

Dissertationes Forestales 96

The effect of temperature on height growth of Scots pine in northern Finland

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Academic dissertation

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The effect of temperature on height growth of Scots pine in northern Finland

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ABSTRACT

The effect of temperature on height growth of Scots pine in the northern boreal zone in Lapland was studied in two different time scales. Intra-annual growth was monitored in four stands in up to four growing seasons using an approximately biweekly measurement interval. Inter-annual growth was studied using growth records representing seven stands and five geographical locations. All the stands were growing on a dry to semi-dry heath that is a typical site type for pine stands in Finland. The applied methodology is based on applied time-series analysis and multilevel modelling.

Intra-annual elongation of the leader shoot correlated with temperature sum accumulation. Height growth ceased when, on average, 41% of the relative temperature sum of the site was achieved (observed minimum and maximum were 38% and 43%). The relative temperature sum was calculated by dividing the actual temperature sum by the long-term mean of the total annual temperature sum for the site. Our results suggest that annual height growth ceases when a location-specific temperature sum threshold is attained.

The positive effect of the mean July temperature of the previous year on annual height increment proved to be very strong at high latitudes. The mean November temperature of the year before the previous had a statistically significant effect on height increment in the three northernmost stands. The effect of mean monthly precipitation on annual height growth was statistically insignificant. There was a non-linear dependence between length and needle density of annual shoots. Exceptionally low height growth results in high needle-density, but the effect is weaker in years of average or good height growth.

Radial growth and next year's height growth are both largely controlled by current July temperature. Nevertheless, their growth variation in terms of minimum and maximum is not necessarily strongly correlated. This is partly because height growth is more sensitive to changes in temperature. In addition, the actual effective temperature period is not exactly the same for these two growth components. Yet, there is a long-term balance that was also statistically distinguishable; radial growth correlated significantly with height growth with a lag of -2 years.

Temperature periods shorter than a month are more effective variables than mean monthly values, but the improvement is on the scale of modest to good when applying Julian days or growing-degree-days as pointers.

Keywords: Needle density, needle trace method, NTM, *Pinus sylvestris*, time-series

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Rovaniemi, October 2009

Hannu Salminen

LIST OF ORIGINAL ARTICLES

This thesis is a summary of the following articles, referred to in the text as Paper I–Paper V.

- I. Salminen, H. and Jalkanen, R. 2007. Intra-annual height increment of *Pinus sylvestris* at high latitudes in Finland. *Tree Physiology* 27: 1347–1353.
- II. Salminen, H. and Jalkanen, R. 2004. Does current summer temperature contribute to the final shoot length on *Pinus sylvestris*? A case study at the northern conifer timberline. *Dendrochronologia* 21: 79–84.
- III. Salminen, H. and Jalkanen, R. 2005. Modelling the effect of temperature on height increment of Scots pine at high latitudes. *Silva Fennica* 39: 497–508.
- IV. Salminen, H. and Jalkanen, R. 2006. Modelling variation of needle density of Scots pine at high latitudes. *Silva Fennica* 40: 183–194.
- V. Salminen, H., Jalkanen, R. and Lindholm, M. 2009. Summer temperatures affect the ratio of radial and height growth of Scots pine in northern Finland. *Annals of Forest Science* 66: 810.

Hannu Salminen was the person responsible for data analysis and writing of all five articles. Risto Jalkanen planned and organized data collection, and prepared the early draft of Paper II. He also participated in the preliminary planning of all studies and commented on all articles on various occasions. Markus Lindholm contributed his comments and discussed methods and text of Paper V.

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ORIGINAL ARTICLES I–V

1 INTRODUCTION

1.1 How trees can react to environmental changes; responses and time scales

Plants on the edge of their distribution range are self-evidently sensitive to those factors that limit their growth. At high latitudes, temperature during the growing season is one of the main controllers of plant growth. Pines accumulate their annual increments and thereby record an indirect measure of the controlling factor to a form that is measurable retrospectively; tree rings and annual shoots. That makes them an interesting source of information about the dependency between growth and environment that can be used both when reconstructing past climate and forecasting future growth under different climatic scenarios.

Carter et al. (1988) classify the effects of climate on plants into direct (radiation, temperature, soil water availability) and indirect but climate-sensitive ones (the availability of nutrients, the interference of pests and disease). A similar direct–indirect approach can be applied when focusing on the effect of temperature on growth. Although temperature is not a primary factor of photosynthesis, it affects growth and development by regulating the rates of the physical and biochemical processes within plants through its effect on the reaction rates of enzyme systems (Downs and Hellmers 1975). Temperature has many effects on growth and it correlates with factors involved in photosynthetic production such as solar radiation and the amount of photosynthetically active radiation (PAR). Soil water deficit is affected by evapotranspiration, precipitation and snowmelt, which all are either temperature driven or at least correlate with temperature. Furthermore, temperature regulates evaporation, which — in turn — affects water and nutrient transportation from roots to stem and leaves. The role of temperature has historically been important because it is relatively easy to measure.

The effect of temperature on annual net growth is intermittent. The annual cycle of tree growth defines those periods when temperature effectively regulates growth. Low winter temperatures are not so influential because north-boreal plants are adapted to tolerate low temperatures in their dormant stage (Kauppi and Posch 1988). However, temperature during spring and autumn defines growing season length, and summer temperatures regulate the rate of biological processes (Kauppi and Posch 1988). Even during the growing season, net growth of trees occurs only above some temperature minimum at which photosynthetic processes proceed at rates greater than those required to maintain respiratory processes and both are greater than zero. For northern boreal forests, this minimum is generally taken to be $+4 - +5^{\circ}\text{C}$. Besides momentary temperatures, the cumulative sum integrated over the whole growing season is a widely used description of temperature at annual level. The heat sum (growing degree-days) is the product of temperatures above the zero-growth level and the duration of those temperatures.

Within the growing conditions of boreal trees, the temperature effect on net photosynthetic rate is unimodal, implying that there is a temperature range that favours photosynthetic production. This nonlinearity is believed to arise from three interacting physiological responses to temperature: an increase of gross photosynthesis at low temperatures, an increase in dark respiration, and deactivation of photosynthesis at high temperatures (Kramer and Kozłowski 1979, Kozłowski et al. 1991). Precise figures for general optimal growth temperatures are seldom declared because temperature response of photosynthesis varies with genotype and environmental conditions, and may acclimate to changes in the prevailing environmental conditions (Medlyn et al. 2002). In general, cold-adapted trees often show maximum photosynthesis at low temperatures (Kramer and Kozłowski 1960).

Responses of plant processes to temperature may vary according to the time scale used (Medlyn et al. 2002). Short-term, seasonal and generation-long perspectives give a different view on the same phenomenon. Time scales of weather-induced responses in trees vary from almost instant to several generations. Long-term adaptation to environment means changes in the genetic structure of a population. The time scale of phenotypic acclimation is one generation long and comprises environmentally induced changes in tree structure and functions. For pines, fine roots and needles are responsible for the most rapid changes. The immediate responses to environment appear in functioning. They may be both in timing of events (phenology) or the rate of functions such as respiration or photosynthesis. On the other hand, functions and structure are supposed to be in balance, and hence, acclimation by changing functions can cover long time scales.

1.2 Resource allocation – general theories

Adaptation and acclimatisation to past and prevailing conditions at various time scales results in growth strategy. According to Tilman (1988) “plant growth is a function of one to several resources, and plant strategies are adaptations to different combinations of the availability of resources.” The key issue on the ‘survival game’ of nature is how to use limited resources optimally. The optimal resource use theory is based on the assumption that plants take up resources according to their proportional limitation by each of the resources (Rapport 1971, Bloom et al. 1985, Tilman 1988). That means that plants optimise their growth allocation according to the ratio of resource availability. For example, if there is much shading (competition for light), more resources are allocated to above ground growth, and correspondingly, in the case of lack of nutrients and water, more resources are allocated to root growth. Allocation is not independent of tree architecture; there has to be a balance between structure and functions. Nikinmaa and Hari (1996) apply Brouwer’s (1962) principle of functional balance to tree architecture as follows: “A balance is assumed to exist between the needles and the roots responsible for nutrient uptake when nutrient requirement of growth is matched by nutrient uptake and relocation from senescing structures.”

A tree responds to environmental conditions and — as Botkin (1993) formulates — “a fundamental question is how this total response integrates the individual effects of separate environmental factors; does each factor act independently on the tree or do factors act together?” One answer is the Sprengler-Liebig Law of the Minimum, which states that of all the biotic or abiotic factors that control a plant, one has to be limiting (i.e. active, controlling the dynamics) (Berryman 1993, van der Ploeg et al. 1999, Berryman 2003). This implies that the effect of one factor or resource depends on whether another one is limiting or not. The level at which the resources are monitored may vary. In common talk, temperature is often assumed a limiting factor for tree growth in the northern boreal zone. Actually, the primary driving factor of growth rate may be the intensity of PAR or nutrient and moisture availability.

The different parts of a plant can be classified into sources and sinks according to their role in production and usage of carbohydrates. The description of many simultaneously active sources and sinks has led to the idea of an internal competition for carbohydrates (Kozłowski 1992).

1.3 Scots pine

The genus *Pinus* belonging to the family *Pinaceae* comprises 94 species distributed over the northern hemisphere. Scots pine (*Pinus sylvestris* L.) has the widest geographical amplitude of all pine species (Jalas and Suominen 1973). Its distribution range covers almost 135 degrees of geographic longitude and about 30 degrees of latitude (Vidaković 1991) (Fig. 1). Although representing the same species, genetically there are several more or less distinct geographical varieties (Wright and Bull 1963). Scots pine forms the northern coniferous timberline in Fennoscandia where it expanded to 7,800 years ago (Willis et al. 1998). It has adapted to the climate prevailing after the ice age but is also capable of acclimating to the present climatic conditions (Hari 1996).

Scots pine forms distinct annual growths; tree rings and annual shoots. On that account, it has been a major source for dendrochronological studies in Fennoscandia. Dendrochronology (Greek *dendron* tree, *chronos* time, *logos* speech, word) is the name given to the archaeological dating technique of past events (climatic changes) through the study of tree ring growth. Since the invention of tree-ring dating in the early decades of the 20th century, it has grown into a multidisciplinary research field of botanists, foresters, geographers, and archaeologists. In addition to tree-ring-width, modern multi-proxy dendrochronology examines physical and chemical properties of the different parts of tree rings, pollen deposition, height increment, and needle dynamics. Likewise, dendrochronology has many subfields such as dendroarchaeology, dendroclimatology, and dendroecology.

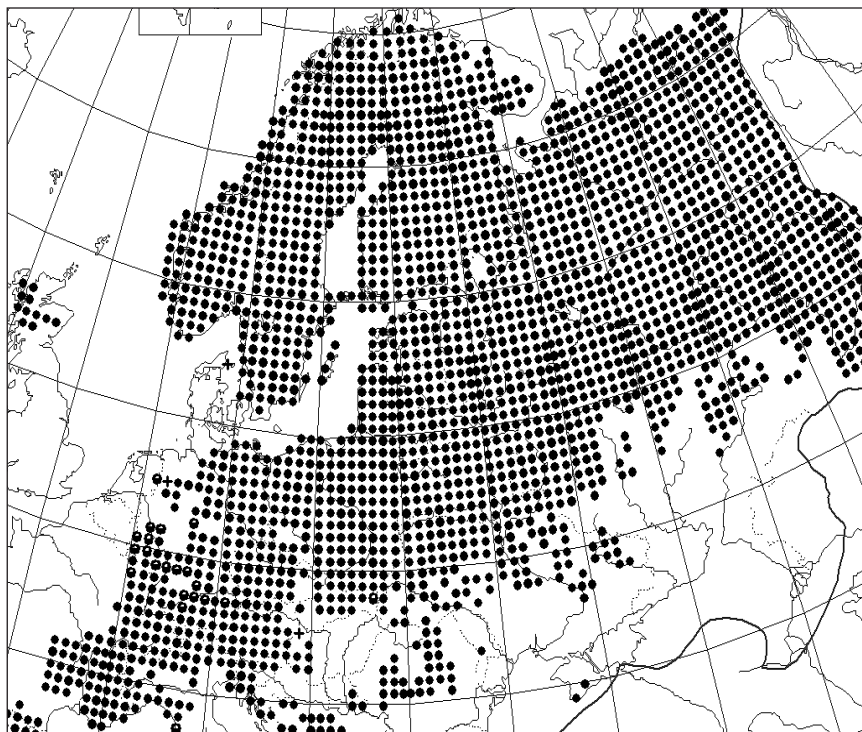


Figure 1. The distribution range of *Pinus sylvestris* L. in Europe (Jalas and Suominen 1973).

Similarly to many empirical research aims, dendrochronology relies on the uniformitarian principle, which states that physical and biological processes that link current environmental processes with current patterns of tree growth must have been in operation in the past (Grissino-Mayer 2009). Especially, dendrochronologists know that climate has been and is continuously changing and the growth environment of trees is not stable. Therefore, the dependencies between tree growth and its environment may also change over time. Nevertheless, by understanding the climate-tree growth relationship of the past, we can better predict and manage environmental conditions of the future.

Dendrochronological observations have shown the most pronounced climatic signal in geographical areas where only one strong growth-limiting factor exists. This has been generalized into the principle of ecological amplitude; a tree species will be more sensitive to environmental factors at the latitudinal and elevational limits of its range (Fritts 1976). Therefore, Scots pine in northern Fennoscandia is expected to respond to those environmental factors that limit its distribution. From another viewpoint, trees growing on the edge of their natural range have to be not sensitive but robust and tough in order to survive harsh conditions.

Dendroecology applies dendrochronological data and methods in ecological studies. Like other fields of dendrochronology, it relies mainly on information originating from tree-rings. Sampling and measuring tree-rings is relatively easy, but tree-ring width, the most classical source of information in dendrochronology, also has some downsides as a climatic indicator. Compared to height growth, tree-ring width of light-demanding species is more sensitive to changes in spatial competition. It can be suggested that height growth is strategically more important than radial growth in the case of competition for light. This is based on the assumption that allocation in height improves access to light (Falster and Westoby 2003) and that height increment reflects the tree's growth potential and ability to survive more precisely than radial growth (Mäkinen 1998). On the other hand, precise and long height-growth series are more laborious to gather compared to coring tree rings. Leader changes caused by snow damage, insect or pathogen attack or mechanical injuries due to neighbouring trees are more the rule than exception in northern pine stands. Thus, assessing height growths from standing trees may include errors. Altogether, studies based on long time-series of height increment are still novel (Pensa et al. 2005, Lindholm et al. 2009).

In addition to radial and height growth, there are many other useful proxies reflecting the changes in growth environment of trees. Additional proxies such as wood density and ratio of carbon isotopes, analysed from annual tree rings, ice cores, glaciers, coral, and pollen records sampled from soil, may be used alone or combined with each other in a multi-proxy approach (McCarroll et al. 2003, von Storch et al. 2004). Retrospective description of needle dynamics using the Needle Trace Method (NTM) has widened the possibilities of dendroecological studies even further (Jalkanen 1995, Aalto and Jalkanen 1998, Jalkanen et al. 1998, Jalkanen 2000, Jalkanen et al. 2002).

1.4 Height growth of Scots pine

In forestry terminology, growth means the biological phenomenon in general and increment is a technical term referring to the quantitative and irreversible change in girth, diameter, height, basal area, volume, quality or value over time (Davis 1966, Helms 1998). In simplified terms, tree growth is the net accumulation of organic matter. It comprises formation, differentiation and expansion of new cells, tissues or organs. Net accumulation results from gross photosynthesis, which is reduced by the amount of energy used in respiration. Photo-

synthetic production is either stored within the leaves or exported via the phloem to the rest of the tree, to the stem and roots (Botkin 1993). Photosynthesis is based on solar energy, atmospheric carbon dioxide (CO₂), and water uptake by the root system. The rate of photosynthetic production is driven by genetic and environmental factors the most important of the latter being the intensity of PAR, availability of soil moisture, availability of nutrients, and temperature.

Meristems are tissues that are capable of cell division and therefore form the growing points of trees. Kramer and Kozlowski (1960) list three growing regions of trees: apical meristems in stem and root tips, primary cambiums, and secondary or cork cambiums. Increase in length (extension) and reproductive growth, both derived from apical meristems, are called primary growth while increase in girth or thickness (growth from lateral meristems) is called secondary growth.

After its first year since germination, Scots pine has determinate or fixed growth (Lanner 1976). That means that height growth is a two-year process consisting of two separate phases. First, there is a morphogenetic phase in which the bud is initiated. Primordial initiation is affected by temperature, nutrition, photoperiod, light quality, photosynthetic photon flux density and soil water deficits (Bollman and Sweet 1976, Cannell and Cahalan 1976, Slee et al. 1976, Pollard and Logan 1977, Morgan et al. 1983, Linder and Rook 1984, Bollman et al. 1986). During next spring, after a period of dormancy (winter rest), the preformed bud elongates during growth phase 2 (Lanner 1968, Lanner 1978). Internodes laid down in the bud divide rapidly and produce cells whose elongation accounts for growth in length (Kramer and Kozlowski 1960). Doak (1935) introduced the concept of height growth units that refer to all internodes needed to form an internode, i.e. the cells between sequential short shoots including the short shoot. Within this framework, the total shoot elongation is a function of the number of growth units and elongation of each growth unit (Lanner 1968). Needle density expresses the number of needle fascicles (short shoots) per shoot centimetre. Based on its definition, needle density reflects the average growth length.

Shoot elongation and winter bud formation of temperate pines are supposed to coincide with height growth cessation; either overlapping (Lanner 1978, Bachelard 1980) or bud formation begins after shoot elongation has practically ceased (Lanner 1976). Shoot elongation begins with a slow phase that accelerates to a period of maximum rate and continues with a gradually diminishing growth (Hertz 1929, Kienholz 1934, Odin 1972, Norgren et al. 1996). In practice, however, it is difficult to judge the precise timing of the cessation, and it is usually defined as the time at which 95% of the final length has been attained. Sucoff et al. (1971) found that primordia for axillary buds forming the shoots in year n+1 of *Pinus resinosa* Ait. began to appear about 2 months after the year n shoot started elongating (late April) and the last ones were set in early September. There is no detailed information about the actual timing of the bud formation on *P. sylvestris* in Fennoscandia but it can be supposed to follow the same kind of pattern as in *P. resinosa*, i.e. bud formation begins when shoot elongation gradually ceases.

The actual elongation of the terminal bud starts in the early phase of the growing season when the soil may still be partly frozen. Therefore, it is natural to study to what extent trees use stored carbohydrates instead of current production. Ericsson (1978) found that shoot growth of 20-year-old Scots pine trees was mainly based on photosynthates from 1-year-old needles until the current year needles reach approximately half of their final length and turn from sink to source. Hansen and Beck (1994) reported that bud break and sprouting in spring is supplied by the recent photosynthates of the 1-year-old needles, while later in the summer, growth of the new shoots is supported by their own photosynthesis. Based on studies on one

to two-year-old seedlings, Lippu (1998) concluded that height growth of Scots pine is to large extent (96%) based on photosynthates produced during the current year. Von Felten et al. (2007) studied 30-year-old mountain pines on the alpine tree line and found that 42% of carbon used for new wood growth came from storage, but that the needles were built up almost completely from current-year photosynthates. The trees of their experiment were exposed to labelled carbon during the whole growing season as opposed to autumn labelling.

Besides the amount of growth, the timing of events in the annual cycle of development is under genetic and environmental control. As defined by Sarvas (Sarvas 1972, Sarvas 1974), the annual cycle of development refers to the sequence of all developmental events that are repeated each year basically in the same way. Annual rhythm, the timing of events in the annual cycle of development, is regulated by the interaction of the genetic properties of tree (adaptation), and environmental factors (acclimation) prevailing at the growing site (Hänninen 1990). Consequently, it has been assumed that geographical variation in climate has resulted in ecotypical differentiation in Scots pine with respect to the air temperature regulation of timing of growth onset (Hänninen and Hari 1996).

1.5 Research aims

The overall objective is to study the effect of monthly mean temperatures on height growth of Scots pine trees at high latitudes. In addition to mean monthly values, temperature periods that were defined as days and growing-degree-days are explored. Intra-annual and inter-annual growth is investigated separately. In Paper I, it is hypothesized that intra-annual height growth is temperature driven and photoperiod does not affect height growth cessation. The main research questions are: 1) what is the relationship between temperature (accumulation) and intra-annual height growth, and 2) is there a constant temperature-sum threshold attained at the time of growth cessation.

In Papers II–III the main emphasis is on inter-annual height growth. A first step is to examine whether current May, June and July temperatures affect the final length of the apical shoot in one experimental stand (Paper II). Thereafter, data from a total of five stands are used in order to model the effect of temperature and precipitation on height increment, the main questions being (Paper III): 1) How much of the height-increment variation is due to changes in temperature and precipitation? 2) Do trees from different latitudinal locations have similar dependency on climatic factors?

Records of annual needle density (needles per unit length of a shoot) reflect to a large extent changes in height growth. Hence, besides needle density range and variation, also height growth is one of the key issues in Paper IV. The main questions are: 1) What is the needle density range of Scots pine at high latitudes? 2) What is the relationship between apical extension and needle density near the northern tree line? 3) Do temperature and precipitation affect needle density and height increment differently?

The aim of Paper V is to examine the relationship between growth components (radial and height growth). This is done by the following steps: modelling the autocorrelation structure of height and radial-growth series measured from the same trees, construction of respective standwise chronologies based on the treewise measurements, and finally, examining the relationship between growth components and temperature variables. The ratio of height and radial growth is used to reveal possible differences in climate-induced changes in growth allocation.

2 MATERIAL AND METHODS

2.1 Study sites and field work

The empirical materials of Papers II–IV originate from five experimental stands (1A, 3A, 5A, 6A and 7A) selected and measured during EC Environment and Climate Research Programme (contract: ENV4–CT95.0063 (FOREST), Climatology and Natural Hazards). These pine stands are located along a 400-km-long latitudinal transect from the Arctic Circle to the northern timberline in Finland (latitudes 66N 35E–69N 45E) (Fig. 2). Additional field data was gathered near experimental stand 5A. These data included intra-annual observations from stand 5B (Paper I) and two new longitudinal growth series: from a 150-year-old stand 5C and a 50-year-old stand 5D (Paper V). Intra-annual growth was also observed in stands 2B and 4B near the Arctic Circle (Paper I).

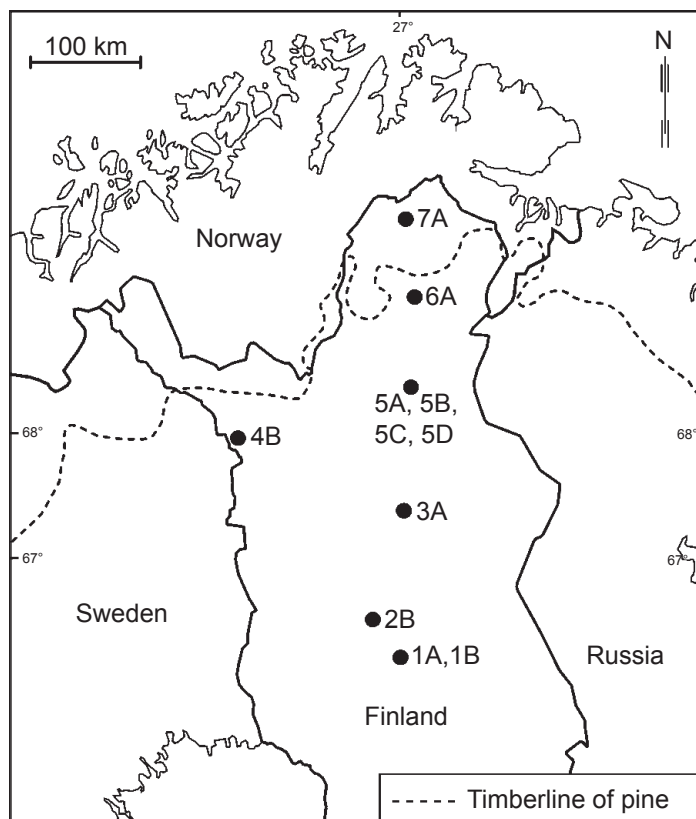


Figure 2. Location of the experimental stands and northern timberline of Scots pine in Finland; seven sites (1–7) and one to four stands (A, B, C, D) per site. Stands 1A, 3A, 5A, 6A and 7A were used in analysis of inter-annual height growth and needle density (Paper II, III and IV). Stands 1B, 2B, 4B and 5B were used in analysis of intra-annual height growth (Paper I). Stands 5C and 5D were used when analysing inter-annual radial and height growth (Paper V).

Table 1. Stand characteristics.

Stand	1	2	3	4	5	6	7
Locality	Rovaniemi, Vanttaus- koski	Rovaniemi, Perunka- järvi	Sodankylä	Muonio, Kätkä- suvanto	Inari, Laanila	Inari, Kaa- manen	Utsjoki, Kenes- järvi
Latitude	66°22'	66°45'	67°22'	68°08'	68°30'	69°07'	69°40'
Longitude	26°43'	26°00'	26°38'	23°21'	27°30'	27°15'	27°05'
Altitude, m	150	164	180	250	220	155	110
Vegetation type ¹⁾	EV	MCCI	UVE	MCCI	UEM	UVE	EV

¹⁾EV=Empetrum-Vaccinium -type, MCCI=Myrtillus-Calluna-Cladina -type, UVE=Uliginosum-Vaccinium-Empetrum -type, and UEM=Uliginosum-Empetrum-Myrtillus -type.

The data from experimental stands 1A, 3A, 5A, 5D, 6A and 7A were collected according to general guidelines of NTM (Kurkela and Jalkanen 1990, Jalkanen 1995, Aalto and Jalkanen 1998). The number of sample trees per stand was 10–25. They were selected from open-growing dominant trees that were visually assessed to be healthy with straight, unbroken stems and regular-shaped crowns and not suppressed by competition. In stand 5C, selection of sample trees was based on absence of visual signs of disturbances or suppressions. At the time of sampling in year the 2005, these 150-year-old trees were dominant but their history is unknown. According to the forest inventory from the year 1940, the dominant age of that specific forest compartment was 150 years, and selective cuttings had been conducted in that area. All the stands were growing on a dry to semi-dry heath that is a typical site type for pine stands in Finland (Table 1).

The sample trees used in studies of inter-annual growth were felled and analysed according to NTM (Aalto and Jalkanen 1998), which aims to produce consistent time series of annual needle dynamics as well as height and diameter growth. The height increments were measured in the field from the branch whorls of the main trunks of the felled trees from 1.3 metres up to the top. Annual rings and shoots were cross-checked in order to produce complete and continuous time-series. Annual radial growth and needle densities of each shoot were assessed in the laboratory (Aalto and Jalkanen 1998). As compared to traditional growth measurements, this procedure is laborious because it necessitates tree felling and laboratory analysis but, on the other hand, the results are precise. This is important since the height growth of pine in the north is rarely undisturbed (Hustich 1948, Hustich 1978).

Stands 1A, 3A, 5A, 6A and 7A were sampled in autumn 1996 and stands 5C and 5D during 2004–2005. There were also differences in the breast-height age of the sample trees. Thus, the time span of sampling varied from stand to stand (Table 2).

Intra-annual observations in stands 1B, 2B, 4B and 5B consisted of measurements of leader shoot length of the sample trees (I). For accurate twice-weekly measurement of growth accumulation, a permanent pin was inserted through the main stem of the previous-year shoot. Air temperature was recorded hourly at the site either throughout the year or during the growing season using a data logger equipped with an external sensor (range -40° to $+125^{\circ}\text{C}$ and resolution 0.4°C at $+25^{\circ}\text{C}$).

Table 2. Measured inter-annual height growth (iH).

Stand	1A	3A	5A	5C	5D	6A	7A
Time span	1962– 1996	1945– 1996	1961– 1996	1826– 2005	1953– 2004	1947– 1996	1954– 1996
Number of sample trees	9	10	10	10	25	10	10
Mean, min. and max. age of sample trees at breast height, yrs	33 29–35	51 43–55	34 31–37	158 137–178	42 32–49	42 39–45	46 42–53
Mean, min. and max. dbh of sample trees, cm	13.0 10–16	12.1 11–14	12.0 10–14	30.5 27–35	14.7 13–17	11.0 10–14	10.2 8–13
Mean, min. and max. Height of sample trees, cm	9.8 9–11	11.0 10–13	8.9 8–10	17.6 14–20	10.9 8–14	8.7 7–10	8.7 7–10
Mean iH (st.dev.), cm	26.3 (8.4)	19.2 (6.3)	22.4 (7.9)	10.0 (6.7)	23.2 (7.5)	15.7 (6.7)	17.6 (5.9)
Min.–Max. iH, cm	7–47	3–40	3–44	0–40	1–49	1–39	2–237

For each stand, the records of the nearest weather station of the Finnish Meteorological Institute were used. Meteorological measurements included temperature and precipitation values since 1958–1961. The climate records were extended with the models of Ojansuu and Henttonen (1983) and the mean monthly temperatures of the years 1802–1957 from Tornedalen (Klingbjør and Moberg, 2003). Evapotranspiration and the effect of snowmelt on water balance were calculated using the WATBAL model (Starr 1999).

2.2 Methodology

2.2.1 Methods of dendrochronology

Tree-ring and height-growth measurements of a tree consist of sequential observations and are in that sense typical time series. Most time series can be described in basic terms such as trends, seasonal or cyclic components, serial dependency (autocorrelation), and the remaining (residual) variation called white noise (Harvey 1993). Trends, cyclic components and autocorrelation can be modelled and mathematically formulated and utilized in interpretations and predictions but, on the other hand, they disturb the independence of observations and make analysis of time series more complex. Traditional dendrochronological analysis

is based on the assumption that annual increment of a tree integrates internal and external factors affecting and controlling tree growth. Thus, a series of annual increments can be deconstructed into different parts reflecting those factors. Cook (1985, 1990) presented a linear aggregate model that condenses the deconstruction of ring-width growth to five discrete signal classes:

$$R_t = A_t + C_t + \delta D1_t + \delta D2_t + E_t \quad (1)$$

where

R_t = measured series

A_t = age related growth curve

C_t = macroclimatic signal; typical to all trees in a stand

$\delta D1_t$ = the endogenous and local disturbance; unique to a single specimen

$\delta D2_t$ = the exogenous disturbance; common to most or all trees in a stand

E_t = unexplained variability

t = time

That part of the information that is relevant to the study is called signal while the irrelevant part is noise. Dendroclimatology concentrates on the effect of climate on tree growth and the reconstruction of the past climate based on observed dependencies. From that viewpoint, macroclimatic signal is the most important component. Dendroecological studies have a broader view being interested also in signals related to tree age and various silvicultural and environmental factors.

One can deconstruct a series of annual increments using various tactics and a broad selection of models. Cook et al. (Cook and Kairiukstis 1990) divide methods into deterministic and stochastic. The deterministic methods apply *a priori* information about phenomenon related to growth, fit a selected deterministic function to the data, and use the residual in the next steps of analysis. The most common example is fitting either a negative exponential or polynomial function that captures the age effect on growth. Similarly, linear functions can be used to “straighten” long-term trends. The stochastic methods such as smoothing using moving average or smoothing splines may be chosen by *a posteriori* selection criteria. A double-detrending procedure applies deterministic and stochastic methods consecutively. Either way, the analyst must judge which frequency range carries the signal and what is noise. Cook et al. (Cook et al. 1990) prefer stochastic methods due to their flexibility; deterministic methods depend more on prevailing theories. However, the downsides of this flexibility are the problems of *ad hoc* model selection and overfitting. Moreover, the degree of filtering and smoothing is still arbitrary and often selected on a trial-and-error basis (Lindholm 1996).

In addition to trends, time series may include serial dependency. Autocorrelation may reflect buffering in the physical environment such as groundwater balance or persistence arising from the internal state and balance of a tree. Examples of the latter are the effect of stored resources and the changes accompanying increasing tree-age and size (Fritts 1976). Thus, serial dependency can comprise relevant information about the studied trees and stands but, on the other hand, it may interfere with multivariate analysis of time-series. Differencing series or modelling the autocorrelation structure using appropriate autoregressive models can remove serial dependency. In time-series analysis, removal of serial dependency is called prewhitening and the resulting series is called white noise.

Removal of non-climatic variation from tree-ring data is called standardization, detrending or indexing (Lindholm 1996). Applying program ARSTAN (Cook 1985) is the *de facto*

standard procedure of dendrochronological standardization. It comprises trend removal, stabilization of variance and mean and optional prewhitening. First, the program fits a selected model to each series, either determined function or smoothing spline or both, and divides measured values by predicted values usually in order to remove low-frequency, age-related trends (Fritts 1976). The user specifies the shape or “stiffness” of fitted curves or smoothing splines. Next, a series of index values called standard chronology is calculated using biweight robust mean estimation, where each value is weighted by its nearness to the median (Cook et al. 1990). The resulting chronology index values, called the standard chronology vary around a mean of one and may contain autocorrelation. ARSTAN can also remove autocorrelation by selecting the appropriate ARMA model based on the minimum Akaike information criterion (AIC). The prewhitened series is called residual chronology.

Besides being time-series, the empirical data measured from trees often represent multiple levels. The lowest level consists of consecutive measurements of an individual tree, and the autocorrelation associated with measurements is nested within them (Henttonen et al. 1986, Miina 2000, Hox 2002). Trees from the same stand or plot form a second level; they share common general environmental conditions and silvicultural history although there is a lot of local variation specific to each tree. Considering that climate affects growth level of each year, the annual increments can be cross classified according to growing years (Saksa et al. 2005, Miina and Saksa 2006).

The empirical data of this study are longitudinal and hierarchical, and the research questions are dendrochronological. Hence, the methodology relies on time-series analysis, multi-level modelling and dendrochronology.

2.2.2 Modelling intra-annual growth

Height-growth phenology was followed in four different Scots pine sapling stands in the northern boreal zone in Lapland, Finland, through one to four growing seasons of 2000–2003 (Paper I). Height accumulation was recorded from 5–15 sample trees per stand using a measurement interval of 1–7 days until height growth was ceased. According to the preliminary data exploration, intra-annual height growth followed a classical non-linear curve. The selected model was a simplification of logistic Gompertz-function that is a classic model for S-shaped growth patterns:

$$H(GDD) = \frac{100}{e^{b \cdot (GDD - c)}} \quad (2.1)$$

where GDD (growing degree-days) is temperature sum from the beginning of the growing season, expressed as degree-days relative to the long-term average temperature sum of each study site, parameter b is a component of the maximum growth rate, and parameter c is the date on which half of the total elongation is completed. Tree height was expressed as a relative value to the annual shoot length. Thus, the upper asymptote is fixed to 100 (percentages of shoot elongation), which reduces the number of parameters to be estimated down to two.

The structure of the data is hierarchical: trees within stands, and stands crossed with years. This design implies multilevel random nonlinear modelling. Statistical models were constructed using procedure NLMIXED that fits nonlinear mixed models by maximizing an approximation to the likelihood integrated over the random effects (SAS User’s Guide

2002b). Procedure NLMIXED fits models by numerically maximizing an approximation to the marginal likelihood using a dual quasi-Newton algorithm (Littell et al. 2006). According to the syntax of NLMIXED, all random effects are supposed to be clustered according to the same subject, which reduces possibilities to estimate multi-level mixed models (Littell et al. 2006). That led to a four-model approach. First, the course of the relative intra-annual shoot elongation and the response of shoot elongation to temperature were modelled using the whole data and only fixed variables. Second, introducing random tree-wise components and estimating parameters for each stand and each year one by one explored the possible differences between trees within stands (results not presented). Third, the differences between stands were studied using a balanced subset of the data and omitting random tree-effects but including random variables for stands:

$$H_{ij}(GDD) = \frac{100}{e^{(b+z1_i)(GDD-(c+z2_i))}} + \varepsilon_{ij} \quad (2.2)$$

where $H_{ij}(GDD)$ is the relative height of tree j in stand i at relative growing degree days of GDD . Parameters are divided into fixed (b and c) and random ones ($z1_j$ and $z2_j$), which allows the model shape and scale to be specific for each stand. The two random effect parameters are assumed to be independent and normally distributed with mean zero and variances σ_{z1}^2 and σ_{z2}^2 and covariance σ_{z1z2} . Likewise, the residual errors ε_{ij} are assumed to be normally distributed with mean zero and variance σ_e^2 . Fourth, differences between years were modelled using Eq.2.2 and replacing random stand-effect by random year-effect.

2.2.3 Modelling inter-annual growth

The empirical material of inter-annual growth was analysed using slightly different methods in Papers II, III, IV and V although they all share similar general approach. Data analysis included four phases; data validation, production of stand-level growth chronologies, analysis of the dependence of mean monthly temperature and growth chronologies, and modelling the dependence of growth and meteorological variables in more detail.

As an additional study, the applicability of temperature variables representing periods shorter than one month was explored (Paper V). Daily temperature values were available from 1961 onwards, which constrained the length of the compared series. A direct-search algorithm was used in order to screen for the temperature periods yielding the highest linear correlation with the residual growth chronologies, radial and height growth of each stand (5C and 5D) separately. As a comparison, monthly periods were also used. Both Julian days and degree-day accumulation (threshold +5°C) were used when defining the start and end of the compared temperature periods.

The quality and uniformity of the measured inter-annual growth series were analysed with the program COFECHA (Holmes 1983, Grissino-Mayer 2001). It is a computer program that assesses the quality of crossdating and measurement accuracy of growth series (Grissino-Mayer 2001). COFECHA removes low-to-mid frequency variation from all series and calculates correlations (Pearson's) between segments of the series. The output provides information about the similarity of series, potential missing observations, divergent year-to-year changes, and statistical outliers.

Prior to correlation analysis, height increment and temperature series were detrended and prewhitened if unit root or white noise tests indicated that the series included a statistically significant trend or autocorrelation. Detrending and prewhitening served two purposes. First, the aim was to enhance the climatic signal and filter other effects out. Second, at least one of the two studied series should be stationary if techniques such as cross-correlation analysis are to be used. Three methodological approaches were applied.

1) When studying the effect of temperature of growing season on height growth of one stand (Paper II), the measured time-series were pre-processed by fitting a linear or quadratic trend and an autocorrelation model and using the residual series in correlation analysis.

2) The climatic response of height increment (Paper III) and the dependence of needle density on annual height growth (Paper IV) were modelled by fitting multilevel mixed effects models in three phases. In the first phase, standardized height-increment chronologies, both an overall mean chronology and standwise chronologies, were predicted by a multilevel mixed effects model of height increment (Henttonen 1990, Miina 2000).

A general linear model can be written:

$$\log(Y_{ijt}) = \beta_{0ijt} + \beta_{1ijt}X_{ijt} + \varepsilon_{ijt} \quad (3.1)$$

where Y_{ijt} is the response variable of tree j of stand i in year t ; β_{0ijt} is an intercept, X_{ijt} is a vector of explanatory variables associated with parameters β_{1ijt} (slope), and ε_{ijt} is the residual error term that has normal distribution with a mean of zero. The structure of data can be regarded as a multilevel model where annual height-increment measurements are level-1 observations (shoot level, within-tree). Each measurement occasion is nested within a tree at level-2 (tree level, between-tree-within-stand), and trees are nested within a stand at level-3 (stand-level, between-stand). The measurements are also correlated within a year, which means that measurements of a certain year have something in common. This year-effect is considered similar in all the stands because it is caused mainly by annual temperature variation that is common to all studied sites. Therefore, year-effect is regarded to be effective at level-3. The general model allows random components to be incorporated both in intercept and in slope. The parameters of random slope were small and appeared to be statistically insignificant and the random part in slope was omitted. Intercept of the final model includes random components representing the hierarchy of the data:

$$\beta_{0ijt} = \beta_0 + z_i + u_{ij} + w_t + k_{it} \quad (3.2)$$

where β_0 is an intercept (mean value), z_i is a stand effect, u_{ij} is a tree effect, w_t is a year effect, and k_{it} is an interaction of year and stand. The random effects were supposed to be independent and to have normal distribution with a mean of zero. Because slope is fixed, β_{1ijt} of Eq.3.1 reduces to β_1 . Thus, the model applied in the standardization was:

$$\log(Y_{ijt}) = \beta_0 + X_{ijt}\beta_1 + z_i + u_{ij} + w_t + k_{it} + \varepsilon_{ijt} \quad (3.3)$$

For random effects, a diagonal-only covariance matrix structure was applied, and a distinct variance component is assigned to each effect. The residual error term was assumed to have a first-order autocorrelation structure. The fixed part of the model was used to remove the growth trend due to tree age (Paper III) or the needle density trend due to height growth (Paper IV). In the beginning, an empty model (“null model”) without explanatory variables was used to get estimates for the fraction of variation at each level of the model (Snijders and Bosker 1999). After adding a 2nd degree polynomial function of tree age as a time-variant explanatory variable, the estimates for $w_t + k_{it}$ were used as chronology for each stand. Stand-level fixed effects were not used. Hence, all between-stand variation is included in random effects. Procedure MIXED of SAS statistical software was used to estimate the parameters of the model using restricted maximum likelihood (Littell et al. 2006).

3) When comparing radial and height growth (Paper V), standwise chronologies were produced by detrending procedure (Holmes et al. 1986), which is commonly used in dendro-chronological studies. Growth series were detrended by fitting a cubic smoothing spline with 30 years filter length using program ARSTAN. This reduces the amplitude to less than 50% in the 30 years and longer frequency range (Cook and Peters 1981) and thereby extracts the short-term variation and enhances the climatic signal. Thereafter, the detrended series were prewhitened using the autocorrelation-modelling feature of program ARSTAN. To avoid bias in comparisons of radial and height growth and 150 and 50-year-old stands, each series was processed in exactly the same way.

The dependence between growth and mean monthly temperatures, as well as the dependence between radial and height growth (III, IV, V) were studied by cross-correlation analysis (SAS User’s Guide 2002a). This is suitable for data-driven inspection of dependency between two time-series and was used when screening for variables of the more detailed growth models.

Modelling the dependence of growth and meteorological variables was again based on three different approaches.

1) The first attempt to quantify the effect of temperature on height growth (Paper II) was based on simple transfer function (SAS Institute Inc. 2001). The general form of the model was:

$$y_t = T_t + f(U_t) + N_t + \varepsilon_t \quad (4)$$

where T_t is a nonstationary trend, $f(U_t)$ are linear or nonlinear relations between the outputs and any specified inputs, denoted here by the vector U_t ; N_t is coloured (assumed to be AR(1)) noise; and ε_t is a zero mean, serially uncorrelated white noise sequence. The output series y_t was height increment, and input series U_t were monthly temperatures with different lags, and t denotes time. A linear trend or a quadratic polynomial function of tree age was used as a regressor T_t to remove the possible age trend of height increment but to retain high and medium–frequency signal. Monthly temperature variables were added to the model according to their significance and the general fit of the model indicated by the Akaike information criterion.

2) Secondly, a multilevel-modelling approach (Papers III and IV) studied those meteorological variables that were found to be statistically significant by using them as explanatory variables in the term $X_{ijt}\beta_j$ of Eq. 3.3 according to their statistical significance and contribution to the overall fit of the model. The latter was determined by means of likelihood ratio statistics and the Akaike information criterion (Littell et al. 2006). This time, the estimates for $w_t + k_{it}$ were considered as yearly variation unexplained by selected climatic variables. When back-transforming the results from logarithmic to normal scale, a bias correction were added

(Flewelling and Pienaar 1981). The relative change of random variance components due to inclusion of $X_{ijt}\beta$ was used as an estimate of the proportion of explained variance (Snijders and Bosker 1999). If denoting variance of random effects $\sigma_e^2 = \text{var}(\varepsilon_{ijt})$, $\sigma_u^2 = \text{var}(u_j)$, $\sigma_w^2 = \text{var}(w_i)$, $\sigma_k^2 = \text{var}(k_i)$, and $\sigma_z^2 = \text{var}(z_i)$, the fraction of total variance that is attributed to different levels can be expressed using equations adapted from Snijder and Bosker (1999):

$$\rho_{\text{within-tree}} = \frac{\sigma_{e0}^2}{\sigma_{e0}^2 + \sigma_{u0}^2 + \sigma_{w0}^2 + \sigma_{k0}^2 + \sigma_{z0}^2} \quad (5.1)$$

$$\rho_{\text{tree}} = \frac{\sigma_{u0}^2}{\sigma_{e0}^2 + \sigma_{u0}^2 + \sigma_{w0}^2 + \sigma_{k0}^2 + \sigma_{z0}^2} \quad (5.2)$$

$$\rho_{\text{year}} = \frac{\sigma_{w0}^2 + \sigma_{k0}^2}{\sigma_{e0}^2 + \sigma_{u0}^2 + \sigma_{w0}^2 + \sigma_{k0}^2 + \sigma_{z0}^2} \quad (5.3)$$

$$\rho_{\text{stand}} = \frac{\sigma_{z0}^2}{\sigma_{e0}^2 + \sigma_{u0}^2 + \sigma_{w0}^2 + \sigma_{k0}^2 + \sigma_{z0}^2} \quad (5.4)$$

where σ_{e0}^2 , σ_{u0}^2 , σ_{w0}^2 , σ_{k0}^2 , and σ_{z0}^2 , are variances of the model without independent variables (empty model, null model). The amount of explained variance at different levels due to adding independent variables was calculated applying the method presented by Snijders and Bosker (1999):

$$R_{\text{within-tree}}^2 = 1 - \frac{(\sigma_{e1}^2 + \sigma_{u1}^2 + \sigma_{w1}^2 + \sigma_{k1}^2 + \sigma_{z1}^2)}{(\sigma_{e0}^2 + \sigma_{u0}^2 + \sigma_{w0}^2 + \sigma_{k0}^2 + \sigma_{z0}^2)} \quad (5.5)$$

$$R_{\text{tree}}^2 = 1 - \frac{\left(\frac{\sigma_{e1}^2}{n} + \sigma_{u1}^2 + \sigma_{w1}^2 + \sigma_{k1}^2 + \sigma_{z1}^2\right)}{\left(\frac{\sigma_{e0}^2}{n} + \sigma_{u0}^2 + \sigma_{w0}^2 + \sigma_{k0}^2 + \sigma_{z0}^2\right)} \quad (5.6)$$

$$R_{\text{year}}^2 = 1 - \frac{\left(\frac{\sigma_{e1}^2}{nm} + \frac{\sigma_{u1}^2}{m} + \sigma_{w1}^2 + \sigma_{k1}^2 + \sigma_{z1}^2\right)}{\left(\frac{\sigma_{e0}^2}{nm} + \frac{\sigma_{u0}^2}{m} + \sigma_{w0}^2 + \sigma_{k0}^2 + \sigma_{z0}^2\right)} \quad (5.7)$$

$$R_{\text{year}\times\text{stand}}^2 = 1 - \frac{\left(\frac{\sigma_{e1}^2}{nm} + \frac{\sigma_{u1}^2}{m} + \sigma_{k1}^2 + \sigma_{z1}^2\right)}{\left(\frac{\sigma_{e0}^2}{nm} + \frac{\sigma_{u0}^2}{m} + \sigma_{k0}^2 + \sigma_{z0}^2\right)} \quad (5.8)$$

$$R_{\text{year}}^2 = 1 - \frac{\left(\frac{\sigma_{e1}^2}{nm} + \frac{\sigma_{u1}^2}{m} + \sigma_{w1}^2 + \sigma_{z1}^2\right)}{\left(\frac{\sigma_{e0}^2}{nm} + \frac{\sigma_{u0}^2}{m} + \sigma_{w0}^2 + \sigma_{z0}^2\right)} \quad (5.9)$$

$$R_{\text{stand}}^2 = 1 - \frac{\left(\frac{\sigma_{e1}^2}{nmp} + \frac{\sigma_{u1}^2}{mp} + \frac{\sigma_{w1}^2}{p} + \frac{\sigma_{k1}^2}{kp} + \sigma_{z1}^2\right)}{\left(\frac{\sigma_{e0}^2}{nmp} + \frac{\sigma_{u0}^2}{mp} + \frac{\sigma_{w0}^2}{p} + \frac{\sigma_{k0}^2}{kp} + \sigma_{z0}^2\right)} \quad (5.10)$$

where σ_{e1}^2 , σ_{u1}^2 , σ_{z1}^2 , σ_{k1}^2 and σ_{w1}^2 are variances of the model with all independent variables, n and m are the average number of observations per tree and total number of sample trees per year, p is the number of sample trees per stand, and k is the number of stands. The basic idea of these equations is to approximate the proportional reduction in mean squared prediction error for a randomly drawn unit of the level under inspection (Snijders and Bosker 1999). The higher-level R^2 gets “its share” from the lower-level variation according to group sizes.

3) The third modelling alternative is based on methods developed for analysis of multiple time series (Tiao and Box 1981, SAS User’s Guide 2002a). The standard height and radial growth chronologies produced by ARSTAN were used when estimating parameters of vector autoregressive models with exogenous variables (VARX). The aim was to simultaneously model both autocorrelation within radial and height growth, and the dynamic relationship at various lags between radial and height growth (Paper V). Both growth chronologies were considered as dependent (endogenous) variables. Additionally, temperature series were added as an independent (exogenous) variable. For example, a tree growth model of order one can be written as follows:

$$\begin{cases} iD_t = \delta_1 + \phi_{11}iD_{t-1} + \phi_{12}iH_{t-1} + \Theta_1^*x_{t-1} + \varepsilon_{1t} \\ iH_t = \delta_2 + \phi_{21}iH_{t-1} + \phi_{22}iD_{t-1} + \Theta_2^*x_{t-1} + \varepsilon_{2t} \end{cases} \quad (6)$$

where iD_t and iH_t are observation vectors (radial and height growth), x_t is a vector of temperature effects with its associated parameters in matrix Θ_i^* , ε_t is an error term (white noise vector that is assumed to be independent and normally distributed with a mean of zero), δ_1 and δ_2 are constant vectors, matrix Θ comprises autoregressive parameters, and t denotes time. It is assumed that the independent variables x_t are not correlated with residuals ε_t . The parameter estimation of VARMAX procedure uses the two-stage estimation method, which computes the estimation of deterministic terms and exogenous parameters and then maximizes the log-likelihood function (SAS User’s Guide 2002a). The results from the autocorrelation analysis of the growth series and cross-correlation analysis of growth and temperature series were utilized in selecting possible independent variables and specifying the order of autocorrelation.

3 RESULTS

3.1 Intra-annual growth; phenological temperature thresholds (Paper I)

The elongation of the leader shoot was temperature driven; temperature sum as degree-days corresponded with height growth. Total shoot length correlated with the growth rate but not with the length of the height-growth period; both height increment per degree-day and height increment per growing day were the higher, the longer the annual shoot was at the end of the season (Table 3). The timing of bud break had no effect on total height growth or growth rate. Height-growth cessation was defined as the date when 95% of the total shoot length was achieved. The within-stand (between-tree) phenological differences were about the same each year; the trees that reacted rapidly to increasing temperatures started and ended their height growth earlier than other trees each year. According to the constructed model, height growth ceases when on average 41% of the relative temperature sum of the site has been achieved (observed minimum and maximum were 38% and 43%). The relative temperature sum is calculated by dividing the actual temperature sum by the long-term mean of the total annual temperature sum for the site. Although there were differences both in the timing of phenological events in different years and the absolute temperature sum at the time of height growth cessation in different stands, this model based on relative values captured the common temperature dependency of intra-annual height growth at stand level.

Table 3. The mean height growth, mean duration of height growth and growth rate of *Pinus sylvestris*. Growth cessation is defined as the accomplishment of 95% of the annual shoot length.

Stand	Year	The mean height growth (mm)	Height growth duration from 5% shoot length (days)	Height growth duration from 5% shoot length (deg.days)	BB	iH-5	iH-95
1B	2000	303	38	310	—	May 26 th	July 2 nd
	2001	195	45	303	May 2 nd	May 18 th	July 1 st
	2002	163	44	317	April 30 th	May 14 th	June 26 th
	2003	137	49	312	May 6 th	May 20 th	July 7 th
2B	2001	277	30	240	May 3 rd	June 2 nd	July 1 st
	2002	247	35	285	April 29 th	May 20 th	June 23 th
	2003	221	42	259	May 11 th	May 25 th	July 5 th
4B	2003	112	48	268	May 6 th	May 22 th	July 8 th
5B	2000	139	53	206	—	May 25 th	July 13 th
	2001	114	38	246	May 16 th	June 2 nd	July 9 th
	2002	132	36	213	May 2 nd	May 26 th	June 30 th
	2003	76	50	233	May 13 th	May 25 th	July 13 th

3.2 The effect of temperature on inter-annual height growth of Scots pine (Papers II, III, and IV)

The observed inter-annual height growth indicated a latitudinal trend, an age trend and dependence on temperature (Fig. 3, Fig. 4, Fig. 5). The average height growth of stand 5C during its sapling stage was lower than in others stands (Fig. 4).

The effect of the mean July temperature of the previous year on height increment proved to be very strong at high latitudes. In the three northernmost stands (5, 6, and 7), correlation between height increment and the previous July temperature was higher than in the two southernmost stands (Paper III). The mean November temperature of the year before the previous year had a statistically significant effect upon height increment of the 50-year-old trees in the three northernmost stands. Mean monthly temperatures of the current growing season did not correlate statistically significantly with the annual height increment at stand level except in stand 5, where the current June temperature also had a positive correlation with height increment. Observations of each tree were analysed separately only in stand 6A (Paper II). The results confirmed that there is a lot of variation within the studied stand; six out of ten trees gave results similar to mean growth, whereas one height-increment series correlated positively also with the current June and July temperatures ($r = 0.50$). Three tree-wise increment series did not correlate statistically significantly with monthly temperatures at all.

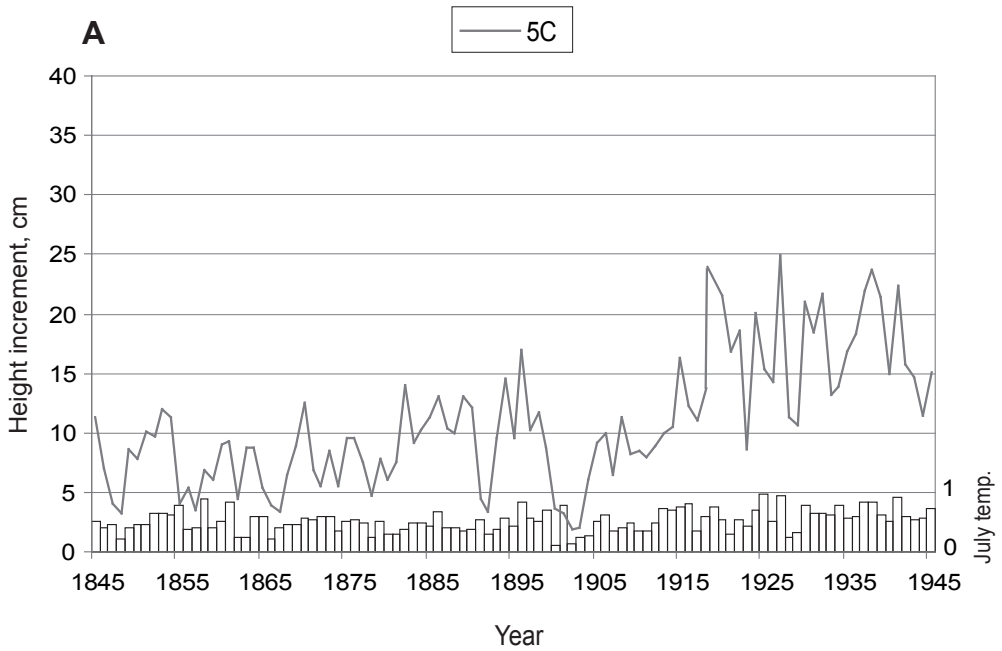
Neither was there any correlation between height increment and precipitation nor between height increment and potential evapotranspiration in any of the sites (Paper III). However, the results from needle-density analysis (Paper IV) suggested that April–May precipitation might fine-tune height growth to some extent.

The multilevel height increment model based on stands 1A–5A included tree age, long-term mean temperature sum of the site, and the mean July temperature of the previous year as independent variables. Assuming the other variables of the model are fixed, a change in July temperature of one degree results on average in a 1.8 cm change in next year's height increment (Paper III). The warmer the July is, the longer are next year's shoots. There was a modest but significant polynomial age effect (Fig. 6). Using the approach described by Snijders and Bosker (1999), the proportion of explained variance (at the year level) was 74%. The dependence of the July temperature on height increment was shown to be very strong, suggesting a high value of height increment in climate modelling near the tree line areas.

A simple transfer function based on observations from stand 6A gave similar results as the multilevel model; the explanatory variable was mean July temperature of the previous year. In addition, a linear negative trend captured the age effect (Paper II). The regression factor of mean July temperature was 1.2, which corresponds to the effect of one degree temperature change on next year's height growth in centimetres if age effect is fixed at its mean value. The measured mean height increment in Stand 6A from 1957 to 1996 was 15.7 cm (Table 2). The mean error of predicted versus measured annual height increment values was 9% (Paper II)

3.3 Needle density with respect to height growth (Paper IV)

The mean overall needle density was 7.8 short shoots per shoot centimetre. Needle-density variation in measured data was mostly due to within-tree differences. From the total variance, within-tree variation yielded 46%, between-tree, 21%, and between-year, 27%. There was a very strong negative correlation between height growth and needle density, and height growth and age explained 50% of the between-year variance. The standwise residual vari-



Continues on fig. B

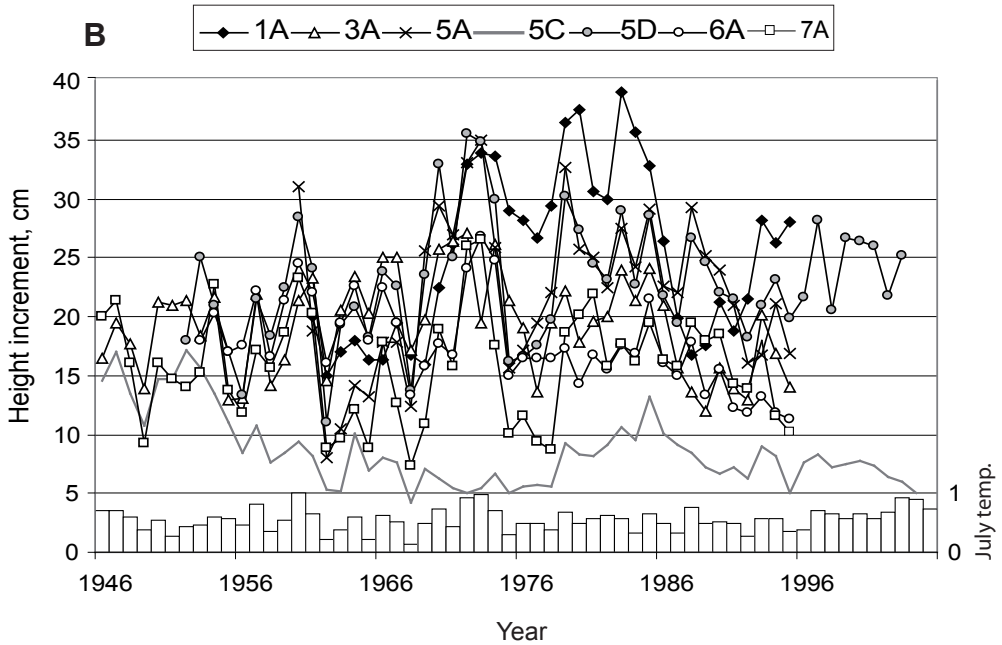


Figure 3. Measured intra-annual height growth in stand 5C in years 1845–1945 (A) and in stands 1A, 3A, 5A, 5C, 5D, 6A, and 7A in years 1946–2005 (B). July temperature index (the mean July temperature of the previous years scaled to 0.0–1.0) is presented as a bar chart.



Continues on fig. B

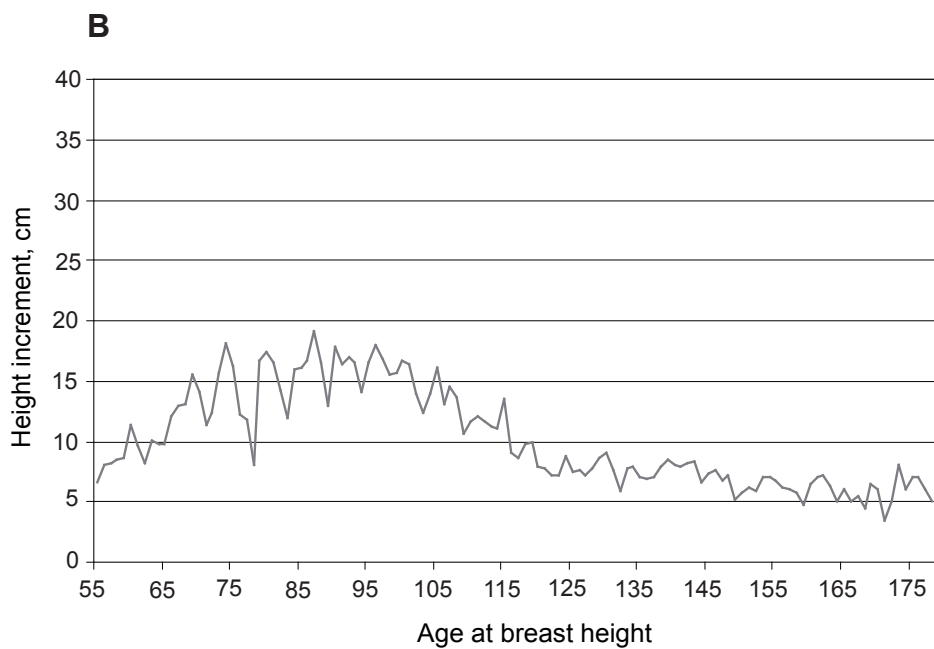


Figure 4. Measured intra-annual height growth in stands 1A, 3A, 5A, 5C, 5D, 6A, and 7A with respect to stand mean age at breast height (A). Height growth chart of stand 5C continues on figure B.

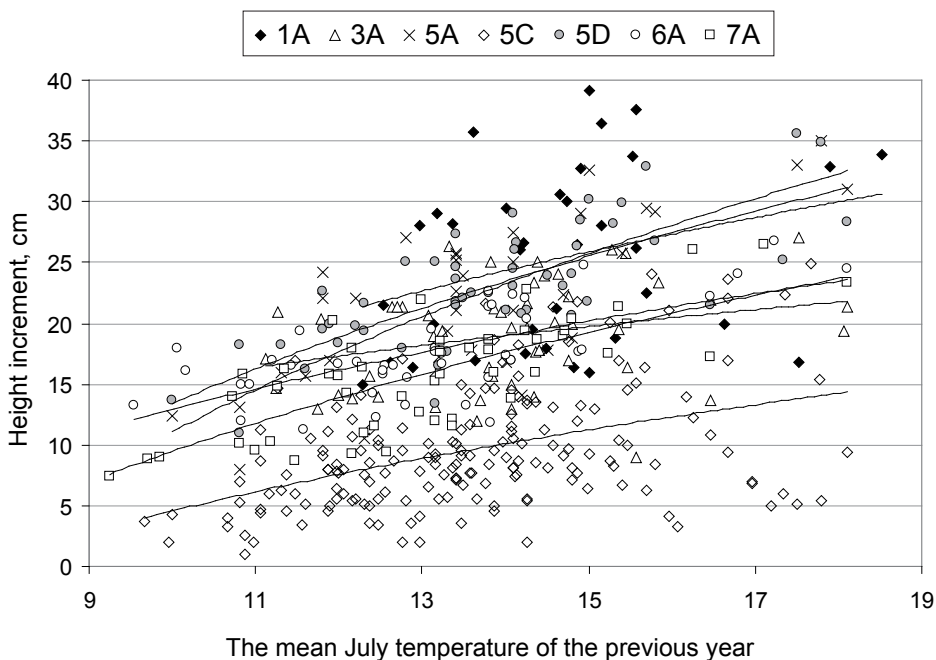


Figure 5. The measured mean height increment at stands 1A, 3A, 5A, 5C, 5D, 6A and 7A and the mean July temperature of the previous year. Lines produced by simple logarithm function illustrate the mean measured temperature response of stands.

ations and their correlations with the temperature and precipitation time series were further analysed with cross-correlation analysis in order to screen for additional independent variables. The only possible additional independent variable was the precipitation of April–May (precipitation of May in the two northernmost stands). When it was added to the multi-level model, the proportion of explained between-year needle-density variance was 55%, but the residual variation remained at the same level. The effect of spring precipitation indicates the role of snow coverage and snowmelt on the growing conditions in the three southernmost stands. In general, stand-level needle-density variation is mostly due to changes in height growth.

There were clear differences between individual trees regarding mean needle density; some trees had constantly lower needle density levels than others. For example, needle density of tree 1 in stand 5A is low, whereas tree 6 in the same stand yields constantly higher-than-average densities (Fig. 7). The trees with a relatively high needle-density level also had more year-to-year differences in needle-density, and lower than average height growth. The within-stand needle-density series became more coherent southwards; when analysing the balanced subset of the data (years 1969–1996) with program COFECHA, the mean correlation of individual trees with the standwise master series in the three southernmost stands was 0.6–0.7, while the respective figures in their northern counterparts were 0.2–0.4. The two northernmost stands both had at least one tree that did not correlate significantly with the needle-density series of any other tree in the stand.

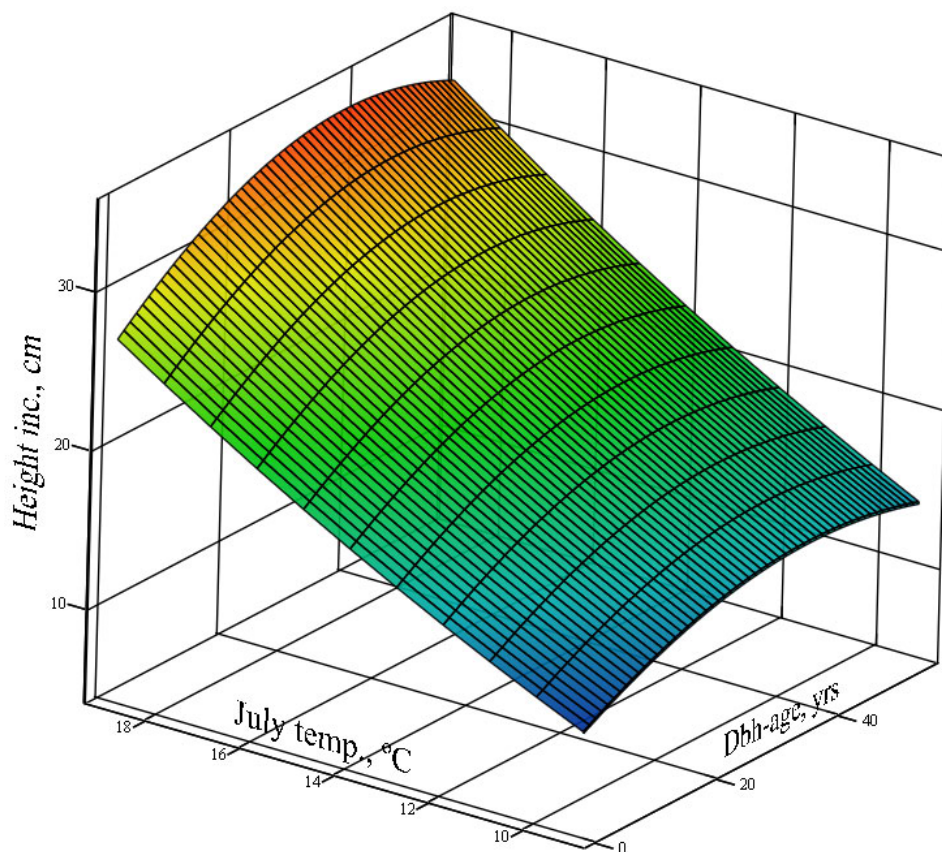


Figure 6. Application of the height growth model; the effect of tree age and July temperature of the previous year on annual height increment.

3.4 The effect of temperature on the ratio of height and diameter growth (Paper V)

The height-growth chronology correlated significantly with radial growth with a lag of 1 year, and radial growth with height growth with a lag of 2 years when the effect of temperature is omitted (cross-correlation analysis). In the VARX-model (Eq. 6), the positive effect of previous year's radial growth on the current height growth was dissipated when the temperature of the previous July was included as an independent variable. On average, low and high growth years represented cool and warm average growing seasons. Summer temperatures (June, July and August) had the strongest effect upon growth, but height and radial growth had a different set of effective temperature periods. Furthermore, July temperature variation affected height growth more strongly than radial growth. Those years when radial growth was relatively higher than next year's height growth (high radial/height-growth ratio) did have cooler than average July temperature and lower growth in general. In contrast, those years with low radial/height-growth ratio had high mid-summer temperatures.

The temperature sensitivity of radial and height growth to other than monthly periods was further examined by screening for the temperature period that yielded the highest correlation

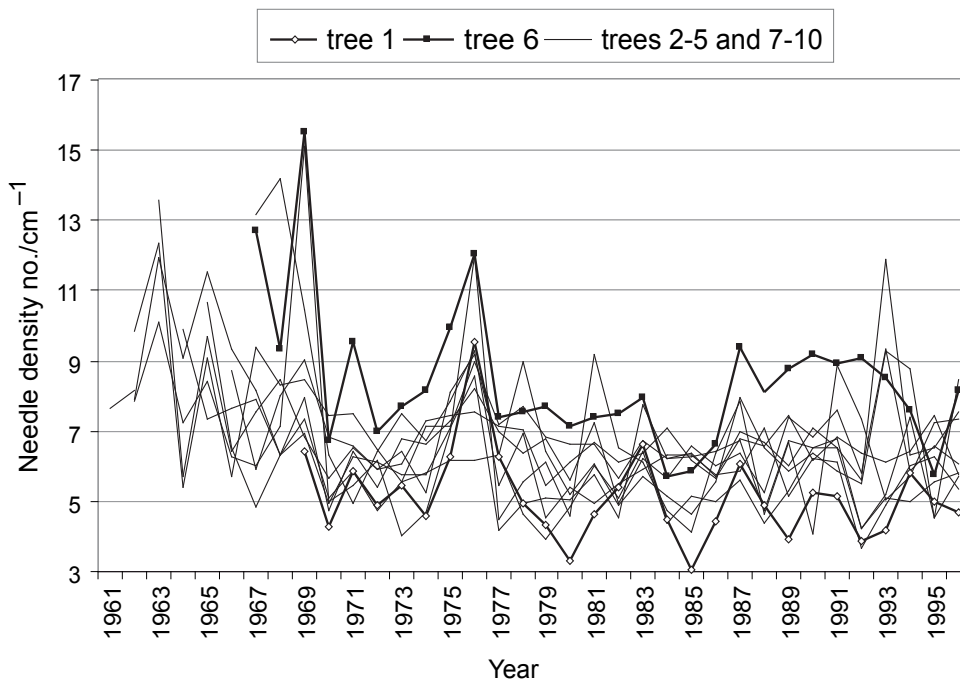


Figure 7. Needle density of sample trees in stand 5A.

with the four residual growth chronologies (radial and height growth of both stands)(Paper V). Four chronologies and two temperature period definitions — based on either Julian days or relative growing-degree-days — resulted in eight separate optimization tasks. The biggest improvement achieved by incorporating these new temperature periods was the correlation coefficients of the height growth chronology of the 150-year-old stand. The period from July 9th to July 25th resulted in a correlation coefficient of 0.45, and the period from 35% to 52% degree-day accumulation (relative to the long-term average) resulted in a correlation of 0.44, while mean July had a correlation of 0.30. On average, Julian days and degree-days gave similar results when they were used for defining temperature periods; correlation coefficients were at the same level and always better compared to those of growth and mean monthly variables. When defining temperature periods by degree-day accumulation, the length of the periods was, in the 50-year-old stand, almost as long as when using Julian days. In the 150-year-old stand, Julian days always resulted in clearly longer periods than degree-day –based definitions.

Several instances were noted where a cool growing season followed two or three warm growing seasons and radial growth maintained its level during the cool year while height declined. This suggests that radial growth uses carbon stored during previous and favourable years. In general, the time lagged effect of several favourable or unfavourable years should be noted although their statistical dependence is difficult to confirm due to the limited length of temperature records. When comparing predicted and measured annual height increments, there appeared to be individual years or periods of some years when the dependence between summer temperature and growth was weak.

4 DISCUSSION AND CONCLUSIONS

Height growth cessation depends on the temperature of the current growing season. As a rule of thumb, height growth of Scots pine ceases when approximately 41% of the long-term average temperature sum corresponding to their origin has accumulated (Paper I). Under the scenario of warming climate, it implies that height growth ceases relatively early despite increasing annual growths. Early cessation may increase the chance of lammas growth, which can be regarded as a disturbance of the normal monocyclic growth rhythm of Scots pine (Lanner 1976). If height-growth cessation precedes and partly triggers earlywood–latewood transition (Jayawickrama et al. 1997, Uggla et al. 2001, Rossi et al. 2009), climate warming may be presumed to increase latewood proportion.

The start of the growing season has advanced during the last few decades (Schwartz et al. 2006). Consequently, phenological events and the time of actual growth may have changed (Tuovinen et al. 2009). For example, because the growing season starts earlier than it used to, spring and early summer temperatures are more important for height growth now than in the 20th century. This affects the interpretation of the effect of monthly climate variables on decadal-long dendrochronological time-series. Temperature periods shorter than a month proved to be more effective variables than mean monthly values, but the improvement is on a scale of modest to good, at least when applying only Julian days or growing-degree-days as pointers. This approach should be elaborated further by combining days and growing-degree-days simultaneously with longer data sets. Then again, optimization techniques should be applied with care because they simply maximize or minimize the selected objective and ignore causality.

The importance of mid-summer environmental conditions on the next season's height increment has been reported since the early 1900's (Hesselman 1904, Laitakari 1920, Mikola 1950, Martynov 1978, Junttila and Heide 1981). The temperature of July proved to be the best monthly variable when modelling height growth. The importance of July is due to its central role in bud formation (MacDonald and Little 2006) and its major contribution to the total temperature sum and net photosynthetic production at the tree line. The current summer did not significantly correlate with the final shoot elongation, except in stand 5A, where the correlation of June was statistically significant in the cross-correlation analysis (Paper II, Paper III). Trees in stand 5A are vigorous and growing well considering their northern location, and their height increment had altogether higher correlations to mean monthly temperatures than in the other stands.

The mean November temperature two years prior to the growing season had a negative effect on height growth in the three northernmost stands (Paper III). It can be hypothesized that a warm period during late autumn increases respiration, which results in consumption of carbohydrates and, because there is no net production in the late autumn, decreases the amount of stored energy available at the beginning of the next season. A tree's vigour and available resources during bud formation are more important than conditions during the final elongation, which explains why the November mean temperature prior to bud formation is more important than the November temperature prior to shoot elongation, which also has a negative but statistically non-significant correlation with final shoot length.

Monthly precipitation did not affect height increment (Paper III). Precipitation alone is probably not sufficient to describe accurately the availability in soil moisture in the studied stands although rainfall is an important part of the annual variation of soil water content. Precipitation records originated from the nearest official weather stations and on-site meas-

urements were not available. Variability of rainfall has large spatial differences (Heino 1994), which reduces the applicability of precipitation records that are not measured on-site. Nevertheless, drought is not considered a significant factor in northern Fennoscandia because of the humid climate and abundant availability of melting snow for the early growing season (Gärdenäs and Jansson 1995). According to Mikola (1950) soil moisture is almost always sufficient in the northern part of the boreal zone. However, periodical loss of temperature signal in the tree line area may be connected with lack of water (Seo et al. 2009).

The constructed growth model that is based on five stands along a 400 km transect predicts a one degree change in July temperature resulting in a 1.8 cm change in next year's height increment (Paper III). Junttila and Heide (1981) reported similar results; the coefficient of mean June–August temperature in their linear shoot length model was 1.85, which translates into marginal growth effect in centimetres. Their model was based on empirical material collected near stand 7A of this study.

In normal, undisturbed conditions, needle count is predetermined similarly to height growth. Needle density may exceed the predetermined figure if elongation of height growth units is disturbed due to damages or extreme weather. Likewise, needle density decreases if shoot elongation is higher than expected due to extremely favourable conditions. In general, needle-density variation is mostly due to changes in height growth. The only additional independent variable found during modelling was the precipitation of April–May (precipitation of May in the two northernmost stands). When it was added to the multi-level model, the proportion of explained between-year needle-density variance was 55%, but the overall fit of the model improved only slightly (Paper IV). The effect of early spring precipitation indicates the role of snow coverage and snowmelt on the growing conditions in the three southernmost stands.

Temperature affected height growth of the 150-year-old stand less than the 50-year-old stand (Paper V). In addition, the radial growth of the 150-year-old trees was more sensitive to temperature than their height growth. This, together with the relatively low height growth level implicates that there are other factors than temperature that control shoot length of those trees. It is possible that these trees have originally belonged to the understorey, which could partly explain their lower height-growth level and temperature sensitivity.

Both radial and height-growth time series include autocorrelation (Paper V). It implies that the conditions of consecutive years affect growth. This effect was stronger on radial than height growth. It was found that radial growth maintains its growth level achieved during a period of favourable years that are followed by a cool year. In general, the time-lagged effect of several favourable or unfavourable years should be accounted for when judging the effect of climate on growth. There were also individual years or periods of some years when the dependence between summer temperature and growth was weak. Therefore, factors other than temperature may occasionally be the main growth-limiting factor or the accuracy and scale of measurements used in this study were insufficient to describe the temperature dependence during some periods.

Radial growth of the previous year and height growth of the current year both reflect mainly the growing conditions of the previous season. Height growth is more sensitive to temperature changes and in young trees also to shorter temperature periods in midsummer than radial growth. Therefore, the ratio of radial and height growth is not stable from year to year. That ratio is further affected by variation in the phenology of radial and height growth. In spite of the occasional “asymmetry” in the level of these annual growth components, a long-term balance was also statistically distinguishable (Paper V).

Good annual height increment usually also means that needle production is abundant. The youngest needle sets are the most important net producers of carbohydrates. Thus, high needle production predicts high net photosynthesis during the following couple of years assuming that other growth conditions are not limiting. Especially older needles sets also play an important role as a storage organ (Ericsson 1978). Stored resources can be reallocated e.g. into new secondary growth. Accordingly, radial growth was found to correlate with height growth at a lag of two years. The ability to buffer resources is exemplified in the growing season of 1975, which was cooler than average but still attained a relatively wide annual ring. The reason for this is most probably the utilization of stored resources from the preceding favourable growing seasons. Several authors note a carry-over effect of the growing conditions of the previous season on current wood production of Scots pine (Hansen and Beck 1990, Berninger et al. 2004, Zweifel et al. 2006, Vaganov et al. 2009).

The competitive position of a tree is composed of its relative height and its distance to the nearest neighbours (Oliver and Larson 1990, Nilsson 1993). Height growth must be strategically important because it is the only way to reach for a better position within the canopy. It is so important that trees even take a risk by predetermining the amount of height growth and thereby partly allocating next year's resources already during the previous season. Maximum height and diameter growth are focused on different parts of the growing season (Seo et al. 2010), which reduces the amount of simultaneously active meristems and in that way simplifies the hormonal control system (cf. Wang et al. 1997). Compared to tree-rings, height growth is prone to disturbances caused by e.g. snow, insects and fungus, but it is also a sensitive indicator of climate in northern Finland. Based on Scots pine from southern and central Finland, Mäkinen (1998) concluded that height increment gave no marked benefits compared to environmental signals obtained from radial increment. In those conditions, the signal strength of height increment did not pay off the laborious and error-prone measurements.

Pine growth can be considered to comprise of partly overlapping two-year periods; radial growth and bud morphogenesis during the first year, and bud burst and shoot elongation during the second one. The latter overlaps with radial growth and morphogenesis of a new bud. The question is why this kind of growth rhythm is so beneficial that evolution has favoured it. The main reason arises from the shortness of the growing season. Preformed growth pattern, which is typical for many alpine species, aims at a rapid burst into vegetative growth as early on in spring as possible (Billings and Mooney 1968, Arft et al. 1999, Bliss). Height and needle growth and flowering are strategically important, and the early and middle part of the growing season is usually the most favourable time to proceed with them, due to the availability of radiation, warmth and moisture. Furthermore, the photosynthetic capacity of the new needles is important already during their first growing season, and the longer their active period, the better. There is a self-explanatory basis for the sequential pattern; support and transport organs (radial growth, root system) have to be built before apical growth relying on them can proceed.

Air temperature regulates annual variation of increment and phenology of Scots pine in northern Finland. However, soil temperature may be equally as important as air temperature, but appropriate soil data was not available for this study. It is still obvious that other limiting factors appear in extreme years or single stands or trees. For example, it was found that the height increment of usually at least one or two trees out of ten trees did not correlate with monthly temperatures as strongly as the stand mean chronology (Paper II). Similarly, the mean height increment of the experimental stand in Sodankylä showed clearly a lower temperature response than the other stands (Paper III). Furthermore, the exceptionally warm growing season of 2002 was followed by lower than expected growth in the next season

(Paper I). This can be due to a relatively low temperature during bud morphogenesis within the warm season or limited availability of soil moisture caused by the exceptionally low soil water table level during the first years of this decade and low precipitation during the year 2002 (Seo et al. 2009).

The empirical observations of this study are sampled from stands located along a 400 km long latitudinal transect but representing the same soil fertility range. Sampling was focused on dryish heath because it is a typical site type for pine stands in Finland. The effect of temperature on height growth was positive in all studied stands, but the dependency at inter-annual scale was not equally strong in all locations (Paper III) and in stands from the same area but of different age (Paper V). Therefore, it can be suggested that the results are applicable only on a general level for Scots pine in northern Finland.

Climate and weather fluctuation includes variation that can be regarded as random and causes uncertainty in long-term forecasts. Temperature is the major determinant of annual height growth variation in northern Finland, which induces random variation into height growth as well. Due to the predetermined growth habit, the next year's height increment is easy to predict, but long-term annual predictions depend heavily on climate. From another viewpoint, the strong dependence between July temperature and next year's height increment makes height growth of northern Scots pine a useful bioindicator of changing environmental conditions, especially when combined with other ecological observation series.

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