

Modelling Variation of Needle Density of Scots Pine at High Latitudes

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The relationship between apical extension and needle density and the effect of temperature and precipitation on needle density was modelled using data gathered from forty-nine felled sample trees in five stands of Scots pine (*Pinus sylvestris* L.) located along a latitudinal transect from the Arctic Circle up to the northern timberline. The lengths were measured and needle densities assessed from all annual shoots located above 1.3 metres using the Needle Trace Method (NTM), resulting, on average, in 39-year-long chronologies.

The mean overall needle density was 7.8 short shoots per shoot centimetre. Needle-density variation in the measured data was mostly due to within-tree differences. Of the total variance, within-tree variation yielded 46%, between-tree 21%, and between-year 27%. The dependence of needle density on annual height growth was studied by fitting a multilevel model with random stand-, tree- and year-intercepts, the independent variables being tree age and height growth. There was a very strong negative correlation between height growth and needle density, and the proportion of between-year variance explained solely by height growth and age was 50%. The stand-wise residual variations 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 found 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. The effect of late winter and early 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.

Keywords dendroclimatology, temperature, precipitation, fascicles, needles, NTM, *Pinus sylvestris*

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1 Introduction

Trees react to environmental changes through growth and senescence processes in order to balance their structure and function. In conifers, shoot growth and changes in needle mass, i.e. production of new and shed of old needles, are easily observed reactions. Needle density is a measurable attribute arising from the proportion of needle production and shoot elongation (Jalkanen et al. 1998). Length of an annual shoot and the number of needles it bears affect visual appearance but also reflect the resource allocation of a tree, and reveal extraordinary years caused by extreme climatic conditions or catastrophic events such as insect or pathogen attack. Regarding resource allocation, height growth is strategically important if shading and the amount of incoming sunlight are critical factors, but the production of new needles is crucial for the photosynthetic production and functional balance of the tree. Hence, it can be hypothesized that the total amount of needle-mass produced each year in normal circumstances should vary less than height growth.

As on most northern pine species, the needle production and height growth of Scots pine (*Pinus sylvestris* L.) are closely related and predetermined processes; the terminal bud, carrying growth initials, is formed during the growing season prior to the actual growth year (Doak 1935, Lanner 1976). During the bud formation, the shoot apical meristem initiates all the major structures that will appear in the elongated shoot, including bud scale primordia and spirally arranged leaf (needle) primordia. Doak (1935) called these structures stem units. They could be fertile units such as branch bud, short shoot, cone, and seed scale, or sterile units such as bud scale and bract.

The number of stem units is fixed during the bud formation, but environmental conditions during shoot elongation may affect internode's length. The total number of short shoots is therefore predetermined but short-shoot density, i.e. the number of short shoots per shoot length (=needle density), is a result of the number of short shoots and the final length of the elongated shoot. Needle density and needle production may be used to approximate mean stem-unit length and the number of stem units, respectively.

Short shoots of Scots pine usually have two leaves (needles) per fascicle. In northern Finland, three needles per fascicle may occur, especially the near-the-node fascicles. Needle is often used synonymously with dwarf shoot in such terms as 'needle density' (Ladell 1963). Needle density is usually defined as the number of fascicles per shoot centimetre after height-growth accomplishment. According to its definition, needle density reflects the proportions of resource allocation to new needle mass on the one hand and to height growth on the other hand. When considering the total needle mass and needle area, in addition to the number of needles, their size should also be accounted for.

The Needle Trace Method (NTM, Kurkela and Jalkanen 1990) is based on determining the length of the primary xylem connecting the living short shoot and the shoot pith. When a short shoot dies, it stops growing by length. This indicates the actual age of the short shoot (Kurkela and Jalkanen 1990). The measurements are based on samples from each annual shoot of the main trunk of a tree. The sample bolts are planed tree ring by tree ring, towards the pith of the shoot, and the number of living needles in each ring is recorded (Aalto and Jalkanen 1998, Kurkela and Jalkanen 1990). As a result, NTM enables studies of needle dynamics by providing empirical time-series of needle production, needle shed and needle density (Jalkanen et al. 1998).

Before the invention of NTM, needle production and needle density studies were usually more or less descriptive and based on only a few measurement occasions (e.g. Ladell 1963, Clements 1970, Garrett and Zahner 1973). Reports based on NTM and dealing with needle density have been published since the late 1990s (Jalkanen et al. 1998, Konôpka et al. 2000, Pouttu and Dobbertin 2000, Jalkanen and Levanic 2001, Fedorkov 2002, Pensa and Jalkanen 2005).

The main questions of our study 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 differently than height increment?

The description of annual needle density variation can be applied in dendroclimatology and

forest health monitoring, as well as in studies of long-term growth dynamics and resource allocation of Scots pine, especially when combined with models of annual height growth.

2 Material and Methods

Based on NTM (Kurkela and Jalkanen 1990), the data was gathered from forty-nine sample trees in five stands located along a latitudinal transect from the Arctic Circle up to the northern timberline in Finland (Fig. 1, Table 1). The height increments were measured in the field from the branch whorls of the main trunks of the felled trees from a height of 1.3 metres up to the top of the tree. Crosschecking of annual rings and shoots was used to reveal possible leader changes that were already healed over and hidden inside the trunk. Obscure annual shoots were cut up and analysed; also, yearly needle densities of each shoot were assessed in the laboratory (Aalto and Jalkanen 1998). The quality and uniformity of the needle-

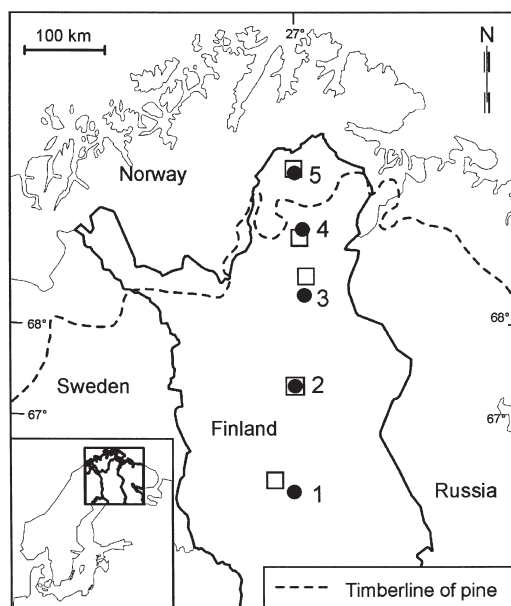


Fig. 1. Location of the experimental stands (●), weather stations (□) and timberline of Scots pine in Finland.

Table 1. Stand characteristics.

Stand Locality	1 Rovaniemi	2 Sodankylä	3 Inari, Laanila	4 Inari, Kaamanen	5 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 a.s.l.	150	180	220	155	110	
Vegetation type ^{a)}	EV	UVE	UEM	UVE	EV	
Species ^{b)}	<i>P. sylv.</i>	<i>P. sylv.</i>	<i>P. sylv.</i>	<i>P. sylv.</i>	<i>P. sylv.</i>	<i>B. pubesc.</i>
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	33	51	34	42	46	-
of sample trees at breast height, yrs	29–35	43–55	31–37	39–45	42–53	-
Mean, min. and max. dbh	13.0	12.1	12.0	11.0	10.2	-
of sample trees, cm	10–16	11–14	10–14	10–14	8–13	-
Mean, min. and max. height of sample trees, cm	9.8	11.0	8.9	8.7	8.7	-
	9.0–11.0	9.5–12.9	7.7–9.7	7.2–9.7	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*.

Table 2. Weather stations and a description of climate in 1961–1990. Abbreviations: 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).

Station Locality	1 Rovaniemi, Apukka	2 Sodankylä	3 Inari, Ivalo airport	4 Inari Toivon niemi	5 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 since	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. (dd.)	914	777	740	698	647

density series were further analysed with the program COFECHA (Holmes 1983). Because the trees were not exactly even-aged, there were also differences in the length of the tree-wise records. When comparing the stands with respect to mean needle density and mean height growth, a balanced subset from years 1969–1996 was selected. Otherwise, the whole data set was used.

For each stand, the records of the nearest weather station of the Finnish Meteorological Institute were used (Table 2). Meteorological records 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 metres already before the year 1956 (stand 4) and before 1947 (stand 5). The climate records were extended with the models of Ojansuu and Henttonen (1983).

Evapotranspiration and the effect of snow-melt 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 (Jensen and Haise 1963) to estimate evapotranspiration and an air temperature index method to estimate snow-melt (Starr, personal communication). In addition to other input data, WATBAL requires monthly cloudiness values (tenths of sky covered), which were available since the year 1961 in stands 1–4 and since 1962 in stand 5. The missing earlier values were replaced by an average 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.

The dependence of needle density on annual height growth was modelled by fitting a multilevel mixed effects model using MIXED procedures of SAS version 8.2 (SAS User's Guide 1992). Parameters for each stand were achieved simultaneously by allowing the estimation of random stand-wise intercepts and slopes. The general form of the model is:

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

where Y_{ijt} is the needle density 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 ε_{ijt} is the residual error term. Within-tree observations were assumed to be first-order autocorrelated. 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). After adding height increment and a 3rd degree polynomial function of tree age as explanatory variables,

the estimates for $w_t + k_{it}$ were used as standardized needle-density chronology for each stand. Graphical pre-modelling examination suggested that the dependence between height increment and needle density is non-linear. Therefore, height increment was introduced as $ae^{b/iH}$, where iH is height increment, and a and b are parameters. This linearized transformation of a non-linear model was used in order to allow the estimation of a multilevel model. Current statistical software packages support only two-level non-linear models, while levels of linear models are basically not restricted, and in this case, the random part of the model can be regarded as having 3-levels (Salminen and Jalkanen 2005).

In the next phase, the dependence of each stand's needle-density chronology on the respective monthly meteorological (climatic) variables of the current and two preceding years (lag 0, 1 or 2) were examined by cross-correlation analysis (SAS User's Guide 2000). Temperature series were centered, detrended and prewhitened if unit root or white noise tests indicated the series to have statistically significant trends or autocorrelation.

In the final phase, statistically significant climatic variables were further studied 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). Graphical residual diagnostics were employed 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 climatic variables were studied. Models were fitted with SAS MIXED procedure. The relative change of random variance components, i.e. z_i , u_j , w_t , k_{it} , and ε_{ijt} , due to $X_{ijt}\beta$ was used as an estimate of the proportion of explained variance (Snijders and Bosker 1999).

3 Results

The mean overall needle density was 7.8 fascicles per shoot centimetre, the normal range being between 5 and 15 (Table 3). The highest measured individual value was 55, while the smallest density value was 3.1. There were four occasions when measured needle-density of a shoot exceeded 20 fascicles per shoot centimetre; these occurred in the three northernmost stands in the years 1963, 1969 and 1978. The variation of annual mean needle densities in different stands was not similar but had common pointer years, e.g. 1978, 1981 and 1990 (Fig. 2). There were

Table 3. Mean needle density and height growth of the stands and the whole material. Minimum and maximum values of individual observations, tree means, and yearly means.

	Stand					Total
	1	2	3	4	5	
Needle density						
Stand mean	7.3	7.6	6.9	8.5	8.2	7.8
st.dev.	2.1	2.1	3.3	2.4	2.9	2.6
min.–max. obs.	4–20	4–17	3–55	4–33	4–36	
Tree mean min.–max.	6–9	6–9	5–8	6–10	6–9	
Year mean min.–max.	5–11	6–12	5–21	6–11	6–14	
Height growth						
Stand mean	26.2	19.2	22.4	17.6	15.7	19.6
st.dev.	8.4	6.3	7.9	5.9	6.7	7.8
min.–max. obs.	7–47	3–40	3–44	2–37	1–39	
Tree mean min.–max.	24–31	16–23	20–26	11–18	7–14	
Year mean min.–max.	15–39	9–27	8–35	11–27	7–27	

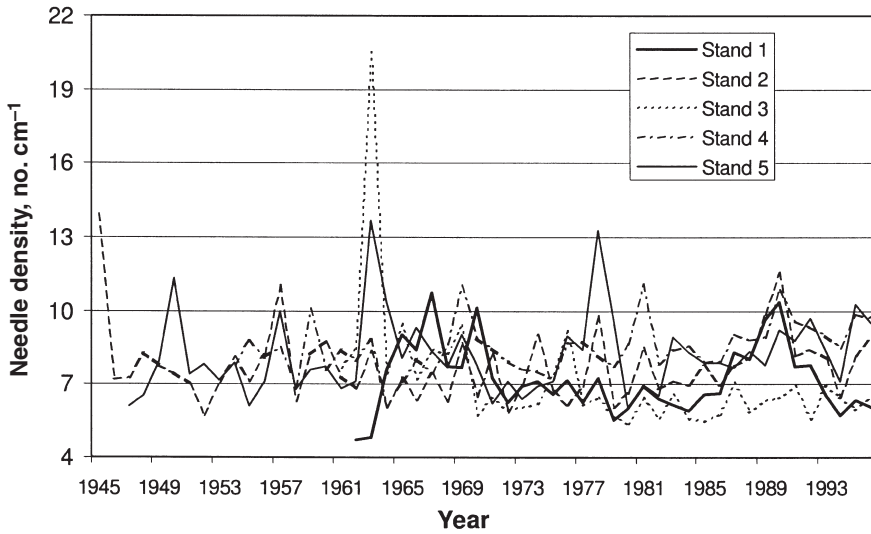


Fig. 2. Mean annual needle density of the five experimental stands.

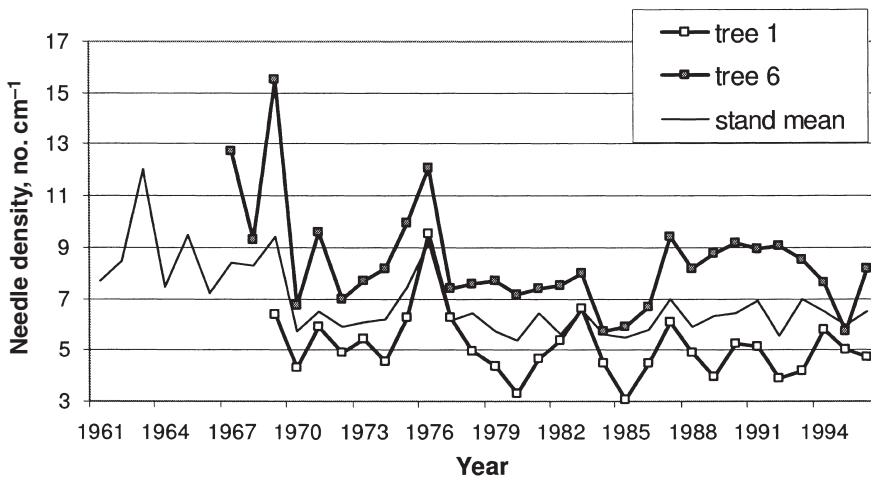


Fig. 3. Example of tree-wise needle densities; stand 3. Needle density of tree 1 is low (average 5.1, standard deviation 1.3), whereas tree 6 yields constantly higher densities than the other trees (average 8.4, standard deviation 2.1).

clear differences between individual trees with respect to the mean needle density; some trees had constantly lower needle density levels than others. For example, needle density of tree 1 in stand 3 is low, whereas tree 6 in the same stand yields constantly higher-than-average densities (Fig. 3). The trees with a relatively high density level also had more year-to-year variation, with occasional peak values and lower-than-average

height growth. The needle-density series of trees within the same stand became more coherent southwards; when analyzing the balanced subset of the data (years 1969–1996) with program COFECHA, the mean correlation of individual trees with the stand-wise 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

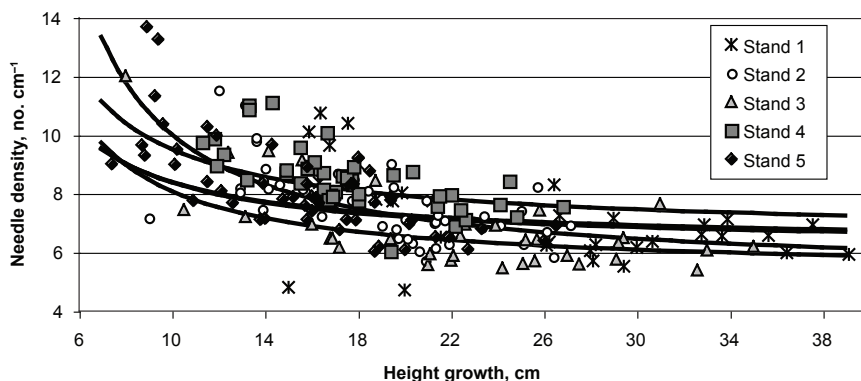


Fig. 4. The relation between needle density and height growth.

had at least one tree that did not correlate significantly with the needle-density series of any other tree in the stand.

The dependence of raw (non-transformed) needle density on climatic variables like monthly temperature and precipitation was similar to that which Salminen and Jalkanen (2005) found for height increment, but the correlation coefficients were clearly lower. In general, the variation was lower for needle density than for height growth, and they related negatively. Furthermore, the dependence between needle density and height growth was non-linear; exceptionally high needle densities coincided with low height growth. When height growth was within its normal range, needle densities were also rather stable (Fig. 4).

The needle-density variation caused by height increment and tree age was removed with a multi-level model. The year-level residual of the model represents a standardized needle-density chronology. When compared to the original measured needle density, there is less variation, which means that height-growth variation affected the original needle-density fluctuation, to a limited degree, however (Fig. 5). When analysing the balanced subset of the data (years 1969–1996) and using height growth as a covariant, the between-stand differences of needle density were not statistically significant.

The stand-wise needle-density chronologies were cross-correlated with the monthly values of corresponding temperature, precipitation and adjusted precipitation. The correlation coefficient

values were rarely statistically significant. The only consistent sign present in all stands was a statistically significant negative correlation between needle density and the precipitation of April–May of the current year in the three southernmost stands (Fig. 6). In addition, the June temperature of the previous year had statistically significant positive correlations in stands 2 and 4.

The fixed part of the final needle-density model includes height increment and tree age (Table 4). April or May precipitation alone were not statistically significant variables, but when precipitation of April–May was used as an independent variable in the southernmost stands, and precipitation of May in stands 4 and 5, this new variable exceeded the significance criteria ($p < 0.05$). Nevertheless, the statistical significance of April–May precipitation was only modest and it improved the fit of the model only slightly. In addition, the contribution of this variable to the total performance of the model was somewhat questionable, because it was actually effective only in the three southernmost stands. Therefore, the model with height increment and tree age as independent variables is preferred.

Needle density decreased with respect to tree age, especially during the juvenile phase and started to increase after the turning point at the breast-height age of 19 years, but the magnitude of the age-effect was rather small, about ± 0.5 fascicles cm^{-1} for the whole study period. The autoregressive correlation coefficient (0.11) was statistically significant. The inclusion of precipita-

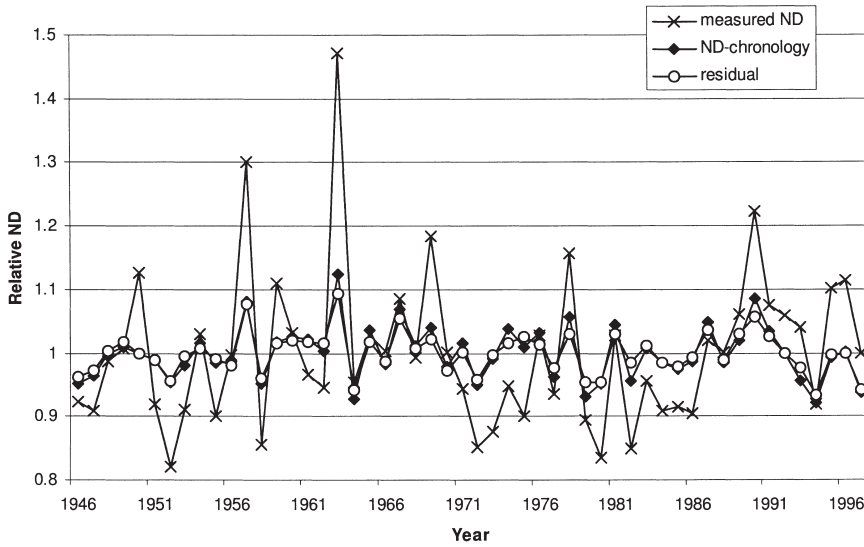


Fig. 5. The measured mean needle density (measured ND), needle-density chronology after age- and height growth effect was removed (ND-chronology), and residual variation after the climatic independent variable was also included (residual). All three series are centered around 1.

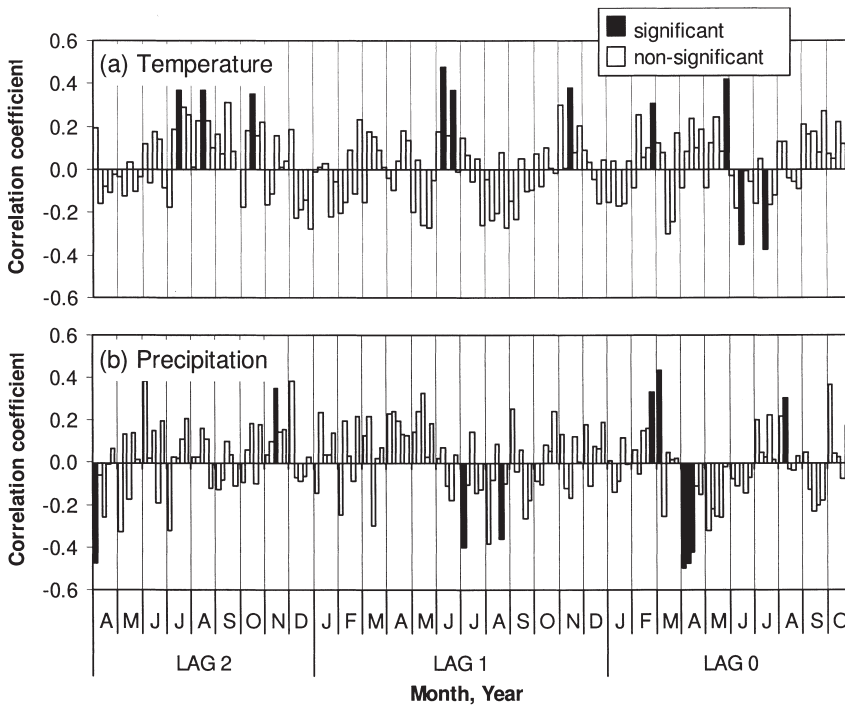


Fig. 6. The correlation of stand-wise needle-density index and monthly mean temperature (a) and the correlation of stand-wise needle-density index and monthly mean precipitation (b). Bars within month column represents correlation coefficients of stands 1, 2, 3, 4 and 5. The years are denoted with LAG 0 (current year), LAG 1(previous year), and LAG 2 (year before the previous one).

Table 4. Summary of parameter estimates of needle-density models (the final model with bold face type) The dependent variable is $10 \cdot \log(\text{ND})$, where ND is needle density, no./cm. Age is measured at breast height. Constant b is 3.19, and iH is height increment in centimetres. 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 independent variables is calculated as described by Snijders and Bosker (1999).

	Empty model		Add tree age and height increment		Add climate variable	
	Value	SE	Value	SE	Value	SE
Constant β_0	20.05	0.40	18.97	0.45	19.52	0.47
Fixed effects $X_{ijt}\beta$						
tree age	—	—	-8.29	2.29	-8.47	2.28
tree age ² /10	—	—	9.70	3.06	9.92	3.06
tree age ³ /1000	—	—	-3.19	1.31	-3.31	1.31
b/iH	—	—	8.41	0.37	8.38	0.37
April–May precipitation ^a /80	—	—			-0.96	0.34
Random effects						
Level-3: stand, z_i	0.52	0.53	0.26	0.32	0.21	0.28
Level-3: year, w_t	0.48	0.21	0.33	0.13	0.24	0.12
Level-3: stand \times year, k_{it}	1.60	0.25	0.69	0.13	0.71	0.13
Level-2: tree(stand), u_j	1.61	0.37	1.51	0.34	1.50	0.34
Level-1: error, ε_{ijt}	3.59	0.14	2.85	0.11	2.85	0.11
Autocorrelation AR(1), $v_{(ijt)}$	0.16	0.03	0.11	0.03	0.11	0.03
		The fraction of variance		The proportion of explained variance		The proportion of explained variance
Level-3: stand		0.07		50%		59%
Level-3: year + stand \times year		0.27		50%		55%
Level-2: tree		0.21		34%		36%
Level-1: within-tree		0.46		28%		29%

^a) In stands 4 and 5, only May precipitation was accounted for.

tion of April–May barely decreased residual error variance when compared to the model with only height increment and tree age as independent variables. Instead, between-year and between-stand residual variation decreased (Table 4). This also results in smaller annual residual variation in needle-density chronology, but there is only a minor improvement, i.e. less year-to-year variation (Fig. 5).

4 Discussion

The use of the needle-trace method enables studies of annual fluctuations of needle density for the life-time history of the tree (Jalkanen et al.

1998). The current study is based on needle-density samples taken from the middle of each annual shoot of the main trunk. This may lead to underestimation of needle density because it is often highest at the upper end of the shoot. On the one hand, normal NTM samples are about 15 cm long (Aalto and Jalkanen 1998), which covers most of the length of the studied shoots, especially in the northernmost sites. On the other hand, the sampling method allows the examination of the annual variation, which was the main issue of our study.

Ladell (1963) used information from two growing seasons to conclude that needle density of Corsican pine (*P. nigra* Arnold) is more or less independent of internode length. Clements' (1970) findings were partly in contrast to

Ladell's; the correlation between fascicle density and shoot length of red pine (*P. resinosa* Ait.) was negative and non-linear. Our study confirms the conclusions of Clements (1970); there was a strong negative correlation between annual height increment and needle density. Similar results have previously been found by Jalkanen et al. (1998). However, the tree-wise dependence of long-term mean needle density on long-term mean height growth was weak but still statistically significant. The long-term mean density is partly due to differences in height growth but may also reflect the photosynthetic efficiency of a tree. In the final modelling phase, tree-level variables such as micrometeorology or topology, which may have explained between-tree variation, were not available.

The trees in the current study had a polynomial age-dependent needle-density trend that was negatively correlated with (reversal to) annual height increment (Fig. 4). The tree-age and the height-growth variation explained half of the annual needle density variation (Table 4). Pouttu and Dobbertin (2000) found that needle density increases with age, but their material was from older trees than in the current study, and the age-dependent effect of declining height increment caused increasing needle densities.

Exceptionally high needle-density values result from disturbances of height growth typical in the juvenile phase of pines at high latitudes (Jalkanen 1985). Otherwise, each tree seemed to have a certain level of needle density, and the annual variation around the tree-wise mean was mainly dependent on changes in height increment. Also Ladell (1963) found that needle density is a feature characteristic to an individual tree, i.e. some trees tend to have constantly higher needle densities than others in the same stand.

Jalkanen et al. (1998) who also acquired their data from a Scots pine stand at high latitude, measured a mean needle density of 10.5 at stand level. Based on an experimental stand in Slovenia, Jalkanen and Levanic (2001) found a mean needle density of Scots pine of 6.9. According to Fedorkov (2002), in the Komi Republic, Russia, the mean needle density in 1967–1988 was 7.3 and the yearly minimum (6.2) and maximum (9.2) values were found in 1984 and 1972, respectively. Pouttu and Dobbertin (2000) found that the mean

annual needle density in the Rhone Valley of Switzerland varied between 6.1 and 11.4. Konôpka et al. (2000) studied needle retention on Japanese black pine (*P. thunbergii* Parl.) and Japanese red pine (*P. densiflora* Sieb. et Zucc.) and recorded needle densities of 9.4 for black and 7.4 for red pine. The mean needle density of Scots pine in North-Finland found in our study, 7.8 fascicles per shoot centimetre (Table 3), was lower than or the same as those reported by Jalkanen et al. (1998) and Konôpka et al. (2000), and a bit higher, on average, than those of Jalkanen and Levanic (2001) and Fedorkov (2002). According to Pensa et al. (2005), needle densities of Scots pine in Finland and Estonia were at the same level although height increment in Estonia was clearly larger. These findings suggest that pines do form nearly the same needle density in normal growing conditions even though their genetic base and local growing conditions, and thus the mean height increment may be different. It can be hypothesized that the needle density, and the final length of height growth units, has an optimum that results from the shading effect of needles. Thus, slightly higher needle densities are expected in less favourable sites where needles tend to be shorter.

The annual variation of needle density in the current study was similar to Jalkanen et al. (1998) but higher than in more southern material (Konôpka et al. 2000, Pouttu and Dobbertin 2000, Jalkanen and Levanic 2001, Fedorkov 2002). Variation of pine growth near its northern limits is effectively controlled by climate (Hustich 1948), which strengthens the climatic signal. In this context, the large range of variation was predictable. However, needle-density fluctuation resulting from climatic forcing was very low after the height-growth and age-related variation was removed. According to our results, the precipitation of April–May accounted only for 5% of annual variation, improving the total proportion of modelled variance to 55% (Table 4). The role of this climatic variable in the needle density model was not important and even somewhat questionable. Therefore, it can be generalized that annual needle density and height increment at stand level respond nearly similarly to changes in temperature and precipitation. Although the general response is the same, it must be noted

that most of the needle density variation is at tree level, and the model presented in this study is able to model only one third of it.

The transformations of height growth and tree age were used as independent variables when constructing stand-level chronologies. Although these variables removed stand-level variation due to height growth and tree age, tree-level variation caused by these effects was reduced but not totally removed when considering the final modelling phase. The interpretation of the possible role of April–May precipitation is that it affects needle density by enhancing the elongation of height growth units, i.e. increasing height growth.

The estimated effect of evapotranspiration is only a rough approximation. Still, it should indicate whether soil water deficiency should be inspected more thoroughly. In the current study, the inclusion of the evapotranspiration effect did not improve the correlations between needle density and precipitation (Table 4). Statistically significant precipitation values were those of April–May; also, evapotranspiration is at its highest during mid-summer and does not decrease soil moisture significantly during winter and spring. The standardized needle-density chronology of the three southernmost stands correlated with the late winter and spring precipitations, which indicates the importance of snow coverage, snow-melt water, soil temperature and melting of ground frost on the growing conditions and stem-unit elongation.

Garrett and Zahner (1973) studied growth responses of red pine to water supply over two seasons. In their material, the needle densities of the untreated, irrigated, and drought-treated trees were 8.8, 7.9, and 12.6 per shoot centimetre, respectively. They concluded that needle density might be affected by some interaction between two growing seasons. If a warm season is followed by a cold and harsh season, the shoot may remain shorter than expected on the basis of the number of height growth units in the overwintered bud. It can be hypothesized that the elongation, especially of the uppermost growth units, remains uncompleted due to the low temperature sum when the photoperiodic control begins to stop growth. However, we could not directly affirm this statistically; independent variables based on differencing monthly temperatures of two adja-

cent seasons were not statistically significant. The hypothesis was not rejected either, because the only meteorological variable of the final model represented the current growing season, and height growth, which is also present in the model, reflects the conditions of the previous season. Based on a subsample of the data of the current study, Salminen and Jalkanen (2005) concluded that the current summer does not affect the final shoot length under normal circumstances. Hence, the effect of two successive seasons might not become significant until there is a large climatic difference between years. This question should be studied more under controlled conditions.

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