>Soil temperature at a 0.1 m below the ground</td>
<td>1.3.1996–28.2.1998 and summer 1998</td>
<td>3 sites on Aakenustunturi</td>
<td>Jyrki Autio</td>
<td>Data logger, model KM1420</td>
</tr>
<tr>
<td>Snow depth and duration</td>
<td>1994–1998</td>
<td>9 sites on Aakenustunturi</td>
<td>Jyrki Autio</td>
<td>Depth gauge</td>
</tr>
<tr>
<td>Delayed snow deposits</td>
<td>1998</td>
<td>Aakenustunturi</td>
<td>Jyrki Autio</td>
<td>Digital aerial photographs by FM-kartta Oy</td>
</tr>
<tr>
<td>Heavy snow load damage to spruce and pine</td>
<td>2000</td>
<td>Aakenustunturi and Yllästunturi</td>
<td>Jyrki Autio</td>
<td>Estimated from the sample plot size of 400 m² at the actual timberline</td>
</tr>
<tr>
<td>Actual timberline position</td>
<td>2000 and 2001</td>
<td>Aakenustunturi, Yllästunturi, Pyhäntunturi (total number of plots is 787)</td>
<td>Jyrki Autio</td>
<td>Yllästunturi (Digita Oy)</td>
</tr>
<tr>
<td>Actual timberline elevation</td>
<td>2000 and 2001</td>
<td>Aakenustunturi, Yllästunturi, Pyhäntunturi (787 plots)</td>
<td>Alfred Colpaert</td>
<td>ArcGis program and elevation model by National Land Survey</td>
</tr>
<tr>
<td>Slope inclination at the actual timberline</td>
<td>2000 and 2001</td>
<td>Aakenustunturi, Yllästunturi (787 plots)</td>
<td>Jyrki Autio</td>
<td>Hypsometer, model PM-5/1520</td>
</tr>
<tr>
<td>Seedling density and mortality</td>
<td>2004</td>
<td>15 sites on Aakenustunturi</td>
<td>Jyrki Autio</td>
<td>Number of seedlings on sample plots (size 300m²/500m²)</td>
</tr>
</tbody>
</table>
| Pollen deposition                      | 1996–2001                | 4 sites on Aakenustunturi  | Sheila Hicks and Raija-Liisa Huttunen                     | Tauber trap
2.2.1 Air and soil temperature

Air temperature measurements were carried out in the closed forest near the economic timberline (330 m a.s.l.), the actual timberline on the northern slope (390 m a.s.l.), the treeline (482 m a.s.l.) and the actual timberline on the southern slope (430 m a.s.l.) along a south-to-north transect across Aakenustunturi. The sites on the actual timberlines were situated close to the climatic forest limit in each case (III, IV). At each site air temperatures were measured at one-hour intervals by means of four-channel data loggers, model KM 1420, at a standard height of 2.0 metres above the ground surface. The temperature sensors were fitted with white plastic covers with ventilation slits to interrupt direct solar radiation. The measurements covered the summer periods of eight years, 1994–2001 (II, III), in addition to which year-round measurements were taken throughout the period from 1st March 1996 to 28th February 1998 (I, III). The vertical distributions of air temperatures at heights of 2.0, 0.3 and 0.1 metres above the ground surface and 0.1 metres below the ground surface in summer 1997 are presented in paper III.

Monthly mean temperatures and effective temperature sums for the normal period 1961–1990, calculated using the model of Ojansuu and Henttonen (1983), were used as reference data (II, III). The measured and calculated data were a quite similar, although the monthly mean temperatures deduced from the model values were usually lower than those for the measurement site at the actual timberline on the southern slope (II). Calculations and definitions of biotemperature, July mean and July mean maximum temperatures, mean tetratherm, maximum and minimum tetratherms, mean tritherm, effective temperature sum, effective temperature sum minimum and length of growing season are provided in paper III.

Soil temperatures at a depth of 0.1 metre were measured at one-hour intervals at the actual timberline on the northern slope, the treeline and the actual timberline on the southern slope at Aakenustunturi all the year round for the period 1.3.1996–28.2.1998, and soil temperatures were measured in summer 1998 (III). Soil and air temperatures were monitored using the same data loggers.

The accuracy of the data logger model at reference temperatures of -100°C to 300°C is ±0.2°C (KM1400 Series 1989), and the accuracy of the instruments was re-tested at reference temperatures of -40°C to +40°C during calibration, where it was found to be ±0.1°C, i.e., at least as good as data loggers such as Tiny-Talk (Data Logger... 2005) and Hammer (Elpro 2005), as used by Mook and Vorren (1996) and Vorren and others (1999).

Missing temperature readings for the treeline station in 1995 were filled in using linear regression based on data for the adjacent actual timberline station during the same period. The square of the correlation (R²) in the regressions ranged between 0.945 and 0.977.

2.2.2 Snow depth and duration, wind direction and velocity

Snow depths were recorded over the period 1994–1998 at nine sites at different altitudes along the south-north transect on Aakenustunturi (III). Digital aerial photographs were used to illustrate the relation between lingering snowpatches and the position of the actual
timberline (IV). Some observations on snowpatches are also included in paper I. Heavy snow load damage to the spruce and the pine were estimated (see Norokorpi & Kärkkäinen 1985) from circular monitoring plots of size 400 m² (radius 11.5 m) bordering on the actual timberline (Fig. 4) and the influence of these factors on the altitude of the actual timberline was assessed (IV).

Wind directions and velocities were estimated on the basis of data available from the Finnish Meteorological Institute’s observation station at Muonio (254 m a.s.l.) and the summit of Yllästunturi (718 m a.s.l.) (II, III).

2.2.3 Actual timberline position and elevation

The actual timberline was drawn along the line where the crown canopy of the continuous or almost continuous forest is still c. 30 % and where the altitudinal position of actual timberline was recorded on GPS receiver. The proportion of canopies, tree species and snow load damage to spruce and pine were estimated from circular monitoring plots of size 400 m² (radius 11.5 m) bordering on the actual timberline. The extents of block or boulder fields were measured by estimating their percentual coverage of the rectangular sample plots of size 400 m². Slope inclination has measured exactly at the actual timberline (black dots).

Fig. 4. Schematic presentation of field data collection at the actual timberline. Black dots illustrate sites where the canopy of the continuous or almost continuous forest is still c. 30% and where the altitudinal position of actual timberline was recorded on GPS receiver. The proportion of canopies, tree species and snow load damage to spruce and pine were estimated from circular monitoring plots of size 400 m² (radius 11.5 m) bordering on the actual timberline. The extents of block or boulder fields were measured by estimating their percentual coverage of the rectangular sample plots of size 400 m². Slope inclination has measured exactly at the actual timberline (black dots).
at the same sites were exposure and slope inclination. Presence and cover of block fields measured just above the actual timberline. Whereas amount of snow damage to spruce and pine and proportions of the tree species were measured just below the actual timberline (Fig. 4). Exposure and the location of the actual timberline were measured at a total of 344 sites on Pyhätunturi. The coordinates (lat, long) of all the sites were recorded on a GPS receiver, model GARMIN GPS 12XL, employing the average position function, which means that the GPS receiver calculates moving averages of the coordinates and measurement is continued until this moving average stabilises, which takes approximately five minutes (Owner’s manual & reference 1998). The accuracy of the position was five to ten metres on average. The elevations of the actual timberline sites were determined using the overlay analysis technique in the ArcGis program and elevation models provided by the National Land Survey. By combining the line connecting the actual timberline sites with digital aerial photographs it was possible verify the accuracy of the actual timberline altitudes whenever they coincided with the lower edges of block fields (IV). In addition, digital aerial photographs were used to illustrate the relation between the actual timberline and environmental factors that lower or raise its position. Treeline altitudes are based on the data published by Autio (1997).

2.2.4 Topography and orographic features

Slope inclination (in degrees) at the actual timberline was measured using an optical hypsometer, model PM-5/1520. The orientations of the actual timberline sites were established in relation to the nearest fell summit. The fell were divided into four sectors, each standing for one cardinal point, with the half-cardinal points serving as sector boundaries, the final exposure of each timberline site then being determined on the basis of the cardinal point of the sector in which the target was situated (IV) (see Perttu 1972).

The extents of block or boulder fields were measured by estimating their percentual coverage of the land area (400 m²) at the actual timberline (IV, Fig. 4). The thicknesses of the humus layers and soil types were measured at the sites used for the air temperature observations (III).

2.2.5 Pollen deposition and seedling density

Annual variation in pollen deposition was measured during the period 1996–2001 by means of Tauber traps placed at exactly the same spots on the transect across Aakenustunturi as were used for the air temperature measurements. The pollen results are expressed as annual pollen deposition (grains cm⁻² year⁻¹) (II).

Seedling density (number of height < 2 m/ha) and mortality (number/ha) were monitored for spruce and pine separately on Aakenustunturi at points immediately above the actual timberline and in the middle of the treeline ecotone on the southern and northern slopes and at the treeline. The total number of plots used was 15. At the actual timberline
plots had an area of 300 m² (radius 9.8 m) and those in the middle of the treeline ecotone and at the treeline had an area of 500 m² (radius 12.5 m) (IV).

2.3 Statistical analysis

Non-parametric statistical analyses were used, because the materials did not follow the normal distribution, which was always checked before application of the Kolmogrov-Smirnov test (SPSS Base 8.0 1998). Spearman correlation analysis was used to examine the direction and intensity of the connection between pollen deposition and the various temperature indicators, i.e., mean monthly temperature and mean monthly effective temperature sum, two-week mean temperature and cumulative effective temperature sums for the current and previous summer (II). Spearman correlation was also used to study the direction and intensity of the correlation between the altitudes of the actual timberline, coverage of block fields, slope inclination and snow damage to spruce and pine (IV).

The altitudes of the actual timberlines with different exposures were analysed with the non-parametric Mann-Whitney’s U test to test the null hypothesis that the groups of sites defined for the four points of the compass would be at equal altitudes (IV). Mann-Whitney’s U test was also used to test the null hypothesis that air and soil temperatures would be identical (III).
3 Results and discussion

The results are described in detail in original papers I–IV.

3.1 Altitudinal positions of the actual timberline and treeline

The average actual timberline elevation varies from ca. 370 metres to 400 metres a.s.l. The lowest vertical forest limit lies at approximately 270 m a.s.l., and the highest continuous forest reaches almost 460 m a.s.l. The difference between the highest and lowest altitudinal positions of the actual timberline on Aakenustunturi and Yllästunturi is greatest at the northern exposure but on Pyhätunturi at the southern exposure (III).

The effect of exposure is significant on the altitude of the actual timberline, which is usually highest on the west and south-facing slopes (Figs. 5, 6, 7) and lowest on the north and east-facing slopes. In some cases, however, the altitude of the actual timberline may remain significantly lower than average even on south-facing slopes, as on Pyhätunturi (Fig. 7), where it is affected by very steep and very rocky slopes (IV).

The average altitudinal position of the treeline is highest on south-facing slopes (473 m a.s.l.) (Autio 1997), where the most favourable thermoclimatic conditions are prevailing (I, II, III), while on north-facing slopes the average altitudinal position of the treeline is 450 m a.s.l. The maximum height of the treeline, 516 m a.s.l., is reached on the south-facing slope of Yllästunturi (Autio 1997).
Fig. 5. Classification of altitudes (m a.s.l.) into four class intervals at actual timberline points on Aakenustunturi. The number of actual timberline points (circles of different colours) for each interval class is also given in parentheses. Contours are presented at 10-metre intervals.
Fig. 6. Classification of altitudes (m a.s.l.) into four class intervals at actual timberline points on Yllästunturi. The number of actual timberline points (circles of different colours) for each interval class is also given in parentheses. Contours are presented at 10-metre intervals.
3.2 Character of the local climate in the timberline ecotone

3.2.1 Temperature

Fell summits are colder on average than areas situated at lower altitudes (I, II, III), because in the standard atmosphere a hundred-metre rise in altitude will bring about a temperature decrease of 0.65°C (Gregg 1949) and high winds will also lower mean temperatures (Tranquillini 1979). The lapse rate of the mean annual temperature deduced from the values observed on Aakenustunturi is much greater between the actual timberlines and the treeline than between the closed forest and the treeline, especially on the south-facing slope (Table 2) (see Mook & Vorren 1996). The drop in mean annual temperature with height between the closed forest and treeline is almost the same as in the standard atmosphere (Table 2; III). The lapse rates of the other temperature indicators that may be regarded as serving best to explain the location of the actual timberline and
treeline behave with increasing altitude in the same way as the mean annual temperature (III). The observations also show that the lapse rates vary seasonally (Table 2, I), a situation also noted elsewhere (Yoshino 1975). Despite the fact that the lapse rate varies with exposure, season and height in a standard atmosphere, it is often used in vertical extrapolation of temperatures from official weather stations due the lack of in situ temperature measurements in mountain areas (Mook & Vorren 1996, McKenzie et al. 2003), especially in timberline environments (Tuukkanen 1999).

Table 2. Lapse rates (°C/100m) of mean monthly temperatures measured at a height of 2 m above ground between the monitoring sites CF (330 m a.s.l., closed forest near the economic timberline) to TL (482 m a.s.l., treeline), ATLN (390 m a.s.l., actual timberline on the north-facing slope) to TL and ATLS (430 m a.s.l., actual timberline on the south-facing slope) to TL on Aakenustunturi. Values are 4-year means (1.8.1994–31.7.1998).

<table>
<thead>
<tr>
<th>Site to site</th>
<th>Difference in height (m)</th>
<th>Jan</th>
<th>Feb</th>
<th>Mar</th>
<th>Apr</th>
<th>May</th>
<th>Jun</th>
<th>Jul</th>
<th>Aug</th>
<th>Sep</th>
<th>Oct</th>
<th>Nov</th>
<th>Dec</th>
<th>Year</th>
</tr>
</thead>
<tbody>
<tr>
<td>CF to TL</td>
<td>152</td>
<td>0.84</td>
<td>0.51</td>
<td>0.79</td>
<td>0.69</td>
<td>1.20</td>
<td>0.92</td>
<td>0.80</td>
<td>0.33</td>
<td>0.30</td>
<td>0.91</td>
<td>0.20</td>
<td>0.18</td>
<td>0.64</td>
</tr>
<tr>
<td>ATLN to TL</td>
<td>92</td>
<td>0.98</td>
<td>0.47</td>
<td>0.71</td>
<td>0.49</td>
<td>1.03</td>
<td>0.79</td>
<td>1.10</td>
<td>0.33</td>
<td>0.71</td>
<td>0.65</td>
<td>0.58</td>
<td>0.90</td>
<td>0.73</td>
</tr>
<tr>
<td>ATLS to TL</td>
<td>52</td>
<td>0.73</td>
<td>0.58</td>
<td>1.40</td>
<td>0.83</td>
<td>1.83</td>
<td>1.73</td>
<td>1.90</td>
<td>1.10</td>
<td>1.44</td>
<td>0.58</td>
<td>0.77</td>
<td>0.63</td>
<td>1.10</td>
</tr>
</tbody>
</table>

The highest July absolute maximum temperatures measured at the actual timberline are always higher than at the treeline and nearly always higher than in the closed forest. The number of hot days (daily maximum temperature +25°C or more) during the period 1994–2001, for example, was 59 at the actual timberline on the southern slope, 35 at the actual timberline on the northern slope, 29 in the closed forest and 18 at the treeline. Temporal and spatial variations were observed in the distribution of temperature stratification within the lowest 2 m of the air mass, in that temperatures near the ground surface were several degrees higher than at 2 m in the middle of the day at the actual timberline on the southern slope and in the afternoon at the actual timberline on the northern slope. Temperatures could be relatively high at night as well at the actual timberline on the northern slope in summer (III). Actual timberlines on south-facing and north-facing slopes with inclinations of 10–15° usually receive more solar radiation than more gentle (2°), forested slopes (Geiger et al. 1995; Whiteman 2000). In the present case the most extreme temperature conditions are to be found at the actual timberline on the southern slope (Autio 1995a, 1995b, Autio et al. 1998, II, III).

Temperature inversions (Huovila 1987, Tammelin 1988, Whiteman 2000) are encountered particularly in winter and can be of over three days’ duration (I, III). When a fell summit is situated about 500 m a.s.l., the greatest temperature difference between the lowest-lying place, the closed forest, which is also the coldest place, and the fell summit, the warmest place, can be as much as 16°C. The top of the inversion is nearly always on the summit among fells where the highest point does not reach more than 500 m a.s.l. (III), but on fells of high altitude, such as Yllästunturi (718 m a.s.l.), the top lies somewhere in the middle of the slope, near the actual timberline (Kurula & Heikkinen 1996). On the other hand, it must be remembered that the height of the top of an inversion varies with the season of the year (Tammelin & Säntti 1992). The observations from Aakenustunturi show, for example, that the top of the inversion sometimes lies at the actual tim-
berline on the south-facing slope (430 m a.s.l.), especially in early winter (I, III). Rapid temperature fluctuations are typical during temperature inversions (II). Inversions of shorter duration, less infrequent and less pronounced than in winter, were also observed during the growing season, mostly in the night and early morning, at which time the cold air slid down the slope, coming to rest in the area just above the actual timberline, where it caused a cold air lake (Tammelin 1988, Whiteman 2000), thus exposing this area to the danger of night frost. Small-scale temperature inversions are also quite common close the ground surface on cold summer nights, being most obvious at the actual timberline, in which case temperatures below 0°C are recorded just above the ground surface while the temperature is above 0°C at a height of 2 m (III). At the treeline, however, the air temperature is more or less the same near the ground surface and at 2 m.

Orographically caused exposure to night frosts is more common at the treeline than at lower altitudes, i.e., at the actual timberline or in closed forests, at the beginning of the growing season, and the late spring and early summer are much colder at the treeline than in lower lying places. By contrast, night frosts occur most commonly at the actual timberline on southern slopes and least at the treeline at the end of the growing season, in August and September (III).

The observations show that the mean minimum tetratherm (+6.3°C, cf. Slettjord 1993), mean July temperature (+12.6°C, Norin 1978, cit. Tuhkanen 1993), biotemperature (+3.3°C, cf. Tuhkanen 1980) and minimum effective temperature sum (455.4 d.d., cf. Nikolov & Helmisaaari 1992) on the treeline coincide with the results of earlier studies, while the mean tetratherm (+10.3°C and +10.1°C, respectively) at the actual timberline on the southern and northern slopes, together with the mean maximum tetratherm (+15.4°C, cf. Mook & Vorren 1996) on the southern slope coincide with the results of earlier studies. In practice the mean length of the growing season is c. 118 days both at the actual timberlines on the southern and on the northern slopes. This is 6 days longer than at the treeline. The growing season becomes shorter by 5 days per 100 m between the closed forest and treeline, but the shortening is more pronounced between the actual timberline and treeline. The mean effective temperature sum at the actual timberline on the southern slope is 704 d.d., which is c. 27 d.d. higher than on the northern slope and c. 85 d.d. higher than on the treeline (III). The thermoclimatic indicators calculated from the observed values and from the climate model of Ojansuu & Henttonen (1983) for the actual timberlines and treeline (Table 3) were mostly higher than in earlier studies (III).
Table 3. 8-year (1994–2001) and 30-year (1961–1990) means (the latter calculated using the model of Ojansuu and Henttonen 1983) of thermoclimatic indicators measured at a height of 2 m above ground at the monitoring sites CF (330 m a.s.l., closed forest near the economic timberline), ATLN (390 m a.s.l., actual timberline on the north-facing slope), TL (482 m a.s.l., treeline) and ATLS (430 m a.s.l., actual timberline on the south-facing slope) on Aakenustunturi.

<table>
<thead>
<tr>
<th>Year Site</th>
<th>July Mean °C</th>
<th>July Mean max °C</th>
<th>July Mean min °C</th>
<th>Tetratherm Mean °C</th>
<th>Tetrath. Mean max °C</th>
<th>Tetrath. Mean min °C</th>
<th>Tritherm Mean °C</th>
<th>Tritherm Mean max °C</th>
<th>Tritherm Mean min °C</th>
<th>Biotemp. °C</th>
<th>Growing season days</th>
<th>Effective temp. sum d.d.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>8-year</td>
<td>13.5</td>
<td>17.8</td>
<td>9.3</td>
<td>10.2</td>
<td>14.2</td>
<td>6.4</td>
<td>11.8</td>
<td>16.1</td>
<td>7.6</td>
<td>3.7</td>
<td>120.1</td>
<td>698.3</td>
</tr>
<tr>
<td>ATLN</td>
<td>13.3</td>
<td>18.0</td>
<td>9.2</td>
<td>10.1</td>
<td>14.3</td>
<td>6.4</td>
<td>11.6</td>
<td>16.2</td>
<td>7.6</td>
<td>3.6</td>
<td>118.5</td>
<td>677.1</td>
</tr>
<tr>
<td>TL</td>
<td>12.6</td>
<td>16.2</td>
<td>8.7</td>
<td>9.4</td>
<td>13.0</td>
<td>6.3</td>
<td>10.9</td>
<td>15.0</td>
<td>7.3</td>
<td>3.3</td>
<td>112.5</td>
<td>619.4</td>
</tr>
<tr>
<td>ATLS</td>
<td>13.5</td>
<td>18.6</td>
<td>8.8</td>
<td>10.3</td>
<td>15.1</td>
<td>6.1</td>
<td>11.8</td>
<td>17.0</td>
<td>7.3</td>
<td>3.7</td>
<td>118.3</td>
<td>704.0</td>
</tr>
<tr>
<td>30-year</td>
<td>12.1</td>
<td>17.8</td>
<td>9.2</td>
<td>10.1</td>
<td>14.2</td>
<td>6.4</td>
<td>11.6</td>
<td>15.0</td>
<td>7.3</td>
<td>3.3</td>
<td>112.5</td>
<td>619.4</td>
</tr>
</tbody>
</table>

*Note: Year mean values are displayed in the 8-year column, and the 30-year mean values are displayed in the 30-year column.*
The period for which air and soil temperature measurements were carried out was longer and the network more extensive in this case than in any other study of timberlines and the treeline undertaken in Finnish Lapland (III). Thermoclimatic characterizations of the timberline ecotone and the effects of climate on the formation of timberlines and treelines in northern Norway (e.g. Mook & Vorren 1996) and in Sweden (Perttu 1972) are also usually based on shorter time series than this. The sparseness of representative records of air temperatures (Tranquillini 1979, Mook & Vorren 1996, Tuhkanen 1999, McKenzie et al. 2003) and soil temperatures (Holtmeier 2003) in the timberline ecotone together with the indeterminacy of the concept of timberline and its highly variable nature both physiognomically and taxonomically create difficulties in comparing the present results with earlier ones.

### 3.2.2 Snow cover

The depth of the snow cover on fells varies greatly on account of altitude, exposure, the vegetation cover, land surface structure and roughness, i.e., microtopography and geomorphic landforms, wind direction and velocity (III, Holtmeier 1974, 2003). The depth continues to increase above the actual timberline, but eventually decreases towards the fell summit, where the maximum depth will be less than 0.3 m. There are also places, usually convex surfaces, where no snow accumulates at all because the wind blows it away. Reindeer grazing also left some snow-free places behind on the fell summit in the present case. The largest amount of snow, c. 4.0 m, accumulated in lateral meltwater channels near the actual timberline on the north-facing slopes (I, III), where the snow patches usually persist until the end of July each year. The convex microtopography on the fell summits and the sun-exposed slopes of the meltwater channels usually become clear of snow during April, at which time the maximum depth of snow, 1.65 m, is to be found in front of the actual timberline. The hardness of the snow varies locally, with that in wind-exposed places, if not rapidly removed, becoming increasingly compacted and hardened by the wind while that on more or less forested slopes is softer. Thus the heat insulation effect of the snow is weaker at places between the actual timberline and the fell summit than in places below the actual timberline. Rime accretion on trees between the actual timberline and the treeline was sometimes very heavy, especially in early winter (III). Newly falling snow can easily accumulate on rimey or icy trees, causing a heavy snow load, sometimes some thousands of kilogrammes (Jalkanen & Konopka 1998), which can break the crowns and branches, so that about 80% of the trees forming the actual timberline have been damaged by heavy snow loads (IV), and about 100% at the treeline (Mustonen 1997). Spruce appeared to be more resistant to snow breakage than pine (IV).

### 3.2.3 Wind

Wind speeds commonly reach storm proportions (21 m/s) in summer time at Yllästunturi (III) and sometimes hurricane proportions (>32 m/s) during the winter (Lehtonen 1992).
The mean wind direction in western Lapland for the months June-September is from the south (III), but that prevailing two weeks before and after the flowering of spruce, pine and birch (in June-July) is from the east (II).

3.3 Environmental factors influencing the actual timberline and its physiognomy

The actual timberline reaches its highest altitude (456 m a.s.l.) on slopes with a gentle inclination and few or no block fields, where soil properties are similar to those in the closed forest and in sheltered furrows where there are no snow patches. Finally, its position is controlled by many climatic features that are unfavourable for tree growth and regeneration (IV). Those slopes are characterized by a gradual progression from forest to treeless or almost treeless terrain, in which case the actual timberline does not form an easily distinguishable or delineable line that can be perceived in the field or in aerial photographs (Fig. 8A, see also Fig. 1 point B).

Many climatic factors of significance for forest growth and regeneration deteriorate at the actual timberline relative to their state in closed forest. The length of the growing season is shorter, for instance, and it can be delayed considerably (II, III), the snow tends to be deeper and it melts much later (I, III, IV), snow load damage to the trees is much more frequent and more severe (IV), wind velocity is greater, night frosts are more common during the growing season and summer temperatures are more extreme (II, III). Interaction between the factors mentioned above results in a situation where forest regeneration is slower and more chancy and seedling mortality may be more common at the actual timberline than in the closed forest (IV). The regeneration process in spruce from bud formation to seed maturation, for example, takes two warm summers, so that certain climatic conditions must be fulfilled during the summer preceding that of seed maturation in order to ensure successful formation of the regenerative buds, flowering and seed formation (Sarvas 1970). Correspondingly, the regeneration process for pine takes three warm summers (Sarvas 1962). Thus the probability of achieving conditions propitious for the successful regeneration for either pine (Kellomäki and others 1997) or spruce is low at the actual timberline. Not only are summer temperatures relevant to the process of tree regeneration, but severe snow load damage to trees, breaking the crowns and branches, is also frequent in places where the regeneration process is taking place. Heavy snow load damage increases with altitude, and pine is more susceptible to it than spruce, while birch is the most resistant. Asexual and sexual reproduction appear to be most successful in birch, as this is the dominant tree species at the highest actual timberlines (IV). On the other hand, it is pine which achieves arboreal form and size at the highest altitude at the treeline (Autio 1997). Pine and spruce reach equal altitudes as tree species forming the actual timberline (IV). Monotonous wind direction may also delay forest regeneration (II), in that trees growing on wind-shadow slopes may be prevented from pollinating. According to Sarvas (1962), pollination is the key minimum factor for seed yield.

Seedling mortality appears to be dependent on exposure, as mortality is 28.0% for conifer seedlings on north-facing slopes but only 4.4% on south-facing slopes. Delayed
snow melting and its consequences on the northern slopes are the key factors causing the
difference in seedling mortality, although the total number of conifer seedlings also var-
ies between north and south-facing slopes, the former having only 1/5 of number to be
found on the latter (IV).

The most severe winter frosts (-31.3°C) appear not to pose any problems for fully
grown trees at the actual timberline (III), as these are well adapted to severe (Sakai &
Eiga 1983) and fluctuating conditions (Hustich 1983). On the other hand, the Red Belt
phenomenon observed in connection with repeated temperature inversions (Jalkanen &
Närhi 1993) may affect the actual timberline locally by destroying the parts of the trees
extending above the surface of the snow, probably through pronounced inversion and the
rapid temperature fluctuations which were typical during the inversions observed here (I,
III). Frost dehydration in the late winter, i.e., in April and May, can also pose a threat
(Tranquillini 1979, Havranek & Tranquillini 1995, Kjällgren & Kullman 1998), as there
were numerous occasions when the air temperature rose to +10°C while the ground was
still frozen (III).

One problematic feature of the climate at the actual timberline is the tendency for cold
air to slide down the slopes in the early and late summer and become trapped to form cold
air lakes (cf. Tammelin 1988, Whiteman 2000). The more compact and abrupt the limit of
continuous forest is, the longer this cold air will remain trapped. In such a situation seed-
lings and new shoots may be damaged or even destroyed (see Luomajoki 1993, III, IV).

The snow patches which form in lateral meltwater channels (Fig. 8B, see also Fig. 1
point C) and between an abrupt actual timberline and a steep slope (Fig. 8C, see also Fig.
1 point D) prevent any rise in the altitude of the actual timberline on sheltered north-fac-
ing or east-facing slopes (I, III, IV). Delayed snow melting will also slow down the rise in
the actual timberline on south-facing slopes (III, IV). Slopes with a great number of lat-
eral meltwater channels (Kujansuu 1967, Abrahamsson 1974) are characterized by unfor-
ested patches, which are result of delayed snow melting. Finally, the generation of contin-
uous or almost continuous forest is prevented by snow patches situated at the actual tim-
berline (Fig. 8B). This timberline is in practice a clearly defined abrupt line in places such
as snow patches, where its altitude is evidently lower than average.

One consequence of delayed snow melting is that the growing season is shortened
(Holtmeier 1974), often to the extent that it is too short for tree growth at all (III,IV), the
soil temperature is kept low until early summer by high soil moisture or even waterlog-
g (Holtmeier 2003) and evergreen conifers are threatened by parasitic snow fungi
(Holtmeier 1973, Ellenberg 1986). Such conditions prevent the establishment and growth
of seedlings, and sites will remain treeless (III, IV). The length of the growing season is
likely to remain even shorter than that determined on the basis of temperature because the
snow cover hardly ever disappears from the open ground, which is one of the criteria for
the start of the growing season as defined by the Finnish Meteorological Institute (Ter-
minen kasvukausi… 2005).
Fig. 8. Influence of slope inclination, landforms and block fields on the physiognomy of the actual timberline. The main types of actual timberline are as follows: A – gradual transition from continuous forest to scattered and often crippled trees bordering on upper oroboreal vegetation, B – abrupt timberline caused by a snow patch on a lateral meltwater channel, C – abrupt timberline caused by a snow patch situated between the compact timberline and a steeper barren slope, D – abrupt timberline bordering on block fields, E – slope inclination in degrees. Idea from Norton and Schönenberger (1984) and Holtmeier (2003).

The proportion of block fields is the most significant and visible single factor controlling the position and physiognomy of the actual timberline (Fig. 8D; see also Fig. 1 point D) (IV). Timberlines dictated by block fields make up at least 9.7% of the total length of the actual timberline on Aakenustunturi, 52.5% on Pyhätunturi and 28.0% on Yllästunturi. Slope inclination essentially increases the occurrence of block fields (Fig. 9). For example, the lowest altitude of the actual timberline (272 m a.s.l.) is the result of an extremely high proportion of block fields (about 80% of the land surface) and steep slopes (inclination more than 30°). Trees have difficulties in taking root on precipitous and rocky slopes and their roots have difficulties in taking up nutrients and water. In such areas the actual timberline is forced to withdraw and is not able to reach its climatic altitude. On slopes with a steep topography (inclination 30°–40°) the actual timberline elevation may also be reduced by avalanches (IV; see Autio & Heikkinen 1999). The influence of paludification force the actual timberline to lower altitudes, too (IV).
3.4 Environmental factors influencing the formation of the treeline

The treeline is a result of many factors that are unfavourable for tree regeneration and growth (Fig. 10), the main one being temperature during the growing season. The long-term minimum effective temperature sum for the normal period 1961–1990 calculated for the treeline using the climatic model of Ojansuu and Henttonen (1983) is 415 d.d., which is 40 d.d. lower than the measured value for the years 1994–2001 (III). This figure of 415 d.d. is also clearly lower than those of 470 d.d. and 450 d.d. quoted by Nikolov and Helmisaaari (1992) as coinciding with the northern treeline of spruce and pine, respectively. This implies that the effective temperature sum is too small in some years. Low temperatures during the growing season can mean a negative carbon budget, i.e., negative dry matter production in the trees (Tranquillini 1979).
Fig. 10. Main factors determining the position and structure of the treeline, combined mainly from author’s and Holtmeier (2003) results.

Short and cool growing season (II, III; Fig. 11) reduces remarkably seed germination rate and development of the seedlings. In addition in nutrient poor, dry and stony soils sprouting of the seeds are usually failed, because the ability to obtain nutrient and water is prevented (Holtmeier 2003, Holtmeier et al. 2003). Night frosts impede the seedlings survival and increase mortality of them during the growing season (III). More than half of all conifer seedlings are dead at treeline (IV). Short and cool growing season can also mean that trees are not able to complete their annual cycle on account of deficient lignification and poor development of terminal buds, rendering them susceptible to damage by night frosts (Tranquillini 1979). Thermoclimatic indicators such as the length of growing season variability is larger at treeline than at the actual timberline (II, III), which makes the regeneration of trees even more uncertain (see Sarvas 1962, 1970).

A thin or absent snow cover will fail to offer sufficient protection for seedlings against the cold of winter (IV). A thin snow cover is liable to be increasingly compacted and hardened by the wind, which will detract from its insulation properties even more, and the penetration of cold air into the ground is often improved by a short, scattered bottom and field layer vegetation and a thin humus layer (III). It is obvious that the roots of spruce and pine trees are unable to tolerate long periods of low soil temperatures without damage (III, Sutinen et al. 1997). It is also possible that the roots of conifer saplings may be incapable of reacting sufficiently quickly to the sudden drops in soil temperature that are typical of treeline conditions. In addition, frost dehydration in late winter can pose a threat to trees at the treeline. In summer, when soil temperatures rise at the treeline and in the treeline ecotone, coarse soils with a lack of organic matter may suffer from drought and excessive evaporation (III, Holtmeier et al. 2003). It has been claimed that excessively
high soil temperatures can delay seed germination (Holtmeier 2003) and seedling establishment (Holtmeier et al. 2003).

Fig. 11. Effects of low air temperature during the growing season and short growing season on trees at treeline. Ideas and concepts according to Tranquillini (1979).

The proportion of trees suffering serious snow load damage has been reported to be almost 100% at the treeline (Mustonen 1997), so that damage of this kind is one of the most essential and visible factors controlling the position of the treeline (see Norokorpi 1994).

Snow and ice crystals carried along the surface of the snow or just above it by high winds (III) impose a mechanical stress on the branches, needles and bark of the trees, detracting from their vitality (Holtmeier 1974) and exposing them to frost damage and frost drought (Hadley & Smith 1983, 1989). The high winds (Fig. 12) also lower the air temperature and reduce CO₂ uptake (Tranquillini 1979) and photosynthesis (Holtmeier 1978; Hadley & Smith 1983). The radial and height growth of trees is reduced by high winds (Kronfuss & Havranek 1999, Holtmeier 2003), leading many tree species to adopt flag and mat-like growth forms (Hustich 1966). High winds in conjunction with high maximum temperatures may increase dehydration in the soil and also evaporation from the soil and trees, while at other times they can break the tree crowns and branches, especially in the presence of heavy snow loads. At sites with a convex topography, winds will mainly transport conifer seeds away from the treeline rather than dispersing them at it (Holtmeier 2003), and this is also true of pollen (II). Everything considered, the winds at altitudinal treelines are such that trees are constantly under pressure (Holtmeier 1971, Yoshino 1975).

The trees forming the treeline are the remotest exceptions, which are able to survival in spite of reductions in factors promoting regeneration and growth and the presence of factors increasing mortality. On the other hand, they do not need to compete with each other for nutrients, for example.
3.5 The relationship between pollen production and climate conditions at the timberline ecotone

It is known that the vast majority of the pollen deposits on the ground fairly close to its source and a much smaller proportion is transported further afield (Hicks 2001, II). This means that numerically much more pollen reaches the area at the closed forest or at the actual timberline than the treeline, where pollen deposition can have come from several kilometres away. The dominant wind direction two weeks before and two weeks after the estimated time of anthesis of birch, pine and spruce was from the east, while north-east and northern winds were also common. Southern winds were the least frequent of all, so that contribution of windblown pollen from the south was minimal. In view of the Muonio and Yllästunturi wind direction results, any pollen transported from outside the fell area is likely to originate from the east or north rather than the south or west, an assumption that is supported by the fact that pollen deposition was regularly greater at the north-facing actual timberline than at the actual timberline on the south-facing slope at Aakenustunturi. In fact, the summit of Aakenustunturi serves as a topographical barrier against pollen deposition. The amount of tree (birch, pine and spruce) pollen along the altitudinal gradient from closed forest to treeline usually declined (emphasized when the average value for the six years is considered), with an exception of pine pollen, the amount of which was highest on the north-facing slope of the actual timberline (II).

As the majority of the pollen originates from fairly close to its origin, i.e., the forest on the fell and its surroundings, pollen deposition does indeed reflect local pollen produc-
tion, which is, in northern situations affected by temperature conditions the previous summer (II), a situation which also has been noted elsewhere (Hicks 1999, McCarroll et al. 2003). A big variation in thermoclimatic indicators from one year to the next (II, III) reflects to the amount of birch, pine and spruce pollen, which also varies from one year to the next. This is consistent at all sites of timberline ecotone (II). The timing of estimated anthesis of birch, pine and spruce varies from one year to the next and in different parts of the timberline ecotone. An examination of the correlations between the deposition of pollen of each three tree species and the two-week temperature variables in terms of the sums of deposition at all four sites situated in different parts of the timberline ecotone taken together (n=22) pointed to a clear temporal sequence for the species: birch pollen appeared to be statistically significantly correlated with temperature variables in the early summer, spruce with those for the midsummer period and pine with the late summer variables (II).

It was noticeable that the temperature variables calculated on a two-week basis were more strongly correlated with pollen deposition than monthly temperature variables, and provided more accurate information on which part of the previous year’s growing season was relevant to pollen production among each tree species.

3.6 Potential for actual timberline and treeline advance

Conifer seedlings show a relatively rapid response to climate warming (see Kellomäki et al. 1997), which is reflected in new regeneration and dense stands of sturdy saplings at the actual timberline and in the treeline ecotone, particularly on south-facing slopes (IV). Recent new regeneration near the actual timberline and treeline has also been observed elsewhere in Finnish Lapland. The seedling density of spruce, for example, doubled between the early 1980s and the late 1990s at the actual timberlines in western Finnish Lapland (Juntunen et al. 2002). Temperature conditions during the growing season have been favourable (II, III, IV) for seedling regeneration, so that the regeneration of conifers in high-altitudinal stands in northern Fennoscandia has not been limited very much by summer temperatures during recent decades (Stöcklin & Körner 1999, Kullman 2000). The air temperatures measured here show that the summer seasons were warmer than in the normal period 1961–1990, especially in 1997 and 1999–2001 (II, III), and this situation has been reflected in high deposition of birch and pine pollen, which have been even higher at the actual timberline than in the closed forest (II). At least 3 or 4 good regeneration years for conifers, the result of warm summers in the mid-1920’s and late 1930’s, have been recorded at high elevations in northern Finland (Hustich 1948, 1983), as indicated by the fact that pines and spruces that started their growth in those warm years 70–80 years ago have formed thriving actual timberlines on Aakenustunturi (Aho 1999) and on Pyhätunturi and Yllästunturi (Somminen 1993, Tuovinen 1997). It is possible that the number and successive occurrence of abnormally warmer summers may increase with global and regional climate warming, and this could mean that the regeneration of conifers is ensured in the timberline ecotone. It has been shown that the regeneration of trees in the marginal zone, e.g., in the timberline ecotone, is dependent on summers that are warmer than usual (Sarvas 1967).
The present results and those presented by e.g., Kullman (2000) and Juntunen and others (2002) indicate an advance of the actual timberline and treeline as a result of climate warming, while the response to potential future climate warming will probably differ from site to site in relation to local orographic factors, topography and associated ecological constraints (see Kjällgren & Kullman 2002, Holtmeier 2003). The actual timberline will advance to a higher elevation in the next few decades on the south-facing and west-facing slopes with a gentle inclination and few or no block fields, while the transition will take place more slowly on slopes of other orientations. Actual timberlines caused by block fields and/or slope steepness will hardly change, however, not even in the long term (IV, see also Holtmeier 2003).

Treelines situated close to fell summits will probably advance more slowly than the actual timberlines, or at least the treeless areas are less likely to become stocked with young saplings than they are near the actual timberline (see Holtmeier et al. 2003) This is indicated by the fact that the warm summers of recent decades that were reflected in several good regeneration years at the actual timberline and in the treeline ecotone on the south-facing slopes are not observed at the treeline near the fell summit. On the contrary, seedlings densities are very low there and seedling mortality is high (IV). On the other hand, treelines on south-facing slopes at a greater distance from fell summits, such as that on the high fell of Yllästunturi, might rise faster than those near a fell summit.

The predicted climate warming and its favourable implications for actual timberline and treeline advance may be slowed down or even prevented by many phenomena introduced by climate change itself, e.g., the increased occurrence of strong winds or gales (Holopainen et al. 1996), increased winter rains (Houghton et al. 2001) and an increase in the frequency of extreme climate events (Hänninen 1991). It is predicted that the already rather long open-water season in the Bothnian Bay will become even longer (Kauppi & Kämäri 1996), which may increase rime formation and also the frequency of heavy snow loads on the trees of the fell area in Finnish Lapland (IV, see also Solantie 1974). In association with the more frequent occurrence of strong winds, this would mean an increased risk of severe snow load damage to trees in the timberline ecotone in the future (IV, see also Jalkanen & Konôpka 1998). Strong winds combined with heavy snow loads can easily break tree crowns and branches (Holtmeier 2003). Some authors (Leemans 1995, Fleming 1996, Greifenhagen 1998) also suggest that the present tree species are unable to adapt to drastic increases in temperature. Also, mild winters would mean increased mass outbreaks of *Epirrita autumnata* and its destructive and debilitating effects on actual timberlines formed by mountain birch.

### 3.7 Significance of the present results

In situ measurements of air and soil temperatures based on relatively long time series (8 years for air temperatures and 3 years for soil temperatures) were carried out here for the first time in the timberline ecotone of fells situated between 67°N and 68°N in Finnish Lapland, and in this sense the results provide new knowledge on topographically modified local climatic characteristics and their effects on the formation of the actual timberline and the treeline in that area. The air temperature results can also be utilized in mod-
els developed to predict climate change in high altitude areas, as existing climate models do not make adequate allowance for topographically determined climatic variability (Martin 1996).

This is one of the very few instances in which correlations have been sought between temperature factors and pollen deposition at exactly the same spot, and the results clearly indicate a relationship between them. This opens up possibilities for the quantitative reconstruction of past temperatures at a high temporal (annual) resolution. If the same annual pollen deposition variations can be extracted from peat profiles or annually laminated lake sediments, the pollen record can potentially provide a proxy for summer temperatures which could be set alongside the dendroecological record. The statistically significant correlations between pollen deposition and temperature factors during the preceding summer enable us to make annual forecasts of the intensity of flowering and pollen production in the coming year. This could be of use to people suffering from pollen allergies.

The positions of actual timberlines and the environmental properties prevailing there have been documented from spatial data sources, which provide opportunities to use them in follow-up studies, particularly in the case of temporal changes in actual timberlines.

### 3.8 Evaluation of material and methods, guidelines for future studies

Validity, reliability and sufficiency of climatic data have been discussed in paper III. In addition limitation of pollen deposition data has been discussed in paper II. The accuracy of data loggers used for temperature recording has been evaluated earlier in this synopsis. Although air temperature and pollen deposition were monitored on four sites of Aakenustunturi, it is possible to generalize results also to cover the timberline ecotone of other fells situated in northern boreal vegetation zone. The same concerns also soil temperature data.

The definition of actual timberline was based on the percentual estimation of canopy. Also boulder fields were measured by estimating their percentual coverage of the land area at the actual timberline. In spite of the subjective manner of the used assessment methods, the results here are quite reliable because measurements were carried out by one person, the author. It is true that the errors in the assessment caused by different measurers might vary from 10.9 % to 33.9 % (Haara & Korhonen 2004). The accuracy of the position and elevation of the actual timberline has been discussed earlier in the synopsis.

In future studies, the plan is to do a comparison between visual assessment methods used to estimate percentual canopy and boulder fields of a certain land area in the field and digital classification based on the aerial photographs. Also modern digital tools and use of DEM (Digital Elevation Model) for classifying the aspect and slope inclination will be used in future investigations. One more approach, not treated here, is to use PCA-analysis (Principal Components Analysis) to examine the interaction and significance of environmental factors affecting the position of the actual timberline.
4 Conclusions

The six questions raised at the beginning of this research may be answered in the following ways:

1. The highest average (c. 400 m a.s.l.) and maximum altitudes (c. 460 m a.s.l.) of the actual timberlines are usually found on the south and west-facing slopes with a gentle inclination and no block fields. Altitude differences might be remarkable between the actual timberlines situated on different exposures and even within the same exposure. Nearly everywhere the actual timberline is composed of three tree species, spruce, pine and mountain birch, even at its highest altitudes. The highest average (c. 470 m a.s.l.) and maximum (c. 515 m a.s.l.) altitudes of treelines are found on the south-facing slopes. There the treeline is formed by pine.

2. The actual timberline area, where the sheltered forest encounters a more or less open, windy landscape, is obviously likely to develop a distinctive local climate which is different from that of the open, windy treeline situated above it. The local climatic features that are most typical of the actual timberline are a thick snow cover, delayed snow melting, regular heavy snow load formation on trees, extreme temperatures (i.e. high daytime temperatures and low night time temperatures near the ground surface, night frost in the late summer, hot days in summer time), cold air lakes and rapid temperature fluctuations during inversions. Local temperature and snow patterns are modified greatly by the varying topographical features and geomorphological landforms to be found at actual timberlines.

Thermoclimatic indicators that denote the location of the actual timberline and treeline are usually the highest at the actual timberline on the south-facing slope, even higher than in closed forest. This area represents the most extreme temperature conditions, too. Mean July temperature at the actual timberline is 13.3°C on the southern slopes and 13.3°C on the northern slopes. The mean effective temperature sums for the same places are 704 d.d. and 677 d.d. respectively. Mean July temperature at the treeline is 12.6°C and the mean effective temperature sum is c. 620 d.d. These thermoclimatic factors are higher than the results of earlier studies. Also thermoclimatic indicators such as biotemperature, mean maximum July temperatures, mean temperature for June-September (tetratherm), mean maximum tetratherm, mean temperature for June-August (tritherm), and minimum effective temperature sum for the actual timber-
line and treeline of the area studied are higher than those regarded in earlier research as serving best to characterize these limits.

An open, highly exposed treeline is characterized by a thin or absent snow cover, extremely heavy, regular snow load formation on trees and seedlings, strong winds and gales, a short growing season and the consequent inadequate effective temperature sum, considerable fluctuations in thermoclimatic conditions between years, rapid temperature fluctuations during inversions and night frost at the beginning of the growing season. The snow and wind properties at the treeline differ most conspicuously from those at the actual timberline.

The meteorological effect called ground surface temperature inversion is typical, particularly in winter, when the top of the ground inversion is usually situated around 500 m a.s.l. On the other hand, the height of the top of an inversion sometimes lies at the actual timberline, especially in early winter.

The vertical temperature gradient, i.e., mean lapse rate, between the closed forest and treeline is -0.59°C/100 m, only very slightly lower than the normal vertical gradient of 0.65°C/100 m. On the other hand, the drop in temperature with height is very much greater between the timberlines and the treeline than between the closed forest and the treeline. The observations also show that the lapse rates vary seasonally.

3. The topography and orographic features are the most significant and conspicuous factors regulating the position and physiognomy of the actual timberline. The highest elevation is reached on gentle southern and western slopes, while the lowest elevation is found on steep slopes with a high incidence of block fields on northern and eastern slopes. On steep, rocky slopes the actual timberline is abrupt and easy to define in the terrain or in aerial photographs, whereas it does not form an easily distinguishable or delineable line on gentle slopes without any block field, where the position of the actual timberline is controlled by the many unfavourable climatic features mentioned above. As also mentioned above, the topography and geomorphological landforms modify features of the local climate such as temperature and snow cover. This is in evidence on the steep north-facing slopes, for instance, where snow patches and cold air lakes are formed. These factors and their consequences are the real determinants of the position of the actual timberline there. Thus the factors regulating the actual timberline are often interrelated in a complex way. Heavy snow load damage evidently detracts from tree vitality and reduces the advance of the actual timberline.

4. On account of the great number of current and historical environmental factors and processes that determine or influence the treeline, it is difficult to ascertain which one is ultimately more decisive or more critical for tree growth than the others. One may come to the conclusion that the prevailing environmental conditions, inadequate snow protection, extreme soil temperatures (long periods of low soil temperatures and sudden drops in winter, high soil temperatures in summer), almost ubiquitous heavy snow load damage to trees, wind pressure, an often inadequate effective temperature sum and length of growing season, night frosts in early summer, poor, dry soils that suffer from excessive evaporation, together form a collective minimum factor for tree regeneration and growth.

5. Seven features emerge from the results of the pollen depositon relation to climate conditions: (a) For the majority of individual years there is a fall in the amount of birch, pine and spruce pollen along an altitudinal gradient from closed forest to tree-
line area. (b) There is a big variation in temperature conditions, which in turn causes big variations in pollen deposition from one year to next, which is consistent everywhere at the timberline ecotone. (c) The summit of fell serves as a topographical barrier against pollen access to the pollen trap situated on the opposite slope side to the prevailing wind direction. (d) The temperature variables calculated on a two-week basis were more strongly correlated with pollen deposition than monthly temperature variables, and provided more accurate information on which part of the previous year’s growing season was relevant to pollen production in each three tree species. (e) Each tree species has its own specific temperature period during the preceding summer which influences its pollen production. (f) Annual fossil pine pollen quantities are a potential climate proxy (g) Finally, it is possible to use temperature parameters of the current year to make forecasts of the intensity of flowering and pollen production for the following year.

6. The present results demonstrated the existence of dense stands of thriving seedlings near the actual timberline and in the treeline ecotone, as observed in earlier investigations (Kullman 2000, Juntunen et al. 2002). On the other hand, seedling density along an altitudinal gradient from the actual timberline to the treeline ecotone is high only on south-facing and not north-facing slopes. This observation suggests that any advance of the actual timberline to a higher elevation as a result of climate warming will occur first on the south and west-facing slopes. Elsewhere any such advance will take place more slowly, while actual timberlines caused by block fields and/or slope steepness will hardly change at all, not even in the long term. Pine and spruce trees which started to grow in the warm years of the 1920’s and 1930’s are now forming the actual timberline in many places on these fells, and this together with the recent warming observed here indicates a potential for the actual timberline to advance to a higher elevation in just a few decades. Any such advance may nevertheless be slowed down or even prevented by many phenomena introduced by climate change, such as the possible increase in the occurrence of heavy snow load damage and strong winds. The regeneration and growth of trees at the treeline near the fell summit is uncertain and seedling mortality rate is high, so that the treeline will probably rise more slowly there than at the actual timberline.
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ENVIRONMENTAL FACTORS CONTROLLING THE POSITION OF THE ACTUAL TIMBERLINE AND TREELINE ON THE FELLS OF FINNISH LAPLAND