Modelling the Effect of Temperature on Height Increment of Scots Pine at High Latitudes

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The effect of temperature and precipitation on the height increment of *Pinus sylvestris* (L.) was modelled using data gathered from a total of 49 felled sample trees from five stands of Scots pine located along a latitudinal transect from the Arctic Circle up to the northern timberline in Finland. A multilevel mixed effects model and cross-correlation analysis of prewhitened time series was used to analyse the dependence between height increment and monthly meteorological observations. The effect of the mean July temperature of the previous year on height increment proved to be very strong at high latitudes ($r > 0.7$). The mean November temperature of the year before the previous affected statistically significantly on height increment in the three northernmost stands. There was no correlation between height increment and precipitation in any of the sites. The final height increment model based on all stands included tree age, long-term mean temperature sum of site, and the mean July temperature of the previous year as independent variables. According to the model, one degree's change in July temperature results on average in 1.8 cm change in the next year's height increment. There was a modest but significant polynomial age-effect. The proportion of explained variance (at the year level) was 74%. The July temperature dependence on height increment was shown to be very strong, suggesting a high value of height increment in climate modelling at the tree line.

Keywords height growth, temperature, dendroclimatology, precipitation, *Pinus sylvestris*
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1 Introduction

Height growth on most pine species is a two-year process involving the formation of the terminal bud during year one and shoot elongation in year two (Doak 1935, Lanner 1976). The length of the new shoot is mostly determined by the number of stem units laid down during the bud formation (Cléments 1970, van den Berg and Lanner 1971, Kozlowski et al. 1973, Lanner 1976). The number of stem units formed in a terminal bud is largely determined by environmental conditions during the period of bud formation (Lanner 1985). Thus, the factors affecting bud formation are crucial to height growth (Cleary and Waring 1969, Cléments 1970, van den Berg and Lanner 1971, Kozlowski et al. 1973, Lanner 1976, Pollard and Logan 1977, Lanner 1978, Junttila 1986). Shoot growth of most pine species is partly affected also by the early period of the current growing season when the stem units reach their final length (e.g. Cleary and Waring 1969, Garrett and Zahner 1973, Kozlowski et al. 1973).

In Fennoscandia, the positive effect of the previous year's midsummer temperatures on current year height increment of *Pinus sylvestris* L. (Scots pine) is widely accepted (e.g. Hesselman 1904, Laitakari 1920, Mikola 1950, Martynov 1978). Previous studies on the relationship between temperature and annual height increment of Scots pine in Fennoscandia have mainly dealt with seedlings growing in a controlled environment or are based on periods shorter than 10 years (Junttila and Heide 1981, Junttila 1986) and give minor emphasis on modelling of height growth. Mäkinen (1998) compared radial and height increment with a 70-year-long growth series measured from 28 trees in southern and central Finland. The measurements of our study cover height increment periods as long as 50 years, which also include extreme years and enables thorough statistical analysis of the data. Our empirical material originates near the northern timberline, where the growing season is relatively short and tree growth is usually determined by the temperatures of the high season of the summer (Hustich 1958). Jalkanen and Tuovinen (2001), and McCarroll et al. (2003) used a subset of the present study when comparing the applicability of different proxies to serve as climatic indicators. In addition, Salminen and Jalkanen (2004) used a subset from the present study when exploring the importance of the current-year temperatures on the height increment.

The aim of this study was to model the effect of temperature and precipitation on the height increment of Scots pine at high latitudes. The main questions were:

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?

2 Material and Methods

2.1 Empirical Material

Annual height increment was measured in 1995 and 1996 from five Scots pine stands located along a 400-km-long latitudinal transect from the Arctic Circle to the northern timberline in Finland (latitudes 66°35´–69°45´) (Fig. 1). The

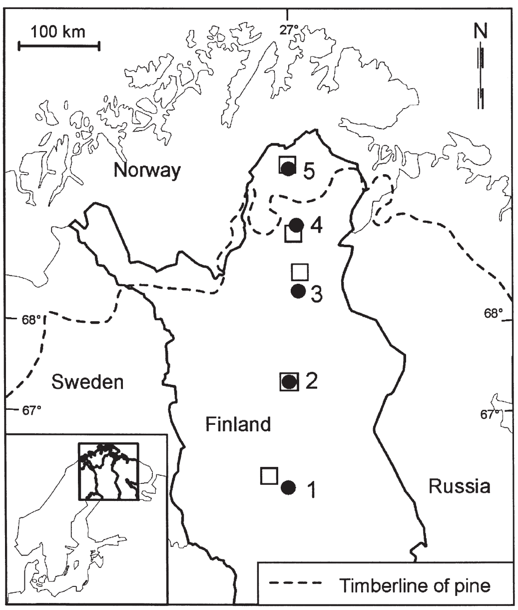

Fig. 1. Location of the experimental stands (●), weather stations (□), and northern timberline of Scots pine in Finland.

Table 1. Stand characteristics.

	Stand 1	2	3	4	5	
Locality	Rovaniemi	Sodankylä	Inari, Laanila	Inari, Kaamanen	Utsjoki, Kenesjärvi	
Latitude	66°22´	67°22´	68°30´	69°07´	69°40´	
Longitude	26°43´	26°38´	27°30´	27°15´	27°05´	
Altitude, m	150	180	220	155	110	
Vegetation type [a)]	EV	UVE	UEM	UVE	EV	
Species [b)]	*P. sylv.*	*P. sylv.*	*P. sylv.*	*P. sylv.*	*P. sylv.*	*B. pubesc.*
Number of stems ha^{-1}	1800	1950	1200	1450	1450	250
Basal area, $m^2 ha^{-1}$	15.4	16.8	9.0	10.1	14.1	1.1
Mean dbh, cm	10.2	10.1	9.4	9.1	10.2	7.4
Mean height, m	8.3	9.4	6.9	7.7	7.5	6.5
Dominant height, m	10.8	12.2	7.9	9.4	9.7	7.3
Total volume, $m^3 ha^{-1}$	72.7	90.3	37.6	45.6	64.3	3.9
Number of sample trees	9	10	10	10	10	-
Mean, min. and max. age of sample trees at breast height, yrs	33 29–35	51 43–55	34 31–37	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	11.0 10–14	10.2 8–13	-
Mean, min. and max. height of sample trees, cm	9.8 9.0–11.0	11.0 9.5–12.9	8.9 7.7–9.7	8.7 7.2–9.7	8.7 7.3–10.0	-

a) EV = *Empetrum-Vaccinium* -type, UVE = *Uliginosum-Vaccinium-Empetrum* -type, and UEM = *Uliginosum-Empetrum-Myrtillus* -type.
b) *P. sylv.* = *Pinus sylvestris, B. pubesc.* = *Betula pubescens.*

aim of the sampling method was to minimize the effects of site fertility between stands, and tree size and competition within stands. All the stands were growing on a dryish heath that is a typical site type for pine stands in Finland (Table 1). The soil type of stand 2 was more even and coarse, grain-size class 0.6–0.2 mm was dominant, and the soil type of stand 3 finer than that of the other three stands (Table 2). A total of 49 sample trees were selected from open-grown dominant trees that were not suppressed by competition and were visually assessed to be healthy with straight, unbroken stems and regular-shaped crowns. The mean height and breast-height diameter of sample trees in the stands were 8.7–11.0 m and 10.2–13.0 cm, respectively, and the stand mean age at breast height was 33–51 years, the oldest trees being in stands 2 and 5 (Table 1). Thus, the growth series of individual trees usually covered the period from the mid 1950's up to 1996. In December 1986, unusually low temperatures in stand 1 damaged roots, which caused severe needle loss during the next growing season (Jalkanen 1988, Ritari 1990, Jalkanen 1993). Later on, it also resulted in an increment loss in both diameter and height. Since the aim of our study was to model height-growth variation under normal conditions, the material from stand 1 was delimited to cover years before 1987.

Table 2. The grain-size proportions (percent by weight) of the soil of the five experimental stands.

Grain size class, mm	Stand 1 (% of weight)	2	3	4	5
<0.06	24	10	36	20	19
0.06–0.2	9	5	19	13	20
0.2–0.6	56	80	39	56	52
0.6–2	11	6	6	11	9

The sample trees were felled and analysed according to the Needle Trace Method, NTM (Aalto and Jalkanen 1998), which aims to produce consistent time series of annual needle dynam-

Table 3. Nutrient content of needles in year 2003.

	Stand				
	1	2	3	4	5
Ca, g/kg	3.17	2.33	2.24	2.00	2.28
K, g/kg	4.04	3.14	3.42	3.61	3.25
Mg, g/kg	1.21	1.19	1.13	1.06	1.32
P, g/kg	1.55	1.64	1.34	1.46	1.61
S, g/kg	0.83	0.96	0.89	0.85	0.90
Zn, g/kg	0.087	0.056	0.059	0.049	0.053
N, % of dry matter	1.18	1.27	1.31	1.29	1.40

Table 4. Weather stations and a description of climate in 1961–1990. Temp, average annual temperature; Prec., average annual precipitation; GS, average length of the growing season (threshold +5 °C); Temp.sum, average annual temperature sum (degree days, threshold +5 °C); July temp., average temperature of July.

	Station and locality				
	1	2	3	4	5
	Rovaniemi, Apukka	Sodankylä	Inari, Ivalo	Inari, Toivoniemi	Utsjoki, Kevo
Latitude	66°35´	67°22´	68°40´	69°04´	69°45´
Longitude	26°01´	26°39´	27°34´	27°07´	27°02´
Altitude, m a.s.l	106	179	123	152	107
Monthly data from	1939–	1908–	1957–	1959–	1962–
Temp. (°C)	–0.1	–1.1	–1.6	–1.5	–1.9
Prec. (mm)	528	446	433	428	370
GS (days)	131	126	122	117	109
Temp.sum. (d.d.)	914	777	740	698	647
July temp. (°C)	14.8	14.1	13.6	13.0	12.8
(range)	(12.3–18.5)	(11.1–18.1)	(10.0–17.8)	(9.5–17.9)	(9.2–17.1)

ics as well as height and diameter growth. The height increments were measured in the field from felled trees along the main trunk from 1.3 metres upwards. Crosschecking of annual rings and shoots were used to reveal possible leader changes that were already healed over and hidden inside the trunk. Obscure annual shoots were marked and collected for a recheck in the laboratory, where they were sawn up and analysed (Aalto and Jalkanen 1998). As compared to traditional height 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, 1978). The method also results in long time series in height increment, which have been rare so far.

For each stand, the records of the nearest weather station of the Finnish Meteorological Institute were used (Table 4). Meteorological measurements included monthly temperature and precipitation values covering the whole study period, except in the two northernmost stands where the three oldest trees had reached 1.3 m already before the year 1956 (stand 4) or 1947 (stand 5). The missing climate measurements were replaced by climate data based on the models of Ojansuu and Henttonen (1983). The average yearly temperature sum of the normal period

1961–1990 varied among the stands from north to south from 647 to 914 degree days (Table 4). The stand altitudes varied between 110 and 220 metres (Table 1). From 1961 to 1996, the mean temperature of November had slightly decreased and March increased. The mean temperatures of December and January have increased from the mid 1980's, but they are still within the range of the long-term variation. In general, the variation of the mean temperature of winter months is larger than that of summer months.

Evapotranspiration and the effect of snowmelt on water balance were calculated using the WATBAL model (Starr 1999). WATBAL is a monthly water-balance model that uses a modified Jensen-Haise radiation equation to estimate evapotranspiration and an air temperature-index method to estimate snowmelt (Starr, personal communication). WATBAL requires monthly cloudiness indexes (tenths of sky covered), which were not available for the whole study period. The missing values were replaced by value 7. To achieve an approximation of the annual net water balance (P_{adj}), original measurements of precipitation were adjusted as follows:

$$P_{adj} = P - E + S \quad (1)$$

where P is measured precipitation, E is modelled actual evapotranspiration and S is modelled snow melt.

2.2 Statistical Analysis

The climatic response of height increment was modelled in three phases (Fig. 2a). In the first phase, standardized height-increment chronologies, both an overall mean chronology and stand chronologies, were calculated by a multilevel mixed effects model of height increment (cf. Henttonen 1990, Miina 2000). The whole empirical material was used in calculations. The fixed part of the model was used to remove the growth trend due to tree age. The random part of the model can be regarded as a 3-level model where annual height-increment measurements are level-1 observations (shoot level). Each measurement occasion is nested within a tree at level-2 (tree level), and trees are nested within a stand at level-3 (stand/year-level) (Fig. 2b). The measurements are also correlated within a year, which means that measurements of a certain year have something in common. The general model applied in the standardization was:

$$\log(Y_{ijt}) = \beta_0 + X_{ijt}\beta + z_i + u_j + w_t + k_{it} + v_{(i)jt} + \varepsilon_{ijt} \quad (2)$$

where Y_{ijt} is the height increment of tree j of stand i in year t; β_0 is a constant (mean increment), $X_{ijt}\beta$ is the fixed part of the model, z_i is a random stand effect, u_j is a random tree effect, w_t is a random year effect, k_{it} is a random interaction of year t and stand i, and $v_{(i)jt}$ is the autocorrelated error term of tree j within stand i in year t, and ε_{ijt} is the residual error term. In the beginning, an empty model ("null model") without $X_{ijt}\beta$ was used to get estimates for the fraction of variation at each level of the model (Snijders and Bosker 1999).

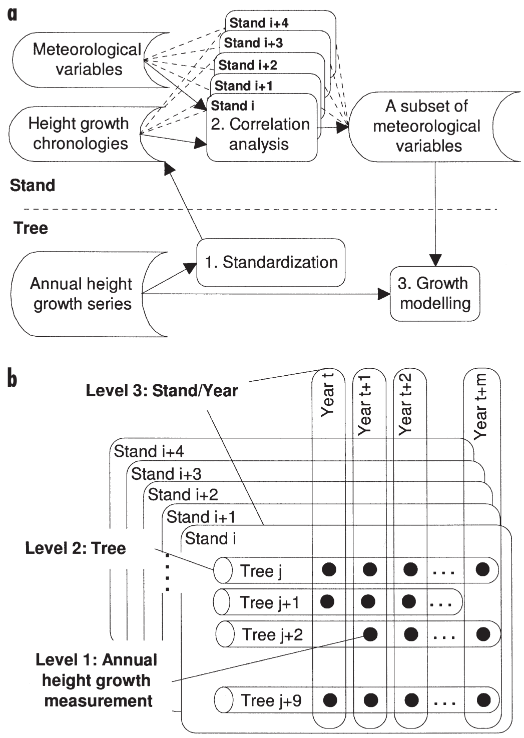

Fig. 2. a) The three phases of data analysis: 1. standardization, 2. cross-correlation, and 3. growth modelling. b) The structure of the data: three hierarchical levels with crossed year effect.

After adding a 2nd degree polynomial function of tree age as an explanatory variable, the estimates for w_t+k_{it} were used as height growth chronology for each stand.

In the second phase, the dependence of each stand height-growth chronology on the respective monthly meteorological variables of the current and two preceding years (lag 0, 1 or 2) was examined by cross-correlation analysis (SAS User's Guide 1992a). Temperature series were centered, detrended and prewhitened if unit root or white noise tests indicated that the series included statistically significant trends or autocorrelation.

In the third phase, those meteorological variables that were found to be statistically significant were further studied by using them as explanatory variables in the term $X_{ijt}\beta$ of Eq. 2 according to their statistical significance and contribution to the overall fit of the model. The latter was determined by likelihood value and the Akaike information criterion (Littell et al. 1996). Residuals were analysed both graphically and with time-series approach throughout the modelling process with an emphasis on yearly variation. Like in the first phase, the whole empirical material was used together. This time, the estimates for w_t+k_{it} were considered as yearly variation unexplained by selected climatic variables. The possible interactions between tree age and weather variables were studied. Models were fitted with SAS MIXED procedure (SAS User's Guide 1992b, Singer 1998). When back-transforming the results from logarithmic to normal scale, a bias correction was added (Flewelling and Pienaar 1981). The relative change of random variance components, i.e. z_i, u_j, w_t, k_{it}, $v_{(i)jt}$, and $\varepsilon_{\mathrm{ijt}}$, due to $X_{ijt}\beta$ was used as an estimate of the proportion of explained variance (Snijders and Bosker 1999).

3 Results

3.1 Cross-correlation Analysis

The correlation between the mean July temperature of the previous year ($\mathrm{TJUL_{LAG\ 1}}$) and height increment was statistically significant in all the stands (Fig. 3). In the northernmost stands (3, 4, and 5), correlation between height increment and the previous summer temperatures (June, July and August) was higher than in the two southernmost stands. In stand 3, also the current June temperature had a positive correlation with height increment. Mean November temperature two years earlier ($\mathrm{TNOV_{LAG\ 2}}$) had a negative correlation with the height increment, this being statistically significant in the three northernmost stands. The mean February temperature of the current year had a statistically significant negative correlation with the height increment in stand 1. The correlations between height increment and precipitation (with or without adjustment) were non-significant. The correlation between potential evapotranspiration and height increment was similar to the correlation between temperature and increment (results not shown). The possible indirect effects due to correlations between climatic variables were studied by cross correlating them. In this meteorological data, the mean February temperature of the current year happened to have a statistically significant correlation with the mean July temperature of the previous year.

3.2 Height-increment Models

The final height-increment model based on all stands included tree age, the long-term mean temperature sum of the site (degree-day average), and $\mathrm{TJUL_{LAG\ 1}}$ (Table 5). There was a significant polynomial age-effect, with maximum annual height increment being achieved on average at 23 years breast-height age. The autoregressive correlation coefficient (0.47) was statistically significant. The positive effect of $\mathrm{TJUL_{LAG\ 1}}$ on log-transformed height increment was clear and linear. The slope of $\mathrm{TJUL_{LAG\ 1}}$ was same in all the stands. The inclusion of mean temperature of previous June or August temperature, either as separate variables or replacing $\mathrm{TJUL_{LAG\ 1}}$ with mean June–August temperature, disimproved the fit of the model. The mean November temperature of the year before the previous year ($\mathrm{TNOV_{LAG\ 2}}$) had a statistically significant negative effect on height increment of the current year, but only when $\mathrm{TJUL_{LAG\ 1}}$ was not included. Therefore, $\mathrm{TNOV_{LAG\ 2}}$ was omitted from the final model.

The model was back-transformed to normal scale and differenced in order to describe the

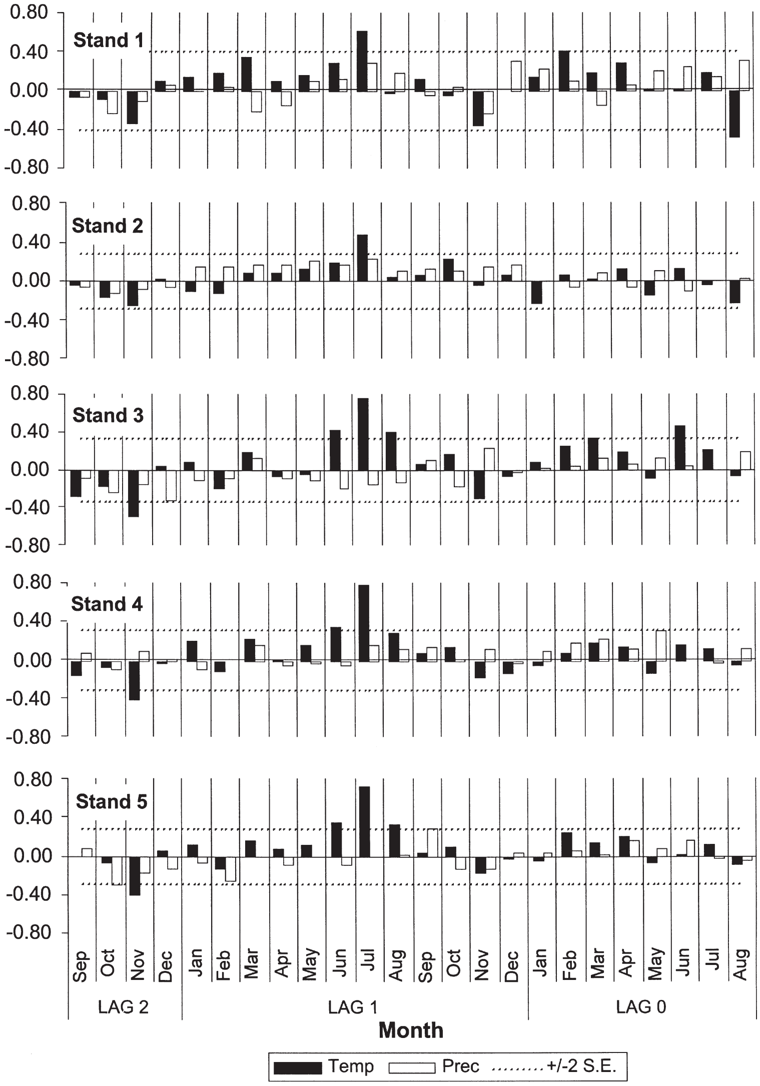

Fig. 3. Correlation between height increment of *Pinus sylvestris* and the mean monthly temperature and monthly precipitation at northern boreal zone. LAG 0 denotes the growth year, LAG 1 the previous year, and LAG 2 the year before the previous. Dotted horizontal lines delineate ± 2 standard error (95%) confidence interval of correlation coefficients.

sensitivity of the model to changes in $TJUL_{LAG\ 1}$. The other explanatory variables were fixed to their average values. The first derivative of the model with respect to $TJUL_{LAG\ 1}$ yields values from 1.5 to 2.2 cm within the measured July temperature range (see Table 4). In simplified terms, the effect of one degree change in the average mean July temperature on the next year's height increment is 1.8 cm and the temperature range of $TJUL_{LAG\ 1}$ results in height-increment range of 15 to 32 cm.

The fraction of variance at the within-tree-level of the empty model (a model without fixed explanatory variables) was 0.49 (Table 5), while

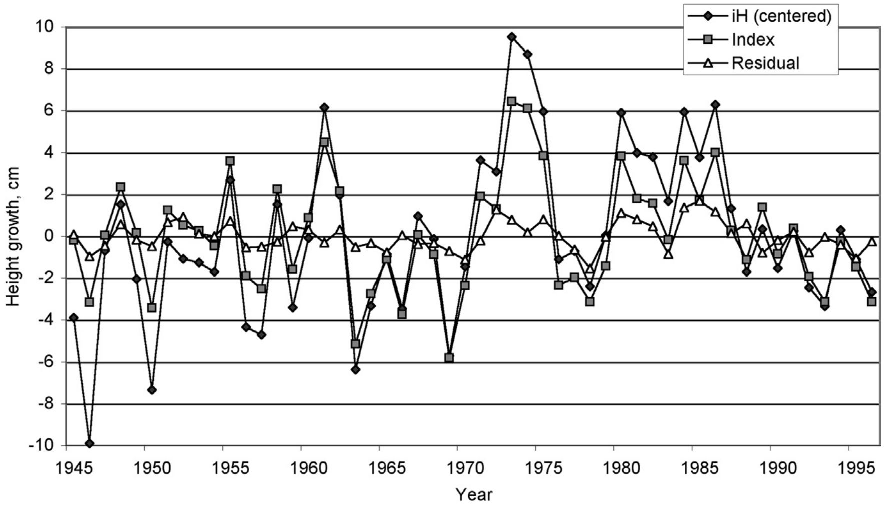

Fig. 4. Measured height growth (iH), height growth indices (Index), and residual annual variation of height increment (Residual) of *Pinus sylvestris*. iH is the annual average of all the stands, and it is centered around zero. Index is w_t of Eq. 2 with climate variables (standardization phase). Residual is w_t of Eq. 2 with climate variables included (growth modelling phase).

Table 5. Summary of parameter estimates of height growth models. SE denotes standard error. The dependent variable is 10*log(1+iH/19.86), where iH is annual height growth, cm. Temp.sum denotes average annual temperature sum (degree days, threshold +5 °C), and $TJUL_{LAG\ 1}$ the mean temperature of previous July. The fraction of variance at each level is calculated using random effect estimates of the empty model. The proportion of explained variance at each level due to the climate variables is calculated as described by Snijders and Bosker (1999).

	Empty model		Add tree age		Add climate variables	
	Value	SE	Value	SE	Value	SE
Constant β_0	6.79	0.47	6.44	0.52	–4.88	1.72
Fixed effects $X_{ijt}\beta$						
Tree age/47	-	-	2.52	0.98	3.60	0.87
Tree age^2/1400	-	-	–1.72	0.59	–2.29	0.54
Temp.sum/647	-	-	-	-	4.61	1.43
$TJUL_{LAG\ 1}$/13.5	-	-	-	-	5.67	0.56
Random effects						
Level-3: stand, z_i	0.99	0.74	1.03	0.77	0.15	0.15
Level-3: year, w_t	0.73	0.19	0.67	0.17	0.11	0.06
Level-3: stand × year, k_{it}	0.49	0.10	0.45	0.09	0.41	0.09
Level-2: tree(stand), u_j	0.09	0.05	0.09	0.05	0.09	0.05
Level-1: error, ε_{ijt}	1.78	0.09	1.80	0.09	1.83	0.10
Autocorrelation AR(1), $v_{(i)jt}$	0.46	0.03	0.46	0.03	0.47	0.03
	The fraction of variance		The proportion of explained variance		The proportion of explained variance	
Level-3: stand	0.24		0%		84%	
Level-3: year + stand × year	0.30		1%		74%	
Level-2: tree	0.02		3%		66%	
Level-1: within-tree	0.44		1%		37%	

the between-tree-within-stand variation was small (0.02). The fraction of variance at year level was 0.27 (includes year × stand interaction) and at stand level, 0.22 (Table 5).

As compared to the empty model, the proportion of explained variance at year level was 74% (Table 5). The original measured year-level variation in the empty model was just noticeably larger than the variation of w_t in Eq. 2 in the standardization model, but inclusion of climate variables reduced the w_t substantially (Fig. 4). The level-1 and level-2 residual variance components were at the same level in all model versions.

4 Discussion

The height-growth material used covered a period of 40 years on average and was very accurate because possible leader changes and other irregularities could be discovered (Aalto and Jalkanen 1998). The experimental stands were located in a 400 km-long transect from the Arctic Circle to the northern timberline, resulting in some variation in site fertility. However, the aim of the sample-tree selection was to eliminate within-stand variation. Thus, the main emphasis of our study was on stand-level development. Daily meteorological data was not measured directly in the experimental stands but the weather stations near to each stand. This causes inaccuracy, at least in precipitation, but presumably not in temperature, as indicated by the highly significant correlation of the temperature data between the five climate stations.

The response of physiological processes to temperature is non-linear, at least if the temperature range is wide (Ford 1980). In the northern boreal forests, temperature is usually a minimum factor for tree growth (Junttila and Heide 1981). It is usually below the range where, e.g., increasing vapour deficit reduces net production. Thus, the linear relation of temperature and growth found in the present study is rational (cf. Fries et al. 2000).

The essential impact of the mid-summer temperature on the next season's height increment was in line with previous studies (e.g. Hesselman 1904, Laitakari 1920, Mikola 1950, Martynov 1978). Junttila and Heide (1981) found that, in northern Fennoscandia, correlation between height increment and the mean June–August temperature of the previous year ($TJUN_{LAG\ 1}$–$TAUG_{LAG\ 1}$) was higher than that between height increment and the mean July temperature ($TJUN_{LAG\ 1}$). In our study, the mean July temperature yielded higher correlations than any combination of mean temperatures of the previous summer months. The importance of July is due to its central role in bud formation and its major contribution to the total temperature sum and net photosynthetic production at tree line. The current summer did not significantly correlate with the final shoot elongation, except in stand 3, where the correlation of June was statistically significant in the cross-correlation analysis. The height increment in stand 3 had higher correlation to mean monthly temperatures than in the other stands. Trees in stand 3 are vigorous and growing well considering the northern location. In the other four stands, there are obviously other growth-limiting factors besides summer temperature.

The mean November temperature in the year before the previous year had a negative effect on height growth in the tree northernmost stands. 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. Drought is not 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). Also the short summers are seldom so warm that drought appears.

The response of height increment to monthly temperature and precipitation was weaker in the two southernmost stands as compared to the northern ones. Stands 3, 4 and 5 are located near the northern timberline, where the summer temperature is clearly a critical minimum factor. In the two southernmost stands there are some latent limiting causes. Although stand 2 was quite dense, the latent factor may arise from slightly more coarse soil. It is also probable that the importance of temperature decreases and the effect of precipitation increases southward (cf. Kellomäki 1995, Mäkinen 1998). These hypotheses should be verified in the forthcoming studies.

The stands were examined together although many relevant factors affecting growth processes were not available. As Junttila and Heide (1981) noted the difference between stands is ascribed to climatic as well as genetic and/or edaphic factors. Therefore, including all the stands in the same model and explaining the difference between the stands solely by annual temperature and precipitation series can lead to misinterpretations. To avoid this and focus more on variation between years, the long-term average temperature sum of each stand was used as a covariate. Independent variables of the final increment model can be classified as time-dependent level-1 variables (tree age), time-independent level-3 variables (long-term temperature sum), and time-dependent level-3 variables (mean monthly temperatures). There was only one level-1 variable and no level-2 variables. Therefore, it was expected that the proportion of explained variance would be higher on level-3 than on the lower levels. If lower level variation is studied, the small-scale spatio-temporal variation in nutritional status, radiation and water deficit should be apparent.

In conclusion, the temperature of the previous mid-summer (lag 1) is the main controller of height growth of pine in northern Finland. July mean temperature of the previous year and the long-term mean temperature sum (degree-day average) explained 74% of the year-level variance of height increment. Warm period in late autumn before winter dormancy in the year before the previous one has a negative effect on shoot elongation near the timberline. The climate of spring and early summer showed some small and statistically non-significant positive effect on height increment. Height increment of the two southernmost stands yielded lower correlations to mean monthly temperatures than their northern counterparts. Whether this is a common north-south difference remains to be verified in the forthcoming studies.

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