

Defoliation by the Common Pine Sawfly (*Diprion pini*) and Subsequent Growth Reduction in Scots Pine: A Retrospective Approach

Timo Kurkela, Tarmo Aalto, Martti Varama and Risto Jalkanen

Kurkela, T., Aalto, T., Varama, M. & Jalkanen, R. 2005. Defoliation by the common pine sawfly (*Diprion pini*) and subsequent growth reduction in Scots pine: a retrospective approach. *Silva Fennica* 39(4): 467–480.

The foliage status in the main stem of Scots pines (*Pinus sylvestris*) was studied retrospectively using the needle trace method (NTM) on a stand, seriously defoliated by the pine sawfly (*Diprion pini*) in the 1980s. Needle density increased abruptly in the seasons following the defoliation. The strongest reduction in annual needle production occurred one year later. As a consequence of lower needle production, the annual number of attached needles decreased three to five years after the defoliation. Needle retention and the average age of attached needles tended to increase after defoliation. In analyses of covariance with the NTM variables, needle density (logarithmic transformed values) and average age of attached needles, had the highest, significant, negative relationship with radial and height increments both in the period prior to the defoliation and in the time when the trees were suffering from defoliation. The relationships between height increment and the number of needles and needle loss were positive and significant. Also radial increment had a positive relationship with the number of needles but not with needle loss. Interestingly, an abrupt increase in the needle density gave a good indication of the effects of a sudden defoliation in pines.

Keywords defoliation, insect attack, needle density, needle production, needle retention, radial growth, height growth, herbivory, NTM

Authors' addresses *Kurkela* and *Varama*, Finnish Forest Research Institute, Vantaa Research Unit, P.O. Box 18, FI-01301 Vantaa, Finland; *Aalto* and *Jalkanen*, Finnish Forest Research Institute, Rovaniemi Research Unit, P.O. Box 16, FI-96301 Rovaniemi, Finland

E-mail timo.kurkela@metla.fi

Received 3 December 2004 **Revised** 8 August 2005 **Accepted** 26 October 2005

Available at <http://www.metla.fi/silvafennica/full/sf39/sf394467.pdf>

1 Introduction

The variation of annual rings in old trees and fossils has been used to explain high, medium and low-resolution climatic changes. This science is called dendroclimatology (Fritts 1976). Although, climate generally determines radial growth, there are still many other factors, which may disturb regular tree ring development (Schweingruber 1996, Ferretti et al. 2002). Numerous pathogen and insect outbreaks result in serious foliage loss, which decreases increment drastically. Using the needle trace method (NTM), annual foliage status in pine trees can be examined retrospectively (Kurkela and Jalkanen 1990, Jalkanen et al. 1995). Changes in growing conditions can be revealed by NTM (Jalkanen 1996, 1998, Jalkanen and Levanic 2001). Jalkanen and Tuovinen (2001) and Hemming et al. (2001) showed that foliage status or height increment in pine trees is a more accurate indication of short-term climatic fluctuations than radial increment at the treeline.

NTM has also been tested to reveal factors causing disturbances in the foliage, and their connection with abnormal variations in tree growth. The type of changes in the foliage may allow identification of the causal agent itself. *Lophodermella sulcigena* (Rostr.) v. Höhn. infects needles of the current year, which are then shed before the end of the next growing season, older needles stay healthy (Jalkanen 1986, Jalkanen et al. 1994). Pine sawfly (*Neodiprion sertifer* Geoffroy) feeds on second-year and older needles leaving usually current year needles intact (Viitasaari and Varama 1987, Jalkanen and Aalto 2000). Another pine sawfly, *Diprion pini* L., feeds on needles of all age classes causing often a serious defoliation in pine stands (Långström et al. 2001). However, the retrospective determination of the feeding in the foliage could be complicated since the insect often eats needles only partially, and the green needle bases may remain alive for years (as illustrated by Uotila and Kankaanhuhta 1999, p. 99).

In this paper, we describe the changes in the foliage status and growth patterns of the stem followed by the attack of the common pine sawfly (*D. pini*) in *Pinus sylvestris* in southern Finland. The relationships between several NTM variables describing foliage status and the radial and height increments were studied.

2 Materials and Methods

Radial and height increment of the Scots pines (*Pinus sylvestris* L.) in relation to their foliage status were studied retrospectively by NTM in trees growing in a dry sandy soil in Pyhtää, Southern Finland, 60°26'N, 26°39'E. The 53-year-old stand with an average dominant height of 11–13 m in 2001 was first attacked by the pine sawfly (*Diprion pini* L.) in 1981. In 1983, the trees in the large areas were totally defoliated. In 1984, 22 survey plots were established in the stand. Treewise foliage loss in annual shoots was assessed in 25% of the four classes until 1988 (Table 1). The minimum value was zero when all needles had disappeared, and the maximum was 3.75 (in 1987) consisting, for example, of three shoots with complete needle sets and a fourth one with 75% coverage. In 1984, only very few larval groups were observed, since many of the cocoons remained in prolonged diapause in 1983 (Viitasaari and Varama 1987), after which some feeding was observed in 1986 and 1988. In this case the defoliation was heavy only in 1983, the trees recovered well and mortality remained negligible.

The sample trees were selected according to their known defoliation history (Table 1). In March 2002, three pines per plot, heavily attacked trees (plots 2 and 3), and unaffected pines (plot 1) were sampled for a retrospective examination of foliage dynamics and tree growth. The trees were cut down and the side of the stem directed toward the east was marked with a chain saw. From each stem, disks were sawn at stump level, at the height of 1.3 m, and at the end of each 2-metre-interval starting from the stump level. The height of the trees was measured as well as the length of the internodes. From each internode above breast height, a bolt of about 15 cm long was taken for counting the needle traces.

Annual ring widths from, North, East, South and West, were measured from the stem disks with a tree ring microscope. Needle traces were counted from each sample bolt according to the protocols presented in Aalto and Jalkanen (1998). Needle traces are the transverse sections of short shoot vascular bundles appearing on the surface of the annual ring revealed by planing. This vascular bundle elongates every season with the rate of radial growth. When a short shoot dies,

Table 1. Characteristics of the sample trees used in the study.

Plot and the degree of defoliation	Retaining needle sets, spring 1984		Tree dimensions spring 2002	
	Upper crown	Lower crown	Height, m	D _{1.3} , cm
Plot 1, Unaffected	2.50	3.00	11.4	10
	2.25	2.75	11.6	12
	2.50	3.00	11.3	11
Plot 2, Heavy defoliation	0.25	0.00	11.5	12
	0.25	0.25	13.3	13
	0.50	0.25	11.5	13
Plot 3, Heavy defoliation	0.25	0.25	11.2	13
	0.50	0.25	11.5	15
	0.50	0.00	10.2	12

its vascular bundle stops growing and can not be seen in the next annual ring. Needle traces are counted from a limited sector in the sample bolts of each annual shoot of the main stem. The data can be obtained concerning needle retention changes over the years. Beginning, for example, on the eighth ring from the pith and advancing toward the pith. When the length of the sample bolt and the annual shoot have been measured it is possible to calculate the primary needle density and needle production in the annual shoot.

To describe the annual foliage status of the trees, needle retention in summer (NR), needle density (ND) or its logarithmic transformation (Ln(ND)), needle loss (NL), total number of currently attached needles (NN), annual needle production (NP), needle age = the final average age of each annual needle set (NA), and average age of the currently attached needles (CNA) were computed. CNA has not been used in any previous papers. It was computed according to the following equation:

$$CNA_a = \frac{\sum_{s=1}^n N_s \left(s - 1 + \frac{t}{12} \right)}{N_a}$$

in which a = year, N = number of needles, s = ordinal number of a shoot beginning from the topmost one, t = time lapse in number of months from the birth of new needles to the autumn yellowing of the old needles, CNA_a = the age of the currently attached needles, N_s = number of needles in the shoot s , N_a = number of needles in the year a . The

data for studying increments and NTM-variables consisted of the years from 1955 to 2001.

ANOVA was used to test annually appearing differences in growth and NTM-variables between defoliated and nondefoliated trees. To further analyse the relationship between the increments and NTM variables, the years from 1955 to 2001 were grouped into three periods: t_1) prior to *D. pini* defoliation, year < 1983, t_2) influence of the defoliation, 1982 < year < 1994, and t_3) recovery, year > 1993. An analysis of covariance (ANCOVA) was used to test the effect of the NTM-variables. For ANCOVA, a linear transformation was applied to some nonlinear NTM variables. Time (= t), plot and tree numbers, were used as categorical variables, NTM variables were used as regression variables, and radial increment (RI) and height increment (HI) were used as dependent variables. All statistical treatments were made using SYSTAT® (2000).

For determining the increment differences between not affected (plot 1) and affected defoliated trees (plots 2 and 3), standardized tree and plotwise radial and height increment chronologies were computed using their average growth during 1972–1982 as a reference value (see Långström et al. 2001). The tree-wise values were averaged to obtain the relative annual increment for each plot. Standardized annual increments were compared to the trend line (value = 100) of the increment in the plot 1. The trend line equation of RI for the trees in the plot 1 was: $y = -2.25x + 127.1$ in which x was numbered from 1 to 37 corresponding with the years from 1965 to 2001. That gave

the annual average deviation from the trend line for each plot, including plot 1. Annual increment loss in damaged plots was obtained by computing relative increment as percentages of the corresponding value in plot 1. The data for HI was treated with the same way. The trend line for HI was $y = -0.223x + 94.57$.

3 Results

3.1 Sawfly Feeding and the Foliage Status

Almost immediate changes in the pine foliage were observed in ND, NP and NN. Conversely, in NL, NA, CNA, and NR the changes were

either delayed or the direction of the change was unexpected. ND increased significantly in plots 2 and 3, in 1984, 1986, and 1988 (Fig. 1, Table 2). In plot 2, ND had the highest average value, 19.4 needles per cm, while without disturbances normal values seem to vary between 5 and 10 cm^{-1} .

In normal years the average needle production (NP) in the plots varied from 150 to 250 per annual leader shoot (Fig. 2). In the defoliated trees, NP was still between these limits in 1984 but decreased sharply two years after the feeding (Fig. 2), being significantly below that of plot 1 in 1983 and 1985–1987 (Table 2). The change in the total number of needles (NN) (Fig. 3) followed NP with a four-year lag, having the lowest culmination in 1989–1990, seven or eight years after

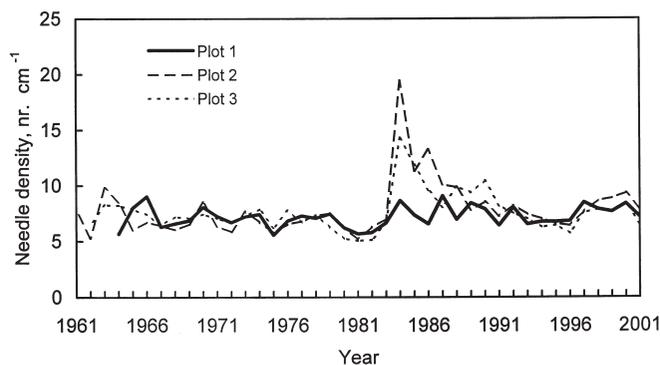


Fig. 1. Needle density (ND), number of needles cm^{-1} , in *Pinus sylvestris* not affected by (Plot 1) and affected by *Diprion pini* (Plot 2 and 3).

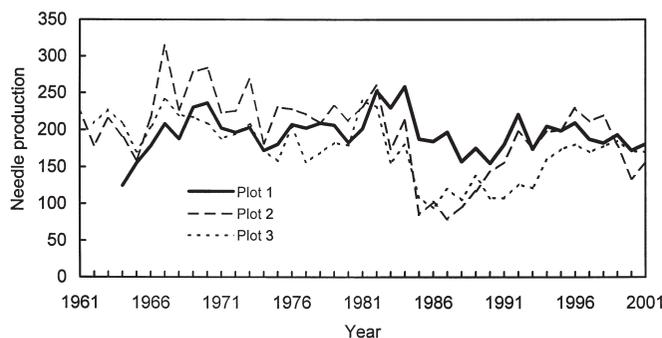


Fig. 2. Needle production (NP), number of needles per annual shoot, in *Pinus sylvestris* not affected by (Plot 1) and affected by *Diprion pini* (Plot 2 and 3).

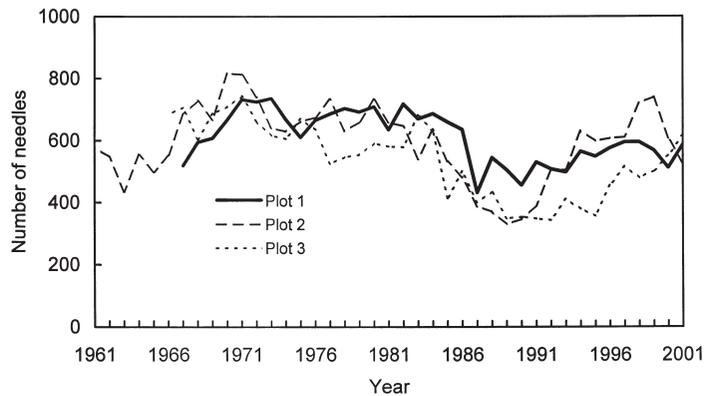


Fig. 3. Needle number (NN), number of attached needles, in *Pinus sylvestris* not affected by (Plot 1) and affected by *Diprion pini* (Plot 2 and 3).

Table 2. Significance of the differences in the NTM variables and increments of pines (*Pinus sylvestris*) between the sample plot not affected and the plots affected by sawfly *Diprion pini*. NL=needle loss, CNA=age of currently attached needles, NR=needle retention, NN=number of currently attached needles, NP=needle production, ND=needle density, RI=radial increment, and HI=height increment. The numbers in the cells are p-values obtained by using an analysis of covariance. Minus sign indicates lower value of the variable in the affected plots. Statistical significant p-values are presented in bold.

Year	Variable							
	NL	CNA	NR	NN	NP	ND	RI	HI
1981	0.088	0.549	-0.831	0.726	0.173	-0.416	0.051	0.060
1982	-0.927	-0.142	-0.095	-0.390	-0.815	0.938	0.247	0.943
1983	-0.065	-0.164	-0.033	-0.091	-0.025	0.772	-0.788	-0.007
1984	0.965	0.584	0.878	-0.131	-0.081	0.021	<0.001	-0.001
1985	-0.361	0.565	0.888	-0.074	-0.007	0.022	<0.001	-0.001
1986	-0.134	0.268	0.414	-0.025	-0.017	0.012	-0.001	-0.002
1987	0.158	0.021	0.013	-0.520	-0.033	1.000	-0.074	-0.050
1988	0.230	0.173	0.084	-0.012	-0.080	0.061	-0.282	-0.041
1989	0.756	0.798	0.429	-0.099	-0.358	0.932	-0.674	-0.542
1990	0.662	0.987	0.656	-0.283	-0.541	0.423	-0.819	-0.483
1991	-0.241	0.886	0.804	-0.301	0.220	0.321	0.969	-0.187
1992	0.447	0.209	0.226	-0.473	-0.147	-0.867	-0.965	-0.200
1993	-0.708	-0.874	0.526	-0.470	-0.367	0.358	0.546	-0.151
1994	-0.798	0.881	0.524	-0.858	-0.451	-0.894	0.695	-0.470
1995	0.097	0.444	0.105	0.921	-0.698	-0.695	0.778	-0.935

the first feeding. The difference in the affected and not affected trees was significant in 1986 and 1988 (Table 2). In the defoliation year, 1983, NR decreased, CNA and NR increased slightly some years after the feeding. The changes in needle loss were irregular and not significant (Table 2).

3.2 Radial Increment

In most years the radial increment had no significant differences between the stem sides. Throughout the data, very significant differences in growth were found among the trees and growth regularly

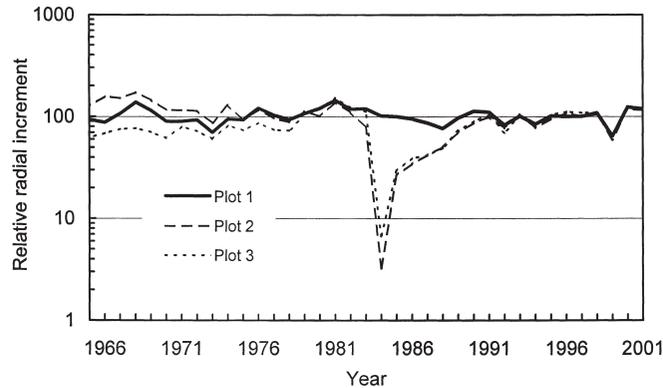


Fig. 4. Relative radial increment (RI) of *Pinus sylvestris* not affected by (plot 1) and affected by *Diprion pini* (plot 2 and 3). The growth in each tree was standardized using the average growth between 1973–1982 as a reference value. Standardized annual increments were compared to the trend line (value=100) of the increment in plot 1 (see text for further information).

increased with increasing measurement height within trees. In the further analyses the annual values of radial increment were averages of the measurements made at different heights and the four directions. The growth (nonstandardized measurements) was less in plot 1 than in other plots before 1983. The differences were significant during 1957 to 1982. Sawfly feeding caused very drastic decreases in RI in plots 2 and 3 in relation to the growth during 1972–1982 and the growth in plot 1. It had its lowest values, only a few percentage points of the normal growth, in 1984 (Fig. 4), and the decreased growth lasted until 1990. In three years, 1984–1986, the difference in RI between the affected and not affected plots was significant (Table 2). During 1984–1988 RI in plot 1 decreased about 25% from the trend line level but it is well within the limits of the standard deviation of the plot mean. Reasons for the decrease could be slight sawfly feeding or climatic factors. About 40% decrease of RI from the trend line level in all plots in 1999 could also have climatic reasons. After 1993, the trees had apparently recovered from the sawfly attack and differences between the plots disappeared.

3.3 Height Increment

In the overall material, from 1964 to 2001 and in the period before 1983, there were no significant differences in height increment between the plots (Fig. 5). An annual comparison showed a slightly significant difference between affected and unaffected trees in 1966 and 1967, with p -values of 0.042 and 0.045, respectively. In the period from 1983–1988, the affected trees had significantly decreased height growth in comparison to the nonaffected trees (Table 2 and Fig. 5). In annual comparisons, significant differences between affected and unaffected trees were found from 1983–1986 ($p < 0.01$), and in 1988 the difference was still significant with $p = 0.041$. After 1993, the height increment in plots 2 and 3 reached the level of plot 1's unaffected trees. In 2000 and 2001, plot 2 grew less than the other plots, for unknown reasons.

3.4 Increments and NTM Variables

The NTM variables which had the highest differences between nonaffected plot 1 and defoliated plots 2 and 3, had the highest correlations also with the growth. Before 1983 (t_1 , $N = 149$) in

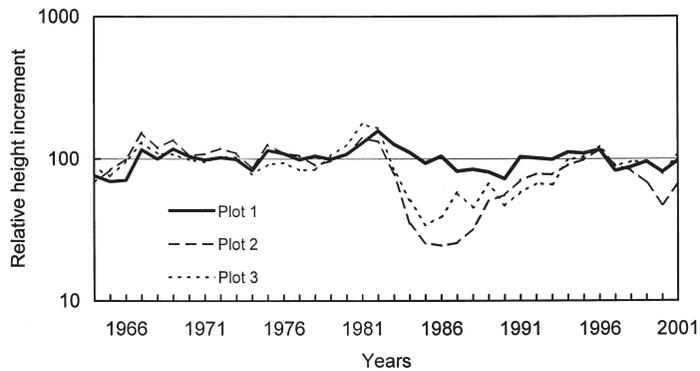


Fig. 5. Relative height increment (HI) of *Pinus sylvestris* not affected by (plot 1) and affected by *Diprion pini* (plot 2 and 3). The comparison between the plots was made same manner as for the case of radial increment. The trend line equation for the trees in plot 1 was: $y = -0.223x + 94.565$ in which x was numbered from 1 to 41 corresponding the years from 1961 to 2001.

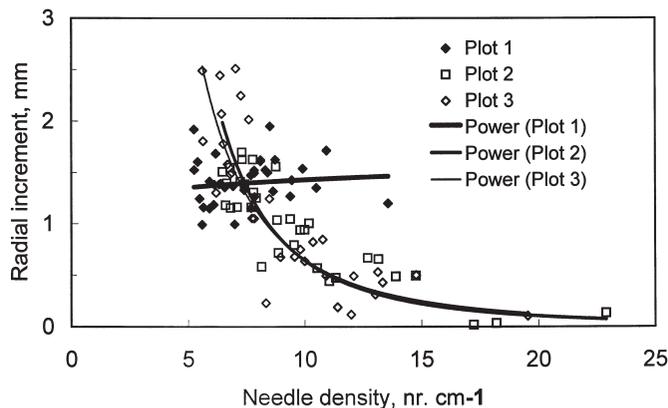


Fig. 6. Needle density (ND, the number of the annually born needles per cm in the shoot) plotted against the radial increment during the time of defoliation and shortly after, 1983–1993. Note: plots 2 and 3 were defoliated, and the results from plot 1 represent nondefoliated trees in which there was no correlation. Trend line equations for the plots 1–3: 1) $y = 1.1906x^{0.079}$, 2) $y = 261.37x^{-2.611}$, 3) $y = 150.44x^{-2.365}$.

the overall material, RI had a slightly significant negative correlation with ND and its logarithmic transformation, $\text{Ln}(\text{ND})$ ($r = -0.272$ and -0.289 with p -values 0.029 and 0.013, respectively), and positive with NP ($r = 0.278$, $p = 0.021$). During that early period, CNA had the highest correlation with RI ($r = -0.321$, $p = 0.002$). In plots 2

and 3 ($N = 104$), RI correlated negatively with ND ($r = -0.335$, $p = 0.018$) and $\text{Ln}(\text{ND})$ ($r = 0.361$, $p = 0.006$). In plot 1 ($N = 45$), RI had no significant correlation with any of the NTM-variables.

In the period of the serious attack by *D. pini* from 1983 to 1993 (t_2 , $N = 99$), RI correlated significantly with needle density, ND and its

Table 3. Relation between NTM variables, and radial and height increments of *Pinus sylvestris* affected or nonaffected by *Diprion pini*, respectively. Lag(HI)=height increment has been lagged by one year. The numbers present correlation coefficients (r) and statistical significance (p) between the compared variables. For abbreviations, see Table 2.

Needle variables	RI		HI		Lag(HI)	
	r	p	r	p	r	p
NR	-0.056	>0.05	-0.182	>0.05	-0.048	>0.05
CNA	-0.154	>0.05	-0.336	<0.001	-0.19	>0.05
ND	-0.583	<0.001	-0.667	<0.001	-0.626	<0.001
Ln(ND)	-0.593	<0.001	-0.723	<0.001	-0.659	<0.001
NP	0.513	<0.001	0.79	<0.001	0.555	<0.001
NN	0.411	<0.001	0.526	<0.001	0.43	<0.001
NL	-0.134	>0.05	0.107	>0.05	0.153	>0.05

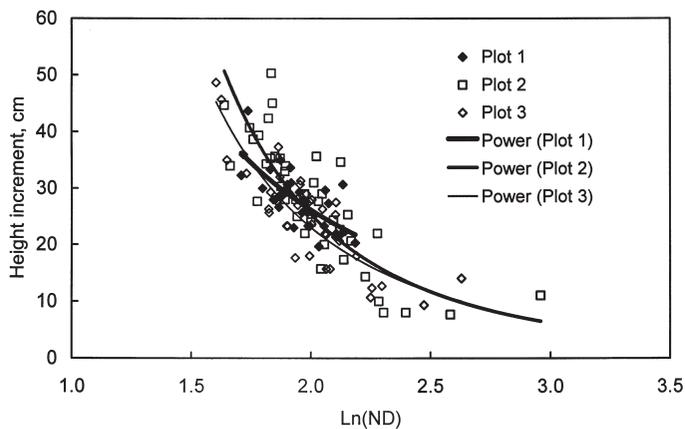


Fig. 7. Ln(ND), logarithmic transformation of needle density (ND) plotted against height increment, HI. The material includes the total investigation period from 1955 to 2001. The dots are averages of three annual observations. Plots 2 and 3 were defoliated and the trees in plot 1 were nondefoliated controls. Trend line equations for the plots 1–3: 1) $y = 110.65x^{-2.079}$, 2) $y = 282.81x^{-3.477}$, 3) $y = 191.88x^{-3.07}$.

logarithmic values (Fig. 6), ($r = -0.718, -0.732$, respectively, with a p-value for both < 0.001 , and with needle production, NP ($r = 0.371, p = 0.006$). After 1993 ($N = 72$), no significant correlation was found between RI and NTM variables.

Height increment correlated with ND in the overall material before 1983 ($N = 149$) (for ND $r = -0.589$, and for Ln(ND) -0.617 , with $p < 0.001$ for both), and in the affected plots ($N = 104$) with ND and Ln(ND)

($-0.672, -0.700$, respectively). HI correlated positively with CNA ($r = -0.390$ with $p < 0.002$). During the period t_2 when trees were defoliated ($N = 66$) the correlation between HI and needle density was about the same level as in the previous period, being slightly lower in the period of recovery (t_3) (for ND $r = -0.639$ and for Ln(ND) $r = -0.647$, both with a p-value < 0.001), CNA had quite a high correlation with HI ($r = -0.603, p < 0.001$).

In the total material from 1955 to 2001 ($N=320$), the correlation coefficients and the number of significantly correlating variables were higher (Table 3) than that computed for any of the shorter periods of the data. The highest correlation (-0.723) in this total material was between the logarithmic transformed needle density values and height increment (Fig. 7), if we omit NP. A high significant correlation ($r=0.706$, $p<0.001$) was between the average radial increment and the height increment. The correlation was even higher when the height increment was lagged with one year ($r=0.719$). For the shorter periods this correlation was less significant.

3.5 Modelling the Influences of the Outbreak

In computing analysis of covariance (ANCOVA), period (t_1 , t_2 and t_3), plot, or tree numbers were used as categorical variables and NTM-variables (CNA, $\text{Ln}(\text{ND})$, NN, and NL) as regression variables. The analysis showed significant ($p<0.001$) differences in average radial increment (RI) between each three periods, which apparently came from the general declining trend of RI with the age of the trees. In the stepwise analysis for the total overall data of RI, the NTM-variables remaining in the model were CNA, $\text{Ln}(\text{ND})$, NN (Table 4). The regression coefficient for CNA and ND was negative, and positive for NN. The values of the standardized coefficients (Table 4) show that from the three NTM variables included in the model, ND had the highest association level with an average RI, followed closely by NN. The categorical variables, period, plot and tree number

affected RI significantly ($p<0.001$).

The RI data was analysed separately in different periods in relation to the feeding. Prior to feeding ($t_1 < 1983$), the regression coefficients for CNA and $\text{Ln}(\text{ND})$ were significant (p -value for both <0.001). From 1983 to 1993 (t_2), $\text{Ln}(\text{ND})$ continued to have a close relationship with RI ($p<0.001$), but CNA and NN were also significant with $p=0.025$ and 0.017 , respectively. After 1993 (t_3), when the affected trees seemed to be recovered, none of NTM variables showed a significant relationship with RI. The only significant differences in RI were found between the trees.

Height increment was analysed similarly to radial increment. In the overall material, ND in the form of $\text{Ln}(\text{ND})$ had negative coefficient and was the most important explanation variable, although, NN was also very important with a positive coefficient. CNA had a significantly negative relationship again. In ANCOVA, all these three variables had p -values <0.001 (Table 5). NL was also included in the model but with a slightly significant positive relation ($p=0.022$). The level of association was highest for $\text{Ln}(\text{ND})$ but NN and CNA also reached quite high levels (see the standardized coefficient in Table 5). The categorical variables, time (t_1 to t_3), plot (1–3) and tree numbers (1–9) significantly affected HI with the p -values 0.002, 0.022, and <0.001 , respectively. The analyses gave the same type of results also for partial data (by plot or by period) according to time. The only exception was that NL was included in the model with a slightly positive significant effect ($p=0.023$) in the period of 1983–1993 (t_2), being insignificant prior to the defoliation (t_1) and during the period of recovery (t_3).

Table 4. NTM-variables explaining the radial growth of pines including both affected and not affected trees between 1955–2001. Variables were selected in stepwise analysis of covariance (SYSTAT® 2000). Variables only with p -values less than 0.150 were accepted. The analysis dropped out NL, and NA. NR were not used. $N=320$, multiple $r=0.693$ for the model. For abbreviations, see Table 2.

Effect	Coefficient	Std error	Std coef	Tolerance	t	P(2 Tail)
Constant	4.123	0.258	0	.	15.97	0.000
CNA	-0.498	0.104	-0.209	0.866	-4.799	0.000
$\text{Ln}(\text{ND})$	-1.403	0.113	-0.515	0.949	-12.391	0.000
NN	0.002	0	0.386	0.883	8.948	0.000

Table 5. NTM-variables explaining the height increment of pines including both affected and not affected trees (plots 1–3) between 1955–2001. Variables were selected in a stepwise analysis of covariance (SYSTAT 10). Variables with p-values less than 0.150 were accepted. NA and NP were not used. N=311, multiple $r=0.932$ for the model. For abbreviations, see Table 2.

Effect	Coefficient	Std error	Std coef	Tolerance	t	P(2 Tail)
Constant	71.953	2.001	0	.	35.962	0.000
CNA	-15.714	0.862	-0.438	0.742	-18.227	0.000
Ln(ND)	-23.782	0.878	-0.591	0.901	-27.096	0.000
NN	0.037	0.001	0.566	0.877	25.604	0.000
NL	1.218	0.529	0.053	0.795	2.301	0.022

3.6 Increment Reduction by Sawfly Feeding

Increment losses were computed as differences between the standardized relative increments in plots 1, 2 and 3. In the trees which suffered from sawfly feeding, the greatest radial increment loss (about 95%) occurred in 1984. Since 1984, the trees gradually recovered (Table 2, Fig. 4).

The effect of the defoliation on height increment was not as abrupt and drastic as it was on the radial increment. The increment loss in annual shoots reached its maximum, about 60–70%, in 1985–1986. Some loss in annual growth apparently occurred until 1993, although, 1988 was the last year with significantly reduced growth in plots 2 and 3 as compared with plot 1 (Table 2, Fig. 5).

4 Discussion

To avoid the nonlinearity in multiple regression analyses, logarithmic transformation of needle density, Ln(ND) was used instead of ND. NP was not used in the models in explaining radial or height increment, since it is a product of HI \times ND (Aalto and Jalkanen 1998), and because it is correlated with NN ($r=0.703$) in the study material (see Ranta et al. 1997). NA was omitted since its value did not describe the situation in the current year. NR and CNA had a very high correlation ($r=0.916$) in the total overall material but because CNA had higher correlations with RI and HI (Table 3) it was accepted to the model and NR

was omitted. Tree number as a categorical variable was preferred to plot number for computing the models, since the plots were selected using the same criteria as the trees, which was according to the defoliation in 1983. However, plot variable was also used in some analyses.

It could be expected that the annual needle loss (NL) changed drastically after the serious defoliation. However, strong feeding in 1983 coincided with low NL values, but was preceded by high values. For keeping the foliage mass in balance, a high annual fall of older needles is often followed by low NL values. Perhaps one reason that the defoliation by the sawflies can not be seen with high NL values in corresponding data is that sawflies often only partially feed on needles (Uotila and Kankaanhuhta 1999) when short shoot bases may remain green and alive for the second or third season from the defoliation. During the critical years 1983–1986, low values of NL could be a consequence from the natural foliage dynamics, according to which high NL in 1982 was followed by low NL values. Apparently, in slowly growing defoliated trees, normal needle shedding was delayed by one or two years. Interestingly, this caused NR to increase. In pine trees, older needles could be activated when a serious loss occurs in younger needle sets (Ericsson et al. 1980). In such cases, needle retention will be increased in connection with slow growth (Pensa and Sellin 2002, Armour et al. 2003), and especially, the increasing gradient of needle retention in pines appears from the south to the north in Finland (Jalkanen et al. 1995).

From NTM variables, ND had the most appar-

ent relation with defoliation. Larvae of *D. pini* finished the feeding on the pine foliage in the late summer long after the formation of apical buds with a normal number of needle primordia. The normally developed buds could not perform the expected elongation in the defoliated trees in the next season, and thus resulted in an increased ND. Although, high ND values had a high negative correlation with height increment in the overall material, the changes of ND after heavy defoliation is more reflective of the pattern of RI than HI. ND appears to accurately indicate adverse changes in the condition of a tree. Heavy defoliation in one year resulted in a significantly increased level of ND for three years. The connection of ND with defoliation and decreased increment was clear in this case. The decreased shoot elongation has a direct connection to the late season defoliation and the consecutive decrease of the amount of starch stored in the remaining needles (Ericsson et al. 1980, 1985, Långström et al. 1990). Generally, an increased ND level does not allow explicit determination of any specific disturbance factor, it is only a sign of disturbance. As an example, increased ND may indicate unfavorable changes in the weather of growing seasons (Jalkanen et al. 1998). An adverse weather episode occurring during the active growing period, may increase the ND values in the shoots of the same season. Stem cankers may also decrease the predetermined shoot growth, which means high ND without preceding defoliation. If pines lose their assimilating organs mainly in the late summer, as occurred in the defoliation caused by *D. pini*, the increase in ND can be seen in the shoots of the next growing season. Other tree species may respond differently to defoliation as *Abies balsamea* (L.) Mill., in which heavy defoliation decreases the number of growing shoots and those remaining may grow exceptionally long with lower ND, although, in later years shoot growth will be retarded with increased ND (Piene and Percy 1984).

Short-term changes in tree health or in the external conditions can be seen as a sudden increase in ND, which then normalizes within a few years. Also long-term changes in ND have been reported. According to Pouttu and Dobbertin (2000), there is a positive trend between ND and the age of pines. That may have a connection also

to the gradually decreasing growth with the age. Jalkanen and Levanic (2001) reported decreasing ND when pines were released from an overstory. In this study, such a long-term trend was not seen. In normal growing seasons when serious disturbances were not affecting the trees, ND was (age < 50 years) between 5 and 10 needles cm⁻¹, which is comparable to that found by Pouttu and Dobbertin (2000). In more harsh conditions, as along the northern tree line, ND can be much higher (Jalkanen et al. 1998).

Needle-pool (NN), the number of needles currently attached in the tree stem, is a sum of the short shoots remaining in annual shoots, usually in two to five internodes. The current-year ND did not correlate with the NN, thus its use with ND in the ANCOVA model was acceptable. However, the significant changes in NN did not appear until three years after the 1983 defoliation. This is because the bases of the short shoot needles may remain attached for the next year or so. Therefore, NN does not reveal the time of defoliation as well as the ND in feeding by *D. pini*.

An artificial defoliation in *Pinus radiata* reduced radial increment more than height increment (Rook and Whyte 1976), but in a different case O'Neil (1962) found that artificial defoliation affected height growth more than diameter growth. In Scots pine stands, infection by *Lophodermella sulcigena* (Rostrup) Höhnelt caused a gradual growth decline, relatively more in the radial increment than in the height increment, in the course of epidemic which lasted several years (Jalkanen 1986). In pines defoliated by *D. pini*, the radial increment had a very drastic decrease in the season following the feeding, and RI returned to the normal level in about seven years. Height increment was less affected than RI but some decrease appeared in the year of feeding, and low growth continued ten or eleven years. It seems that the trees allocated relatively more resources for RI than HI during late 1980s when the active assimilating needle mass was still below the normal level. The losses in radial and height increments found in this study were well comparable with those caused by the heavy infection by *L. sulcigena* (Jalkanen 1986), or with experimental defoliation of the youngest needle sets in the study by Ericsson et al. (1980).

Loss in volume increment. For example, by

using equations presented by Vuokila (1967), it is easy to also calculate the loss in volume increment in defoliated trees. In this case the loss was about 30% when compared with undefoliated trees during 1983–1993. According to Tiihonen (1970), volume-increment loss in several stands, variously defoliated by *N. sertifer*, was about 20% in a series of five year periods prior to, and after, the defoliation. In this study, our sample trees were selected according to the rate of defoliation recorded shortly after the feeding, and NTM variables were used to explain increment variations. Thus the volume increment loss of about 30% in the sample trees seems reliable; however, our material included nine trees, which was not adequate for calculating growth loss at a stand level. According to the original assessment of the number of the remaining needle sets was 0.25 in our six defoliated sample trees (Table 1), which must correspond the defoliation of 80 to 90 percent. That defoliation was at about the same level as the growth reduction, in both RI and HI after one or two years, respectively. Primarily, *D. pini* may cause more serious increment losses at a stand level than *N. sertifer*. The feeding of *D. pini* continues into the late summer, and it often causes complete defoliation, including the current foliage. Although the buds remain usually healthy, the defoliated trees attract secondary pests (Annala et al. 1993), which may result in mortality of a remarkable degree. *N. sertifer* leaves most of the current-year needles intact (e.g. Juutinen 1967). For comparison, Piene (1980) found that in balsam firs, which had completely lost their youngest needle sets in two consecutive years, growth was only half that when compared to the nonaffected trees.

We can conclude that needle density (ND) is the best NTM variable to explain radial or height increment. By examining highly increased values of ND, it is possible to date any acute serious damage, defoliation, wounding, etc., in pine stands within one year's accuracy. We can conclude that damage, like defoliation by *D. pini*, which occurs mainly in the late season, causes the most drastic changes in ND or in the increments in the next season. The living short shoot bases remaining in the tree after defoliation by *D. pini* hamper the exact dating of defoliation. Normally leaf senescence is the signal to activate

the abscission process (Kramer and Kozłowski 1979). However, it seems that short green bases of healthy needles cut by insects do not always give that senescence signal which may cause a delay in the formation of the abscission layer. The Scots pine short shoot may also remain attached for longer time, if only one of the short shoot needles is killed by *Lophodermella sulcigena* (Jalkanen 1986). In retrospect, studied foliage status using NTM reveals occasional changes in the condition of the trees. However, one should remember that the most NTM variables are only secondary indicators but rate of assimilation and the total needle mass are the primary factors determining the dry matter production within the tree. In this study, the immediate needle loss was not possible to determine, since many of the needles were eaten apparently partially and the needle traces did not disappear from the next annual ring after the feeding. However, the increase of the needle density was very closely connected with the growth reduction and showed accurately the time of the defoliation with the lag of one year. A further examination of different cases is required to further supplement the accurate determination of causative factors.

Acknowledgements

We are indebted to Mr. Pekka Närhi for field and laboratory work as well as Mr. Mikko Kukkola for discussions to improve data treatments. We thank Ms. Majella Clarke for revising the English text.

References

- Aalto, T. & Jalkanen, R. 1998. Neulasjälkimenetelmä. The needle trace method. Metsäntutkimuslaitoksen tiedonantoja 681 – Finnish Forest Research Institute, Research Papers 681. 36 p.
- Annala, E., Varama, M., Långström, B. & Niemelä, P. 1993. Pilkkumäntypistiäistuhojen vaikutus männyn elinvoimaisuuteen. Metsäntutkimuslaitoksen tiedonantoja 460: 27–33.
- Armour, H., Straw, N. & Day, K. 2003. Interaction

- between growth, herbivory and long-term foliar dynamics of Scots pine. *Trees* 17: 70–80.
- Ericsson, A., Larsson, S. & Tenow, O. 1980. Effects of early and late season defoliation on growth and carbohydrate dynamics in Scots pine. *Journal of Applied Ecology* 17: 747–769.
- , Hellqvist, C., Långström, B., Larsson, S. & Tenow, O. 1985. Effects on growth of simulated and induced shoot pruning by *Tomicus piniperda* as related to carbohydrate and nitrogen dynamics in Scots pine. *Journal of Applied Ecology* 22: 105–124.
- Ferretti, M., Innes, J.L., Jalkanen, R., Saurer, M., Schäffer, J., Spieker, H. & Wilpert, K. von. 2002. Air pollution and environmental chemistry – what role for tree-ring studies? *Dendrochronologia* 20: 159–174.
- Fritts, H.C. 1976. *Tree rings and climate*. Academic Press, London. 567 p.
- Hemming, D., Jalkanen, R. & Leavitt, S.W. 2001. Preliminary relationships between climate and the apical extension, needle production and ring width of *Pinus ponderosa* in Arizona, USA. *Palaeobotanist* 50: 125–131.
- Jalkanen, R. 1986. *Lophodermella sulcigena* on Scots pine in Finland. *Communications Instituti Forestalis Fenniae* 136. 41 p.
- 1996. Needle retention chronology along a pollution gradient. *Radiocarbon* 1996: 419–426.
- 1998. Fluctuation in the number of needle sets and needle shed in *Pinus sylvestris*. *Scandinavian Journal of Forest Research* 13: 284–291.
- & Aalto, T. 2000. Detecting past needle cast epidemics and sawfly outbreaks by using the needle trace method, NTM. In: Knizek, M. et al. (eds.). *Methodology of forest insect and disease survey in Central Europe*. Proceedings of the IUFRO WP 7.03.10 Workshop, September 24–28. 2000. p. 44–50.
- & Levanic, T. 2001. Growth and needle parameter responses of *Pinus sylvestris* after release from suppression. *Dendrochronologia* 19: 189–195.
- & Tuovinen, M. 2001. Annual needle production and height growth: better climate predictors than radial growth at treeline. *Dendrochronologia* 19: 39–44.
- , Aalto, T. & Kurkela, T. 1994. The use of needle trace method (NTM) in retrospectively detecting *Lophodermella* needle-cast epidemic. *European Journal of Forest Pathology* 24: 376–385.
- , Aalto, T. & Kurkela, T. 1995. Development of needle retention in Scots pine (*Pinus sylvestris*) in 1957–1991 in northern and southern Finland. *Trees* 10: 125–133.
- , Aalto, T. & Kurkela, T. 1998. Revealing past needle density in *Pinus* spp. *Scandinavian Journal of Forest Research* 13: 292–296.
- Juutinen, P. 1967. Zur Bionomie und zum Vorkommen der roten Kiefernbuschhornblattwespe (*Neodiprion sertifer* Geoffr.) in Finnland in den Jahren 1959–65. *Communications Instituti Forestalis Fenniae* 63(5). 129 p.
- Kramer, P.J. & Kozlowski, T.T. 1979. *Physiology of woody plants*. Academic Press. 811 p.
- Kurkela, T. & Jalkanen, R. 1990. Revealing past needle retention in *Pinus* spp. *Scandinavian Journal of Forest Research* 5: 481–485.
- Långström, B., Tenow, O., Ericsson, A., Hellqvist, C. & Larsson, S. 1990. Effects of shoot pruning on stem growth, needle biomass, and dynamics of carbohydrates and nitrogen in Scots pine as related to season and tree age. *Canadian Journal of Forest Research* 20: 514–523.
- , Annala, E., Hellqvist, C., Varama, M. & Niemelä, P. 2001. Tree mortality, needle biomass recovery and growth losses in Scots pine following defoliation by *Diprion pini* (L.) and subsequent attack by *Tomicus piniperda* (L.). *Scandinavian Journal of Forest Research* 16: 342–353.
- O’Neil, L.C. 1962. Some effects of artificial defoliation on the growth of jack pine (*Pinus banksiana* Lamb.). *Canadian Journal of Botany* 40: 278–280.
- Pensa, M. & Sellin, A. 2002. Needle longevity in Scots pine in relation to foliar nitrogen content, specific leaf area, and shoot growth in different forest types. *Canadian Journal of Forest Research* 32: 1225–1231.
- Piene, H. 1980. Effects of insect defoliation on growth and foliar nutrients of young balsam fir. *Forest Science* 26: 665–673.
- & Percy, K.E. 1984. Changes in needle morphology, anatomy, and mineral content during the recovery of protected balsam fir trees initially defoliated by spruce budworm. *Canadian Journal of Forest Research* 14: 238–245.
- Pouttu, A. & Dobbertin, M. 2000. Needle retention and density patterns in *Pinus sylvestris* in the Rhone Valley of Switzerland: comparing the results of the needle-trace method with visual defoliation assessments. *Canadian Journal of Forest Research*

- 30: 1973–1982.
- Ranta, E., Rita, H. & Kouki, J. 1997. Biometria, tilastotiedettä ekogeille. Yliopistopaino, Helsinki. 569 p.
- Rook, D.A. & Whyte, A.G.D. 1976. Partial defoliation and growth of 5-year-old radiata pine. *New Zealand Journal of Forestry Science* 6: 40–56.
- Schweingruber, F. H. 1996. Dendrochronologie – ein jahrgenauer Masstab zur Entschlüsselung der Umwelt- und Menschheitsgeschichte. *Naturwissenschaften* 83: 370–377.
- SYSTAT® 2000. Statistics I and II, version 10. ©SPSS Inc.
- Tiihonen, P. 1970. Ruskean mäntypistiäisen (*N. sertifer* Geoffr.) tuhojen vaikutuksesta männiköiden kasvuun Etelä-Pohjanmaalla, Pohjois-Satakunnassa ja Länsi-Uudellamaalla vuosina 1960–1967. (Summary in German: Über die Einwirkungen des Schadfrasses der roten Kiefernbuschhornblattwespe auf den Zuwachs der Kiefernbestände im südlichen Pohjanmaa, im nördlichen Satakunta und im westlichen Uusimaa in den Jahren 1960–1967). *Communicationes Instituti Forestalis Fenniae* 71(3). 21 p.
- Uotila, A. & Kankaanhuhta, V. 1999. Metsätuhojen tunnistus ja torjunta. *Metsälehtikustannus*, Helsinki. ISBN 952-5118-23-1.
- Viitasaari, M. & Varama, M. 1987. Sahapistiäiset 4. Havupistiäiset (Diprionidae). University of Helsinki, Department of Agricultural and Forest Zoology, Reports 10. 79 p.
- Vuokila, Y. 1967. Eriasteisin kasvatushakkuin käsiteltyjen männiköiden kasvu- ja tuotostaulukot maan eteläistä sisäosaa varten. Summary: Growth and yield tables for pine stands treated with intermediate cuttings of varying degree for southern central Finland. *Communicationes Instituti Forestalis Fenniae* 63(2). 123 p.

Total of 35 references