Growth response of young Scots pines to needle loss assessed from productive foliage

Timo Kurkela¹*, Rein Drenkhan², Martti Vuorinen³ and Märt Hanso²


Abstract. The amount of productive foliage was assessed with the help of the relative significance of each annual needle set in their contribution to the growth of young Scots pines (Pinus sylvestris). The number of needles in the subsequent needle sets was studied retrospectively in twelve-year-old stand, and the worst needle loss years were detected. The growth rate of trees was compared with the number of needles in the annual needle sets and with the loss of needles from the assessed productive foliage. Needles in the 4th and older needle sets remaining in the trees were interpreted as useless or less important if their amount did not correlate with the growth. The second and third needle sets supported both radial and height growth. Most variation in the needle loss during 1999–2002, caused mainly by summer drought and by fungal needle cast due to Lophodermium seditiosum, occurred in the third annual needle set. Decrease in both radial and height increments in relation to the needle loss were apparent in the total material for 1997–2004, but needle loss reduced the annual growth significantly only in two-three years inside that period.

Key words: Scots pine, needle loss, productive needles, senescent needles, Lophodermium seditiosum, drought, radial growth, height increment.

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Introduction

Needle loss, shedding of needles or defoliation in Scots pine (Pinus sylvestris L.) may originate from one to several needle sets or needle cohorts (Ross et al., 1986). Needle loss is related to growth reduction, but this relationship can not be correctly quantified unless the actual growth supporting proportion of the total foliage, i.e. productive foliage, is not specified and unless the needle loss is not related solely to that proportion. Scots pine sheds needles in northern Finland approximately one needle set (needle cohort) annually (Jalkanen, 1998; Muukkonen, 2005). It is difficult to determine the extent of growth reduction due to the defoliation if the needle loss is presented as a part of a certain annual needle set (Williams et al., 2003), since more than one needle set is supporting the growth. Moreover, in natural conditions it has also been difficult or has seemed impossible to determine the amount of the shedding needles belonging to the normal annual shed of the useless to the tree senes-
cent needles, or to the productive needles shedding prematurely (e.g. Zierl, 2004). Appropriate scientific information is, therefore, very sparse.

In the artificial defoliation experiments the effect of the removal of needles had varied according to the age of the removed needles and to the season of this violent action (Linzon, 1958; O’Neil, 1962; Ericsson et al., 1980; Honkanen et al., 1999). The growth reduction in conifers, achieved by the artificial removal of green needles or caused by herbivory (Ericsson et al., 1980; Honkanen et al., 1999; Armour et al., 2003; Pieø et al., 2003; Williams et al., 2003; Kurkela et al., 2005; Straw et al., 2005) can not be correctly compared with the growth reduction in trees caused by abiotic stress situations (like drought) or by fungal needle pathogens (like Lophodermium needle cast). The reason is that the first type of needle removal is accompanied by the additional energy-consuming traumatic effects (resin flow etc.), but the second type is not.

The needle loss from young (usually < 3 years old) needle cohorts or the total needle loss correlates with the growth or growth reduction (Pieø et al., 2003; Williams et al., 2003; respectively). This relationship, however, appears uncertain because loss percentages have not been differentiated between loss of growth supporting foliage and loss of senescent foliage. The needle cohorts of different age have different values in supporting the growth, because: i) the number of needles in the different needle sets among the total foliage is greatly different (Drenkhan et al., 2006); ii) physiological activity (productivity) of different needle cohorts varies (Jach & Ceulemans, 2000, Zha et al., 2002); iii) there exist seasonal functional differences in the different needle sets, e.g. current year needles do not become productive before the middle of the season and the older needles lose their activity when senescence approaches (Clark, 1961; Loach & Little, 1973; Sullivan et al., 1997). Analyzing the foliage structure retrospectively by the needle trace method (NTM), we can assess the relative importance of each needle set even when some loss of needles from a definite needle set has occurred. If the number of remaining needles or, on the contrary, if the needle loss from the older needle sets does not correlate with the growth, it means that these needles did not support the growth, but were merely remaining on the tree because of slow growth (Drenkhan et al., 2006).

Using the NTM, i.e. counting the number of needle traces in year rings in annual shoots toward the pith of a tree, it is possible to obtain the data concerning annual production and shed of the needles in each annual shoot. Most conveniently, the needle trace counting in pines is restricted to the main stem (Aalto & Jalkanen, 1998).

In the literature there may not exist any adequate definitions for the productive or growth supporting foliage. Many published works have described the effect of natural or artificial defoliation on the growth of trees. The needle loss there has always been described as the loss from any particular needle set (Kulman, 1971; Ericsson et al., 1980; Armour et al., 2003) or as the loss from the total green foliage (Alfaro et al., 1982; Williams et al., 2003). When the rate of defoliation is inaccurately defined, it is clear that the relationship between the needle loss and growth rate can be based only on correlations and cannot prove cause and effect (Armour et al., 2003) or open sink and source (Honkanen et al., 1999). Drenkhan et al. (2006) suggested that only three youngest needle sets in Scots pine (P. sylvestris) are supporting the growth in southern Finland and in Estonia.

Based on our definition of the productive, growth supporting foliage (Drenkhan et al., 2006) and using the NTM, we studied foliar dynamics and quantitative effect of the annual loss in the productive foliage on the radial and height increment of young pines in a provenance experiment.
Material and methods

Needle loss and its consequences to the growth of trees, including the number of needles in the annual needle sets, were studied retrospectively in a Scots pine provenance experiment established in 1993. Six provenances were included in this study, two from Estonia and four from Finland (Table 1). The experiment was planned according to a randomized complete block design. Two-year-old nursery grown seedlings were planted in four parallel lines with 100 plants in each and with the replications in four blocks in a clear cut area in Konguta, Tartu Forest District, south eastern Estonia (58°13’N, 26°09’E). Planting density was 0.5×1 m, Vaccinium forest site type (Lõhmus, 2004).

In October 2004 twelve pines per block, two from each provenance, were chosen by randomized sampling among the dominant or codominant trees, which totalled 48 sample trees. After cutting of the trees the annual height increments from 1997 to 2004 were measured. At the height of 5–10 cm a disk was sawn from each stem. From the discs, annual radial increments (RI) were recorded with a tree-ring measuring system in two random directions with an accuracy of 0.01 mm. The averages of these measurements were further used as characters of radial increments of the trees. Bolts (10–25 cm) were cut from each annual shoot of the stems. The number of currently attached needles was directly counted from the youngest annual shoots. The numbers of needles which had been attached on each annual shoot in the succeeding annual rings were counted from the sample bolts using the NTM (cf. Kurkela & Jalkanen, 1990). To find needle traces in the tree rings of the previous years, the bolts of each annual shoot were handled according to the protocol presented by Aalto and Jalkanen (1998). As the single difference from the protocol the lowest bolts analyzed by NTM represented the internodes of the stems grown up one to three years after the planting.

NTM is based on the fact that needles (actually short shoots) of conifers are connected to the pith by vascular bundles through the annual rings as long as they are attached to the shoot (Figure 1). When the needles shed from the shoot the vascular bundles stop growing and can not be seen in the later (outer) tree rings. The transverse sections of these vascular bundles on the planed surface of annual rings are called needle traces. By planning ring by ring the latewood surfaces and counting the appearing needle traces, we can find the number of the needles, which have been attached during every definite year. Usually only a certain section, restricted e.g. by an angle (α) of 45 or 90 degrees from the pith is planed. The counted number is now divided by the length of the bolt and multiplied by eight or four, respectively to the angle, which gives the needle density (ND) for the bolt in the specified annual ring.

Table 1. Seed origin of the tested Scots pine provenance plantations.

<table>
<thead>
<tr>
<th>Provenance</th>
<th>Latitude, N</th>
<th>Longitude, E</th>
</tr>
</thead>
<tbody>
<tr>
<td>Saaremaa</td>
<td>58° 22’</td>
<td>23° 30’</td>
</tr>
<tr>
<td>Rakvere</td>
<td>59° 18’</td>
<td>26° 30’</td>
</tr>
<tr>
<td>Tenhola</td>
<td>60° 03’</td>
<td>23° 20’</td>
</tr>
<tr>
<td>Ruokolahti</td>
<td>61° 26’</td>
<td>28° 45’</td>
</tr>
<tr>
<td>Korpilahti</td>
<td>62° 00’</td>
<td>25° 30’</td>
</tr>
<tr>
<td>Kinnula</td>
<td>63° 32’</td>
<td>24° 55’</td>
</tr>
</tbody>
</table>
of each annual shoot. By multiplying ND by the measured length of annual shoot we obtain the number of needles attached on each annual shoot during the successive years counted from the pith outwards (for the method, see also Armour et al., 2003). As noted earlier, the number of needles in the later text actually means the number of needle pairs = short shoots.

An abbreviation, ANN, was used for the variable showing the number of needles in an annual needle set. Current-year needles on the main stem were marked with ANN (Figure 1). At the end of each growing season the current year needles were about four months old (0.3 years-), the situation which our needle trace countings are describing. The number of the retained needles in the previous year’s shoots in the same annual ring was marked by ANN with 2.3-years-old needles, etc. ANN indicates the number of retained needles in the annual shoot grown n-1 years before the current year shoot but still maintained in the same annual ring (see the list of symbols and abbreviations in the Appendix 1).

As reference value for the needle loss we used the number of the needles attached in the previous season on the same shoot. The original number of needles, i.e. the needles born the previous year (ANN), was used as the base to compute needle loss from the second year needle set (NL), but NL (i.e. the needle loss from ANN) was calculated from the ANN of the previous year. To present the total effect of the needle loss we combined the second and third year needle losses into a new variable NL.

Consequently, annual needle losses (NL) were derived from the needle trace counts as percentages from the number of needles attached in the previous year. The combined needle loss NL from the needle sets ANN and ANN was computed according to the following equation:

\[ NL_{(1-2)} = 100 \times \left( 1 - \frac{ANN + ANN}{ANN + ANN} \right) \]

in which t indicates the current year and t-1 means the year before. To test the effect of the current year needles on RI, we included ANN into the NL equation:

\[ NL_{(1-2)} = 100 \times \left( 1 - \frac{C \times ANN + ANN + ANN}{C \times ANN + ANN + ANN} \right) \]

in which C is a weighting coefficient for current year needles. Alternative values

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Figure 1. Schematic explanation of the origin of different needle sets (ANN) and needle loss values (NL and NL) in the pine stem.

Joonis 1. Asendiskeem erinevate okka vanusklasside (ANN) ja neist arvutatavate okkakao väärteste (NL ja NL) kohta männi tüvelöigul.
from 0 to 1.0 were given for $C$ (1.0, 0.5, 0.3, 0.2, 0.1, and 0). The needle fall from $ANN_4$ was not included as a component in $NL$, since the most important reason for the needle fall after the third season was natural senescence. NL percentages for statistical analysis were then transformed according to the equation:

$$y = 2 \arcsin \sqrt{x}$$

Also, a categorized variable, $CNL_{(1-2)}$ with 10% intervals was used to study the effect of $NL_{(1-2)}$ (Table 2).

Assuming that six whorls from the top could include the most productive foliage (Kellomäki & Oker-Blom, 1983), we constructed a model for the six uppermost branch whorls (Drenkhan et al., 2006). The model was based on the assumption that the annual shoots in each branch decrease exponentially in the succeeding years and according to the branching order. The first order branches were $p$ times the leader shoot (for example $p = 70\%$). The next order shoots in the same branch were again 70% of the previous shoot. Further we assumed that the top end of each branch produced five side branches being again 70% of the tip shoot.

The cause of the needle loss is not possible to determine from the NTM data. We considered the loss from the third needle set (the difference between $ANN_3^{(t-1)}$ and $ANN_4$) as the shedding of the senescent needles since the fourth needle sets ($ANN_4$) had only a few needles attached throughout the study period. In the period from 1999 to 2002, there were two main causes for the premature shedding of pine needles, drought and fungal needle cast ($L. seditiosum$). In 2001 the needle loss was caused mainly by $L. seditiosum$ (Hanso & Hanso, 2001) and in 2002 by the late summer drought (Drenkhan & Hanso, 2006).

Annual differences in radial (RI) and height increments (HI) were analyzed statistically in multivariate general linear models (GLM) using the needle loss as independent covariant or, alternatively, from the needle loss data transformed to a categorized variable with ten percent intervals. Since the NTM-variables were derived from the same needle trace counts, only one NTM-variable could be included in the same model describing the growth. No standardization was used for the increment and needle data. Statistical operations were performed according to SYSTAT® (2000) software. Symbols and abbreviations are listed in the Appendix 1.

<table>
<thead>
<tr>
<th>Needle loss percentage class of $CNL_{(1-2)}$</th>
<th>Class code</th>
<th>$N$</th>
<th>Mean, %</th>
</tr>
</thead>
<tbody>
<tr>
<td>$0–10$</td>
<td>1</td>
<td>148</td>
<td>4.68</td>
</tr>
<tr>
<td>$10.1–20$</td>
<td>2</td>
<td>77</td>
<td>15.39</td>
</tr>
<tr>
<td>$20.1–30$</td>
<td>3</td>
<td>63</td>
<td>24.48</td>
</tr>
<tr>
<td>$30.1–40$</td>
<td>4</td>
<td>45</td>
<td>34.73</td>
</tr>
<tr>
<td>$40.1–50$</td>
<td>5</td>
<td>30</td>
<td>45.26</td>
</tr>
<tr>
<td>$&gt;50$</td>
<td>6</td>
<td>10</td>
<td>57.14</td>
</tr>
<tr>
<td><strong>Total / Kokku</strong></td>
<td></td>
<td>373</td>
<td>18.53</td>
</tr>
</tbody>
</table>
## Results

### State of needle sets and needle loss

The mean number of the current year needles (= short shoots) per shoot ($\text{ANN}_1$) for the total material was 239. In most years our sample trees had their oldest needles in the fourth needle set ($\text{ANN}_4$) which, however, represented as a mean only 2.6% of the total number of needles attached to the main stem (Table 3). One single tree in one year had some needles in the fifth needle set ($\text{ANN}_5$). As expected, the number of needles in different needle sets on the main stem varied during the learned period (1997 to 2004, cf. Figure 2). $\text{ANN}_1$ remained below $\text{ANN}_2$ in 1999 and 2000. $\text{ANN}_3$ had the lowest value in 2002. In about six years after the planting the proportion of needles in each needle sets ($\text{ANN}_1$ to $\text{ANN}_4$) had set to their own level in the pines constructed according to the model including the six uppermost branch whorls. In the model trees $\text{ANN}_1$ and $\text{ANN}_2$ varied around 40%, $\text{ANN}_3$ slightly below 20%, and the rest were for $\text{ANN}_4$.

During the entire study period, no needles from the current year needle sets were lost in the autumns. The average needle loss NL$_1$ in $\text{ANN}_2$ from $\text{ANN}_1$ of the previous year was 3.5% and by the third autumn ($\text{ANN}_3$) the loss (NL$_2$) from the previous years’ $\text{ANN}_2$ was 35.7%. NL$_3$ had the highest average values 67.5% in 2002, and was around 40% in 1999–2001. Before 1999 and after 2002 NL$_2$ was significantly lower ($p < 0.001$), 21 and 18%, respectively (Figure 3). The average combined needle loss NL$_{(1-2)}$ was 18.5%. Among individual trees the differences in NL$_{1}$, NL$_2$ and NL$_{(1-2)}$ were highly significant ($p<0.001$), varying annually from 0 to 100%.

### Radial increment

The average annual radial increment (RI) of the sample trees was 2.4 mm per year. Among the provenances, there were some differences but without a clear north-south gradient. The highest average growth was registered in 1998, 3.0 mm, and the lowest in 2003, 1.8 mm. Radial increments had a decreasing trend from 1997 to 2004, especially after canopy closure in 1999–2000. $\text{ANN}_2$ and $\text{ANN}_3$ were in a significant positive relationship with RI, when analysed separately with year and two categorical variables $\text{RI} = \text{constant} + \text{Provenance} + \text{Block} + \text{Year} + \text{ANN}_n$. The effect of $\text{ANN}_4$ was insignificant ($p = 0.179$). $\text{ANN}_1$ correlated significantly with RI, but possibly without mutual relationship.

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**Table 3.** Mean number of the needles in the annual needle sets ($\text{ANN}_n$) attached in the main stem in the autumn by the provenances.

<table>
<thead>
<tr>
<th>Provenance / Päritolu</th>
<th>$\text{ANN}_1$</th>
<th>$\text{ANN}_2$</th>
<th>$\text{ANN}_3$</th>
<th>$\text{ANN}_4$</th>
<th>$\text{ANN}_5$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>261.9</td>
<td>245.2</td>
<td>156.1</td>
<td>13.1</td>
<td>0.0</td>
</tr>
<tr>
<td>2</td>
<td>229.7</td>
<td>216.6</td>
<td>133.0</td>
<td>11.7</td>
<td>0.0</td>
</tr>
<tr>
<td>3</td>
<td>225.2</td>
<td>208.5</td>
<td>118.1</td>
<td>15.0</td>
<td>0.0</td>
</tr>
<tr>
<td>4</td>
<td>213.5</td>
<td>200.1</td>
<td>138.6</td>
<td>17.5</td>
<td>0.3</td>
</tr>
<tr>
<td>5</td>
<td>221.0</td>
<td>207.7</td>
<td>136.1</td>
<td>14.8</td>
<td>0.0</td>
</tr>
<tr>
<td>6</td>
<td>191.7</td>
<td>180.6</td>
<td>116.9</td>
<td>20.9</td>
<td>0.0</td>
</tr>
<tr>
<td>Mean / Keskmne</td>
<td>239.1</td>
<td>217.0</td>
<td>133.6</td>
<td>15.5</td>
<td>0.1</td>
</tr>
</tbody>
</table>
Height increment
The provenances had similar rates of height growth (HI) with the mean annual growth varying between 39.5 and 29.2 cm, the lowest characterising the northernmost provenance, Kinnula. After canopy closure in 1999-2000, in contrast to the RI, the HI had a clear accelerating trend. ANN$_2$ and ANN$_3$ affected significantly HI ($p < 0.001$), but ANN$_4$ did not.
Effect of needle loss

The relationship between the needle loss and growth rate was analysed with the model: Growth = constant + Provenance + Block + AsinNL + Year. In the total material the growth decreasing effect of NL$_2$ appeared to be higher for RI (p < 0.001) than for HI (p = 0.012). The loss (NL$_1$) in the second needle set had no significant effect on the growth. The effect of NL$_{(1-2)}$ the combined needle loss from ANN$_2$ and ANN$_3$ decreased significantly both RI and HI, with p-values < 0.001 and = 0.001, respectively.

The effect of needle loss on the growth rate varied annually. Needle loss was at a relatively high level from 1999 to 2002, but the effect on RI and HI was different. RI was affected significantly by the needle loss (NL$_2$) in 2000 and 2001 and by NL$_{(1-2)}$ in 2001 (Figure 4). Needle loss in the constructed model trees decreased slightly significantly RI and HI also in 1999 (p = 0.016 and 0.046, respectively). In 1997 and in 2001 there was a significant decrease in HI, associated with the both needle loss variables (NL$_2$, NL$_{(1-2)}$) (Figure 5). Although the needle loss was at the highest level (NL$_2$ = 65.4\%) in 2002, GLM-models revealed no significant effect of NL on the growth (both HI and RI). Needle loss had a lagging effect on RI, which was statistically significant in 2001 and 2002 (p = 0.021 and 0.005, respectively). The lagging effect on HI was not significant in either year.

![Figure 4](image-url)  
**Figure 4.** Effect of needle loss on the radial growth (RI) during the study period. The standardized coefficient of regression (ordinate) shows the relative effect of needle loss obtained with the equation: Growth = constant + Provenance + Block + AsinNL. AsinNL$_2$ = represents needle loss from ANN$_3$, and AsinNL$_{(1-2)}$ represents the combined needle loss of NL$_1$ and NL$_2$. Standardized coefficients are obtained in computing a stepwise regression and are called beta weights by some social scientists (SYSTAT 2000). The numbers in vertical alignment show p-values of the effect of needle loss.

Joonis 4. Okkakao mõju radiaalkasvule (RI) antud uuringuperioodi jooksul. Standardiseeritud regresioonikoeffitsient (ordiaat-teljel) näitab okkakao suhtelisi mõjus, mis on arvutatud valemiga: \(\text{Kasv} = \text{constant} + \text{päritolu} + \text{plokk} + \text{AsinNL} \). AsinNL$_2$ = tähistab okkakadu ANN$_3$-st ja AsinNL$_{(1-2)}$ = tähistab kombineeritud okkakadu NL$_1$-st ja NL$_2$-st. Standardiseeritud koeffitsientid saadakse sammuvisilisel regresioonil ning neid nimetatakse sotsiaalteadustes ka beeta-kaaluks (SYSTAT 2000). Numbrid vertikaaljoonel näitavad okkakao mõju p-väärtusi.
We also tested the dependence of RI from the needle loss when ANN
1 was included partially in the formula for computing the needle loss, giving different weight to the current year needles. Supposing that the current year needles do not affect RI during the whole season, we weighted the number of current year needles by C having different values from one to zero when computing the value for needle loss. Overall, the combined needle loss value, NL
(1-2) gave the highest explanation for the decrease in RI (F = 13.492, p < 0.001) when the current year needles (ANN
1) were totally omitted (C=0) as a component in the computations of NL-percentages (Material and Methods).

The quantitative effect of needle loss on RI was studied in the data of 1999-2001 with the categorized variable CNL
(1-2) derived from NL
(1-2) with ten percent intervals. In these three years the needle loss had a relatively high effect on RI (p = 0.002). Using GLM (Growth = constant + Provenance + Block + CNL
(1-2)) we obtained the growth values for different categories of NL. GLM for RI was computed separately for each year (1999–2001) and adjusted to the same level with the help of the annual mean growth (Snedecor & Cochran, 1968). The regression line of the growth data (18 data points obtained), when plotted against NL
(1-2)-class means, revealed that at the level of 50% NL
(1-2) decreased RI as a mean by 39.2% in these three years (Figure 6).

Similarly, the effect of NL
(1-2) on HI was computed for the data of 1997, 1999 and 2001, when NL
(1-2) had relatively high effect on HI. Sixteen data-points obtained were plotted against ten-percent classes of NL
(1-2) and the regression line for these points revealed 34.8% decrease in HI with the needle loss of 50% (Figure 7).

Figure 5. Effect of needle loss on the height increment (HI) during the study period. The standardized coefficient of regression (ordinate) shows the relative effect of needle loss obtained with the equation: Growth = constant + Provenance + Block + AsinNL. AsinNL
2 represents needle loss from ANN
3, and AsinNL
(1-2) represents the combined NL of NL
1 and NL
2. The numbers in vertical alignment show p-values for the effect of needle loss.

Joonis 5. Okkakao mõju kõrguskasvule (HI) antud uuringuperioodi jooksul. Regressiooni standardiseeritud koefitsient näitab suheltelist okkakao mõju, mis on arvutatud valemiga: Kasv = konstant + päritolu + plokk + AsinNL, kusjuures AsinNL
2 = kujutab okkakadu ANN
3-st ja AsinNL
(1-2) tähistab kombineeritud okkakadu NL
1-st ja NL
2-st. Numbrid vertikaaljoonel näitavad okkakao mõju p- väärtusi.
Discussion

Scots pine has various numbers of needle sets attached, which seems to be regulated by the local site conditions (e.g. Reich et al., 1996) and by climatic factors (Jalkanen et al., 1995; Xiao, 2003; Insinna et al., 2007a). In the previous paper Drenkhan et al. (2006) showed that only the three youngest needle sets correlated positively with the growth, in conditions prevailing in the studied sites in Estonia and southern
Finland, and the effect of the older needle sets appeared to be negligible. The needles in the fourth or fifth needle sets may still assimilate if remaining on the tree, but the younger needles appear to be physiologically most active (Oleksyn et al., 1997; Sullivan et al., 1997; Zha et al., 2002). In pines, it is uncertain whether the changes in the physiological capacity of ageing needles are the result of general degradation or whole-plant reallocation of resources (Muukkonen, 2005). Possibly, the older needles serve as storage for surplus nutrients if assimilation is impeded for some reason. For example, Scots pine definitely stored nitrogen during the winter in the needles grown the previous summer (Millard et al., 2001). Normal senescence of the oldest needles of Scots pine in Estonia occurs in September (Sepp, 1959, Hanso, 1970). The fall of senescent needles in the third autumn (NL₃) was not included in the loss of productive needles. The loss from ANN₄ seems not to be connected with the growth losses. This needle set may merely influence the dry matter production for the new tissues in the next season, if the accelerated reallocation of nutrients stored in older needles is required (Nambari & Fife, 1987; Pensa & Sellin, 2003).

Since the current year needles mature after the shoot elongation, they apparently can not support the current year height increment. Similarly, they can support the radial increment only during the latter half of the growing season (Clark, 1961; Ericsson et al., 1980). By this reasoning, only the second and third year needle sets seem to be most important for the current year growth. It seems that the studies on the relationship between the current foliage and growth, or on the effect of needle loss on the growth, should be focused on that most important part of the foliage of Scots pine.

The needle cast fungus Lophodermium seditiosum Minter, Staley and Millar affects both height and radial increment (Wühlisch & Stephan, 1986). The fungus infects needles in the second half of summer and autumn, and the diseased needle fascicles shed during the next spring, often before the beginning of the new growth (Diwani & Millar, 1987). In Estonia, after a hard L. seditiosum epidemic in 1961 the massive shedding of damaged needles occurred in the first half of June (Hanso, 1970). In every case a great part of the most actively assimilating foliage is lost, together with the nutrients stored in the shedding needles.

Another frequent stressing factor in Estonia − summer drought − mostly reaches the critical level during the later half of the season (Lagergren & Lindroth, 2002). In the current season, therefore, it may affect only the radial growth (Pichler & Oberhuber, 2007).

Ericsson et al. (1980) found that even quite drastic needle removal did not cause an immediate decrease in growth, but it occurred merely with a two-year lag. Growth loss after the defoliation seems to be directly proportional to the loss of productive needles (Van Sickle, 1974; Plattner et al., 1999; Långström et al., 2001). As shown before, in our material the two youngest needle sets in the spring belonged to the productive mass of the foliage. That is also supported by the facts that: i) the elongation period of the current year shoots in the northern conifers may be completed approximately in the middle of the season (Clark, 1961; Kurkela, 1980), and ii) two- and three-year-old needles are not much different in their physiological activity (Oleksyn et al., 1997; Zha et al., 2002; Straw et al., 2005).

The role of needles in the lateral branches can not be neglected as well, because in the branches the proportion of different needle sets may vary from that in the main stem. It could be more correct to count all needles in the uppermost whorls in each needle set in order to reveal the total effect of NL on the growth. Assuming that six
whorls from the top could include the most productive foliage (Kellomäki & Oker-Blom, 1983), we constructed a foliage model for the tops of young pines. Needle loss values obtained using this hypothetical number of needles gave similar results concerning the growth losses as our original needle loss variables which did not include errors generated from the model. For that reason we concentrated to the original NL-variables in our analyses.

Regression between the needle loss and the growth characteristics gave different values depending on the categorization of the needle loss percentages. Six categories with the10% intervals (Table 2) were chosen to avoid the effect of the few deviations with high needle loss values. Supposing that needle loss less than 10% does not cause any growth reduction (Jalkanen, 1998), the estimation of the growth reduction should be compared to that variant (the growth with needle loss from 0 to 10%). This yields a regression line with 2 to 3% less growth reduction than if the line would start from the zero point. Moreover, as the growth reduction could be expected to follow a sigmoid curve, the low level needle loss causes a negligible growth reduction. The growth reduction would be steepest when the needle loss is about 50%. Apparently at least some of the needles lost to summer drought could have been productive in the beginning of the season, and the use of the stored material from the previous season might have some compensating effect for the lost assimilation capacity. Therefore 50% growth reduction was not reached by the 50% needle loss.

Early season needle loss from ANN$_2$ and ANN$_3$ apparently causes the highest reduction in the current season growth. This kind of needle loss is typically caused by the needle cast fungi, e.g. L. seditiosum. Lophodermium needle cast caused a heavy needle loss in Estonia in 2001 (Hanso & Hanso, 2001). Late season needle loss, like that caused by summer drought, may decrease the growth in the next season, apparently detected in RI in our total material as a lagging effect. Although in 2002 the late season drought caused a high needle loss (Drenkhan & Hanso, 2006), its effect was not revealed in our examinations of either the current or the next year’s growth, apparently because there were not much differences in NL between the trees. However, NL in 2000 and 2001, lagging by one year, affected the radial growth almost as strongly as it did to the current year growth, suggesting that the lag effect was real and not connected only with the autocorrelation of the variables. Low growth during the recovery period as a lagging effect of defoliation has been found to last several years in some cases (Kurkela, 1981; Wühlisch & Stephan, 1986; Jalkanen et al., 1994; Lyytikäinen-Saarenmaa et al., 2003).

The lagging effect of NL could also be expected in the height increment but it was not revealed there. The explanation may be that, starting with crown closure, the trees are allocating more resources to the height than to the radial growth. Early senescence in ANN$_3$, because of the late summer drought, might have no observable effect, direct or lagging, on the growth since buds for the next season’s growth are formed during the shoot elongation period. Unfortunately, we could not separate for each year the early season needle loss caused by fungal disease from that caused by summer drought in late season.

Supposing that the current year needles mature by the beginning of July and are productive only in the latter half of the current season (see Clark, 1961, Loach & Little, 1973), we weighted the number of current year needles with various coefficients in determining the total needle loss. After some statistical tests we had to totally exclude the current year needles from the foliage supporting both height and radial growth of trees. Inclusion of the current year needles into the NL-formula as a component
decreased the explanation value of needle loss in the seasons of heavy needle loss. It is not surprising since only about ten percent of the annual radial growth is coming up after the maturation of current year needles in the middle of July (Leikola, 1969; Ericsson et al., 1980; Renninger et al., 2006; Insinna et al., 2007b). In several earlier studies the needle loss from different age classes weighted equally when analyzing the response of the growth of trees to the needle loss (e.g. Piene, 1989). It may give results that are incomparable among different studies. The number of needles in different needle sets (age classes) is very different. Therefore, the growth-inhibiting defoliation should be determined solely as the lost proportion from the effective foliage, and the only reference level should be the number of needles during the previous season for each particular needle set. Applying an appropriate coefficient for the efficiency of each needle set may still improve the models for studying the growth response to the defoliation (Jach & Ceulemans, 2000).

High leaf longevity in pines occurs generally in connection with the slow growth rate (Schoettle, 1990; Jalkanen et al., 1995; Pensa & Jalkanen, 2005; Drenkhan et al., 2006). In the model describing height increment, the effect of the ageing of needles could not be used in the same model with NL since NL had strong correlation with the age of the needles.

During heavy epidemics, *L. seditiosum* may almost equally infect needles in all age classes (e.g. Kurkela, 1979). However, the intensity of infection often increases with the age of the needles (Kowalski, 1982). *L. seditiosum* was considered to be the main reason for needle cast in 2001 and summer drought was very apparent in the foliage in 2002. We interpreted this shedding from the second needle set (appearing in 1.3-year-old needles) as premature, because most of the senescent needles in the sample trees shed at the end of their third growing season (i.e. older than 2.3 years).

**Conclusions**

The results of this study: i) indicate that needle loss at different times of the season may affect differently the height and radial growth, and ii) represent the first report where long-run needle loss solely from the productive foliage was retrospectively assessed and used to explain the effect of the needle loss on the annual growth rate of young Scots pines. In the earlier studies concerning the impact of artificial defoliation or herbivory on the growth rate of conifers, the authors did not present the appropriate definition for the productive foliage nor use it to compute the proportion of total lost foliage. The present results also confirm earlier observations that only the three youngest needle sets correlate with both radial and height increment in Scots pine, but the current year needles have very limited effect even on the radial growth. It seems that only needle loss in the early season, expressed as percentages from the physiologically active (productive) foliage, can explain the relationship between the needle loss and the current year growth. Needle loss in the late season has a minimal effect in the current season, but it may reduce more the radial growth in the next season. To distinguish the early seasons’ and late seasons’ needle loss from each other when using the NTM, one should count the needle traces separately at the outer surface of the late wood and, additionally, at the surface between the early and late wood. That was not done in our material since many of our sample trees had quite thin annual rings. Generally, more studies and more modified methods are needed to confirm our findings.
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References


Honkanen, T., Haukioja, E., Kitunen, V. 1999. Responses of Pinus sylvestris branches to simulated herbivory are modified by tree sink/source dynamics and by external resources. – Functional Ecology, 13, 126–140.


Reich, B.R., Oleksyn, J., Modrzynsky, J., Tjoelker, M.G. 1996. Evidence that longer needle retention of spruce and pine populations at high elevations and high latitudes is largely a phenotypic response. – Tree Physiology, 16, 643–647.


Appendix 1. Symbols and abbreviations.
Lisa 1. Sümbolid ja lühendid.

<table>
<thead>
<tr>
<th>Symbol / Abbreviation</th>
<th>Definition / Definitsioon</th>
</tr>
</thead>
<tbody>
<tr>
<td>ANN\textsubscript{n}</td>
<td>annual number of needles in the n\textsuperscript{th} needle set (downward from the top) attached on the stem</td>
</tr>
<tr>
<td>ANN\textsubscript{1}</td>
<td>number of current year needles, age in October four months or 0.3 years</td>
</tr>
<tr>
<td>ANN\textsubscript{2}</td>
<td>number of second year needles, age 1.3 years</td>
</tr>
<tr>
<td>ANN\textsubscript{3}</td>
<td>number of third year needles, age 2.3 years</td>
</tr>
<tr>
<td>ANN\textsubscript{4}</td>
<td>number of fourth year needles, age 3.3 years</td>
</tr>
<tr>
<td>AsinNL\textsubscript{2}</td>
<td>arc sine transformation of NL\textsubscript{2}</td>
</tr>
<tr>
<td>AsinNL\textsubscript{(1-2)}</td>
<td>arc sine transformation of NL\textsubscript{(1-2)}</td>
</tr>
<tr>
<td>CNL\textsubscript{(1-2)}</td>
<td>the percentage classes (with 10% intervals) of NL\textsubscript{(1-2)} combined from NL\textsubscript{1} and NL\textsubscript{2} (Table 2)</td>
</tr>
<tr>
<td>GLM</td>
<td>multivariate general linear model</td>
</tr>
<tr>
<td>HI</td>
<td>height increment (height growth of tree), cm</td>
</tr>
<tr>
<td>RT</td>
<td>radial increment (radial growth of tree), mm</td>
</tr>
<tr>
<td>ND</td>
<td>needle density, number of needles/cm</td>
</tr>
<tr>
<td>NL</td>
<td>needle loss, %</td>
</tr>
<tr>
<td>NL\textsubscript{1}</td>
<td>needle loss from ANN\textsubscript{2}, difference between ANN\textsubscript{(t-1)} and ANN\textsubscript{(t)}%</td>
</tr>
<tr>
<td>NL\textsubscript{2}</td>
<td>needle loss from ANN\textsubscript{3}, difference between ANN\textsubscript{(t-2)} and ANN\textsubscript{(t)}%</td>
</tr>
<tr>
<td>NL\textsubscript{(1-2)}</td>
<td>needle loss percentage combined from ANN\textsubscript{2} and ANN\textsubscript{3} in the current year</td>
</tr>
</tbody>
</table>

T. Kurkela et al.
Kokkuvõte

Okkakadu ehk defoliatsioon on rahvusvaheliselt kasutatav oluline tunnus puude ja puistute seisundi hindamiseks. Samal ajal kui okkakao laiemat ökoloogilist tähendust metsa elus on uuritud suhteliselt palju, on teadmised okkakao produktsooni-bioloogilisest aspektist veel ebapiisavad. Heitlehiste puudega võrreldes on suhteliselt palju tunduvalt keerukam. Heitlehiste puudega võrreldes on mitme-aastase okastikuga okaspuude lehestiku ja selle kaotuse (ebasoodsate ilmatikuolude, haiguste ja kahjurite läbi) mõju uurimine puude juurdekasvule panduvalt keerukam. Käesolevas uurimistöös püüti aga just seda teha.

Okkakao saadus – okkavaris sisaldab alati erivanuselisi (s.o. erinevatelt okka-aastaküikutest päriseld) okkaid, nii füsioloogiliselt vanu, puule tarbetuid kui ka alles aktiivevaid (produktiivseid) okkaid. Seepärast tuleb okkakao mõju uurimiseks aga omaoksse võtta üksnes kadusid produktiivsest okastikust. Mändide juurdekasv ulitsutsid okaste vägivaldse eemaldamise (noppimise ja lõikamise), samuti okkatakoostumisest seoste vältel, on määratletud, et kahjututakse hulgipaljunemise järel on maailmas tehtud mitmeid uurimisi. Neid ei saa aga võrrelda okkahaiguste ja põuakahjustuste järgsete juurdekasvumuutuste uuringutega, sest esimesed mõjud põhjustavad puudele selliseid energiakadusid (vaiguerituse, jms. näol), mida teised ei põhjusta.


Käesolev uuring kinnitab, seejuures okkajälje (NTM) metoodikat kasutades, et vaid kolme noorima okka-vanusklassi okkad seonduvad Eestis ja Lõuna-Soomes mändide radiaal- ja körguskasvuga. Noorimate, s.o. jooksva aasta okaste mõju puude juurdekasvule on piiratud, avaldudes vaid puude radiaalkasvus. NTM-uuringuid oli maailmas seni tehtud vaid vanematel puudel.

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