Comparison of Methods for Estimation of Needle Losses in Scots Pine Following Defoliation by *Bupalus piniaria*

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In 1996, ca. 7000 hectares of pine forests at Hökensås in SW Sweden were defoliated by the pine looper, *Bupalus piniara* (L.) (Lepidoptera. Geometridae). Following an aerial damage survey using CIR (colour infra red) photography, and estimation of pupal densities in the soil, ca 4000 ha of the most defoliated pine stands were sprayed in early August 1997 with *Bacillus thuringiensis* var. *kurstaki.* The control operation was succeessful but probably redundant, as no further defoliation occurred in unsprayed reference areas. In order to assess defoliation levels in different damage classes for later growth loss studies, 47 circular study plots were laid out in pine stands representing different damage and age classes. The remaining foliage was recorded for each tree using the following classes: 0, 10, 30, 50, 70, 90 and 100%. The defoliation levels in 1996 were estimated by disregarding the 1997 needle age class. Thirteen ca. 40-year-old sample trees representing different damage classes were felled, and the remaining foliage of all branches was estimated by needle age class using the above-mentioned scale. One branch in each of the whorls 1996, 1991, 1986 and 1981 was sampled and its needle dry weight was determined. The sample branch data confirmed the field observations that virtually no additional defoliation took place in 1997. The damage classes estimated from the CIR-pictures only agreed with the field damage estimates at the higher end of the damage scale. In contrast, the field estimate correlated well with plot means derived from tree-wise estimates (R^2 = 0.93), and with with the calculated needle biomasses per tree (R^2 = 0.90). Thus, the field damage classification was supported by the more detailed defoliation estimates, and hence forms a relevant basis for later growth loss studies.

Keywords *Pinus sylvestris*, pine looper, undefoliated foliage, needle biomass, CIR-pictures
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1 Introduction

In Fennoscandia, local outbreaks of defoliating insects in Scots pine forests (*Pinus sylvestris* L.) have occurred during almost every decade of the last centuries (Lekander 1950). Among these defoliators, diprionid sawflies, and especially *Neodiprion sertifer* (Geoffr.) (Hymenoptera; Diprionidae), are the most important species, causing considerable defoliation from time to time (Lekander 1950, Kangas 1963, Ehnström 1985). The pine looper, *Bupalus piniaria* (L.) (Lepidoptera; Geometridae), has had a few major outbreaks in Sweden and Finland, leading to severe defoliation (Butovitsch 1946, Juutinen 1968, Mutanen et al. 1988). Elsewhere in Europe, this geometrid moth is a well known defoliator with more or less regular outbreaks (Straw 1996, and references therein).

Pine stands normally survive one year of severe defoliation, and the main impact is hence growth losses (Butovitsch 1946, Lekander 1953, Straw 1996, Långström et al. 2001). Total defoliation in one year, or repeated defoliation in two consecutive years may, however, render trees susceptible to secondary attacks by stem-attacking insects, such as the pine shoot beetles *Tomicus piniperda* (L.) and *Tomicus minor* (Hart.) (Coleoptera; Scolytinae) or other stem-borers, mainly *Pissodes pini* (Coleoptera; Curculionidae) (L.) (Lekander 1953, Crooke 1959, Långström et al. 2001). The increased risk for beetle-induced tree mortality in defoliated stands is often considered a more important justification for control operations than the growth losses that are saved through the operation (Speight and Wainhouse 1989). The validity of this view was recently confirmed for defoliation in Scots pine by Långström et al. (2001).

Although it is well known that severe defoliation often leads to substantial growth losses, the relationships between needle losses and subsequent growth reductions are seldom well established. Many of the older studies suffer from vague defoliation descriptions that make results difficult to generalize (see overview in Kulman 1971). Conditions may also vary greatly between outbreaks depending on pest and host species, site conditions and stand structures, and the resulting growth losses do also vary accordingly (Alfaro et al. 1991, Straw 1996, Långström et al. 2001, Lyytikäinen-Saarenmaa and Tomppo 2002). As impact studies often lack true controls or are often pseudoreplicated (Day et al. 1997), each independent case has something important to add to the knowledge about defoliation impacts on tree survival and growth.

Visual estimates of needle losses have often been used for assessing insect damage (eg. Annila et al. 1999, Långström et al. 1999a, 2001) or forest decline effects (Wulff 1997, 2002). Horntvedt (1997) also related them to objective estimates derived from sample branches. Piene (1989a, b, 1996) has developed a technique for assessing remaining foliage on live trees that also has been applied to Scots pine (Långström et al. 1998). Other approaches rely on destructive sampling and detailed shoot analysis (Långström and Hellqvist 1991a), but all these are very time consuming and difficult to generalize. The needle biomass of undefoliated trees can be reasonably well predicted by the stem basal area, and especially the sapwood area (Waring et al. 1980, Albreksson 1984), but this relationship does not hold for defoliated trees (Långström and Hellqvist 1991b). Remote sensing techniques based on aerial photography using colour infra red (CIR) film has also been used to classify insect defoliation (Ciesla et al. 1984, Ackerman 1997).

In the autumn 1996, a large outbreak of the pine looper was detected in the Hökensås area in SW Sweden. This event initiated a series of studies aiming primarily at estimating the need for a control operation and secondly at estimating the effect of the control operation on the target and non-target organisms. The entire procedure leading to the control decision, the control operation itself and the subsequent follow up studies are described in more detail below and by Långström et al. (1999b). In summary, the control operation was succeessful but probably redundant, as there was no additional defoliation in the unsprayed reference areas either. Hence, the pine forests at Hökensås suffered only one year of defoliation regardless of whether they where sprayed or not. Consequently, there was no control effect to study, and hence the project was redirected towards studying the impact of a single-year defoliation on stand development.

The first step towards a later evaluation of the impact on stand development by the pine looper outbreak at Hökensås, was to secure information on the needle losses in stands in different parts of the outbreak area. This paper is the first in a series of studies, and its specific aims were twofold: first, to compare different approaches to estimate needle losses, and second, to quantify needle losses due to the pine looper activity in stands sufferring different levels of defoliation.

2 Material and Methods

2.1 Study Site

The Hökensås area (58º05'N, 14º06'E) is an esker made up by glaciofluvial deposits dominated by fine sand, and most of the area is situated at 220–280 m above sea level (Tamm 1937). Annual precipitation is fairly low (550–600 mm), and the water holding capacity of the soil is low resulting in a poor pine heath vegetation. The area is covered with pine forests, and lichens constitute the dominant ground vegetation over large areas. The average site productivity is low (3.8 m^3 per year and hectare) corresponding to T18 (for site classification, see Hägglund and Lundmark 1977). The pine stands are naturally regenerated, and they are managed to promote quality timber production, i.e. young stands are kept dense and the rotation period is more than 100 years.

2.2 Outbreak Description

Pine looper outbreaks have been reported three times before in the Hökensås area, namely in 1886, 1924 and 1943 (Butovitsch 1946). The outbreak in 1996 was much larger than the previous ones, as aerial surveys in the autumn indicated that ca. 2000 ha were severely to totally defoliated, 2000 ha were severely to intermediately defoliated, and 3000 ha were lightly defoliated. In spring 1997, parts of the outbreak area were photographed from the air using CIR (colour infra red) film, and selected stands were then classified from the CIR pictures in different damage classes ranging from class 0 (no defoliation) to class 6 (total defoliation). The intermediate classes 1 to 5 were not clearly defined, but were aimed to represent the classes 10, 30, 50, 70 and 90 percent defoliation. These damage classes were then related to estimates of the density of pine looper pupae that were obtained from ground surveys conducted in late April. The mean number of healthy female pupae increased with increasing damage level from 1.5 to 12.5, whereas the critical number of pupae increased from 1 to 7 in the opposite direction (Olofsson 1998, Långström et al. 1999b). Thus, the totally defoliated stands were at risk of repeated severe defoliation even at a control effect of 90%. In the severely defoliated stands, a control effect of ca 80% would save the stands from additional defoliation whereas no control was needed in the moderately defoliated stands.

With this information at hand, and knowing that the pine shoot beetles were abundant in the area due to a considerable stormfelling in 1995, there was a large risk for substantial growth losses and tree mortality following continued defoliation in 1997. Permission was therefore given by the National Chemicals Inspectorate (KEMI) to control the outbreak from the air using *Bacillus thuringiensis* var. *kurstaki*. After additional CIR-photography of the remaining outbreak area in early summer 1997, the area to be controlled was determined as well as the reference areas that should remain unsprayed in order to facilitate evaluations of the control efficiency (see map in Långström et al. 1999b). In early August, ca 4000 ha of the most badly damaged pine stands were sprayed from helicopter using Foray 48B® at an ultralow volume rate of 3.5 litres per hectare containing 10 600 IU per mg of the above mentioned strain of BT. The cost for the control operation was estimated at ca 440 SEK (i.e. ca 50 Euro) per hectare.

In order to monitor the control effects, sample branches were taken from the mid-crown of sprayed and reference trees using a skylift (for details, see Långström et al. 1999b). The branches were sampled on the day after the spraying, kept outdoors in water for a week and then searched for live and dead larvae. Altogether, 860 larvae were found on the sixty sample branches. This was less than 10% of the expected number based on pupal densities. On sprayed branches, 87% of the larvae were dead, thus indicating good control effect. One of the reference areas was apparently contaminated as larval mortality was high there, whereas the other two control areas had 14 and 16% dead larvae, respectively (probably due to contamination during handling in the field). Thus, the control operation was successful but probably redundant as no additional defoliation occurred in unsprayed reference areas either.

2.3 Field Procedures

In August 1997, we selected stands for this study in different parts of the outbreak area using the information from the aerial survey and the CIR-pictures (scale 1:8000). The aim was to find comparable stands in the areas classified as moderately, severely and totally defoliated in the aerial survey, as well as undefoliated control stands. As the pine looper damage generally increased from west to east within the outbreak area, stands of different damage and age classes were selected along main roads running in east-west direction across the outbreak area (see map in Långström et al. 1999b). Some of the stands were situated in the unsprayed reference areas and the majority in sprayed areas, but it became meaningless to keep these apart as no additional defoliation occurred in the area in 1997.

Within the chosen stands, plot sites were located "at random" by walking ca 20–30 m from the road into the stand. The plot size depended on stand age and density, and ranged from 50 to 300 m^2, aiming at ca 20 trees per plot. As stands of ca 40 years of age were common in the area, and often were severely damaged by the pine looper, we selected to focus on these, but we also included some older and mature stands into our study. The young stands had high stem numbers (up to 5000 stems/ha) and the average diameter at breast height (DBH, i.e. at 1.3 m stem height) was below 10 cm. The old stands had an average DBH exceeding 20 cm and had been thinned to 500 to 1000 stems per hectare. Altogether, a total of 47 study plots were laid out in the outbreak area. Thirty of these were ca 40 years old, eight were 50–75 years old, and the remaining nine ca 100 years old.

For each plot, the defoliation level was assessed visually as a "stand damage class" by checking a few (i.e. 3–5) dominant trees with binoculars. The classification used was the same as the one mentioned above for the CIR-pictures, i.e. classes 0–6, where 0 = no visible defoliation, 1 = 10 (i.e. 1–20), 2 = 30, 3 = 50, 4 = 70, 5 = 90 (i.e. 81–99) and 6 = 100% defoliation. Trees were assigned to class 6 only if no green needles could be detected. Then, all trees within the plot radius were marked and numbered clockwise starting with the nearest tree. For each tree, we recorded its dbh and its vigour as dead (0), weak, i.e. survival uncertain (1), damaged but surviving (2) and healthy (3). The remaining needle biomass present on each tree was estimated using the above-mentioned classes: 0, 10, 30, 50, 70, 90 and 100%. We also tried to reconstruct the situation in 1996 by disregarding the 1997 age class of needles and giving each tree a reading for that year, too.

In 13 of the young stands that represented different damage classes, one ca. 40-year-old sample tree was felled in the vicinity of the plot. The chosen trees were typical for the stand, and were taken at ca 10 m distance from the plot periphery, avoiding suppressed or dominant trees. After felling, these trees were analysed whorl by whorl from the top down to the last living whorl. For each branch, we recorded branch diameter at base (in the middle of the basal internode) in 0.5 mm classes and branch vigour as follows: 0 = dead (no green needles), 1 = weak and probably dying (unhealthy appearance, yellow needled, no buds and few current shoots), 2 = affected but probably surviving (few but healthy needles, new buds), and 3=vital (many healthy needles and buds). The needle biomass present on each branch was estimated for each age class of needles (current, last-year, two-year-old and three-year-old needles, herefter referred to as C, C+1, C+2 and C+3, respectively), using the above-mentioned classes: 0, 10, 30, 50, 70, 90 and 100%. Finally, total tree height and the annual leader growth for the last five years were recorded.

For each of these 13 trees, one randomly selected branch in whorls 1996, 1991, 1986 and 1981 (if present) was taken for additional analysis to the field station, where the branch length and annual shoot lengths were recorded along the main branch axis. Thereafter all needle-bearing shoots were clipped off and collected by age class in paper bags, taken to the laboratory and frozen. In addition to these 13 trees, extra branch samples were taken as described above from two additional undamaged trees from which no stem data were recorded.

2.4 Laboratory Procedures

In the laboratory, all study plots were marked on the CIR-pictures and the defoliation class read from the pictures by the same consultant (Nordpointer AB) that did the original damage classification for the pupal survey. In both classifications, some plots were rated as intermediate, eg. classes 4–5, when they could not be assigned to either category.

The shoot samples from the felled trees were oven-dried at 80ºC for 24 h, all needles removed, redried and weighed. The branch needle biomass was then related to the branch cross sectional area at the branch base (i.e. branch basal area, BBA), and equations were developed for different damage classes (see below).

Tree-wise needle biomasses were expressed in two different ways. For all branches on each tree, we calculated the mean percentage of needles left of each age class, and summed these into a measure of ”accumulated foliage” with a theoretical maximum of 400%, i.e. all needles left of the four age classes (C, C+1, C+2 and C+3) present on pine in late summer before the oldest age class (C+3) is shed. The second expression was based on the assumption that the needle biomass of the sample branches was representative for the whole tree. Originally, we intended to use the equations for the relationships between branch basal area and needle biomass in different damage classes for calculating needle biomasses for all branches, and by summing these to get tree-wise needle biomasses. Because of poor relationships, especially in the highest damage class (see below), we chose to use a quotient method where the tree's needle biomass was derived from the ratio between its total branch basal area and that of the sample branches times the needle weight of the sample branches.

2.5 Statistics

Linear regression analysis was used to compare different defoliation estimates, and to relate branch basal areas to their corresponding needle biomass. Means were compared using one-way analysis of variance followed by Tukey´s test for multiple comparisons. Differences were considered significant when $p < 0.05$. Percentages were arcsin-transformed prior to testing (Zar 1999). Calculations were made using the SAS-program (SAS 1987).

3 Results

3.1 Stand Damage Assessments

The damage classification of the study plots that was done from the CIR-pictures did not correspond well ($R^2 = 0.64$) with the classification results obtained by the initial stand damage classification based on a visual assessment of dominant plot trees (Fig. 1a). Most of the severely or totally defoliated plots were similarly classified in both ways. Assuming that the classification from the ground was more reliable (see below) than the CIR-classification, the latter systematically overestimated the damage levels at intermediate and low defoliation levels. The pattern was similar for young and old stands (< 50 and > 50 years old, respectively; data not shown).

There was a much higher correlation between the initial stand damage class and the average remaining foliage per plot that was calculated as the mean of the estimated foliage classes for all live trees on each plot. The relationship was strong both for 1996 ($R^2 = 0.93$, Fig. 1b) and 1997 ($R^2 = 0.91$, Fig. 1c) but these estimates were really not independent, as the situation in 1996 was reconstructed in autumn 1997 by disregarding the 1997 needles.

There was also a strong linear relationship ($R^2 = 0.90$) between the damage class and the accumulated foliage of the felled sample trees (Fig. 1d). At the time of felling, undefoliated trees carried a little more than three full age classes of needles (> 300%), whereas the totally defoliated trees altogether had only one year class in autumn

1997. More details about the remaining foliage is given below for the sample branches.

3.2 Needle Biomass of Sample Branches

Knowing that branch basal area correlates linearly with the branch needle biomass of undamaged branches (Loomis et al. 1966, Grote 2002), regression equations were calculated for the different damage classes (Fig. 2). Because of the small sample size, we grouped the trees in four categories with minimum 3 trees per group, resulting in the classes 0–1, 3, 5 and 6 (there was no felled trees representing class 2 or 4 in the sample). As could be expected, the fit was better for the undamaged branches (R^2 = 0.55) than for branches suffering severe defoliation (R^2 = 0.20). The two intermediate classes displayed the highest R^2 (0.81 and 0.73, respectively) but did not differ in slope, and were hence pooled in the further analysis.

The sample branches also gave information about the remaining foliage by age class. Undefoliated branches had most of their 1995–97 foliage intact and little of the 1994 age class left, and thus carried an accumulated percentage of foliage amounting to ca 300% distributed over four age classes (Fig. 3a). In contrast, severely defoliated trees only had ca 100% accumulated foliage, and nearly all of that was current needles. There was no significant difference in the percentage of current foliage between the pooled damage classes (ANOVA: F = 1.47, p = 0.26, df = 2,14), whereas all other needle age classes differed significantly (ANOVA: F_{1996} = 43.33, p = 0.0001, df = 2,14; F_{1995} = 41.09, p = 0.0001, df = 2,14; F_{1994} = 39.36, p = 0.0001, df = 2,14). Thus, the pine looper larvae had eaten nearly all the foliage in 1996 in class 6, and more than half of it in classes 3–5. The high percentage of current needles in all defoliation classes shows that virtually no additional defoliation took place in 1997.

The total amount (dry weight) of current needles was, however, significantly lower in damage class 6 than in the other (Fig. 3b; ANOVA: F = 3.96, p = 0.047, df = 2,14). The branches from the most severely damaged trees had nearly no older needles left, indicating a nearly total defoliation, whereas branches of damage class 3–5 carried ca

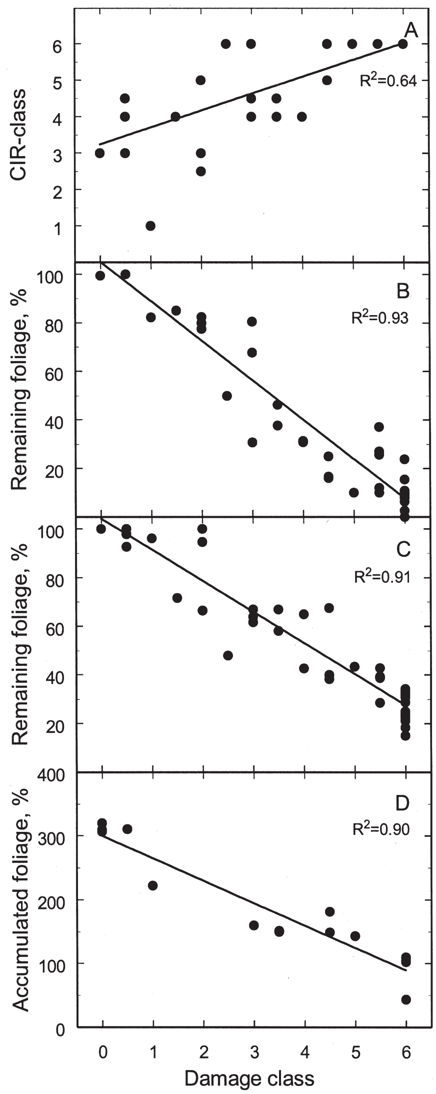

Fig. 1. Relationships between the visually estimated initial stand damage classes, and the damage classification based on CIR (colour-infra-red)-photographs taken from the air in June 1997 (A), the mean percentage remaining foliage per plot, calculated from the the mean foliage percentages of all live trees per plot in 1996 (B), the same in 1997 (C), and accumulated foliage (i.e. the sum of the percentages remaining foliage in each age class of needles) of the felled sample trees as calculated for each branch and needle age class (D). Note that there may be multiple observations in some points, especially in A; further information is given in the text.

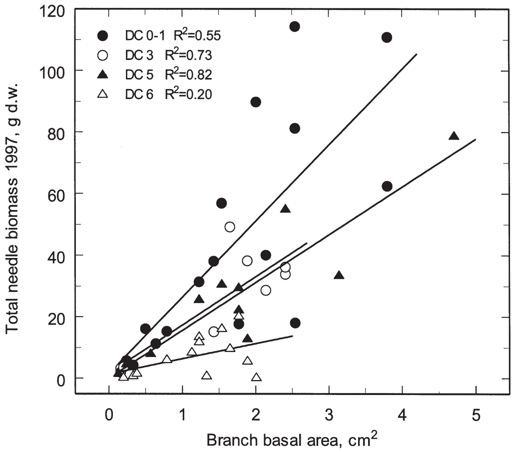

Fig. 2. The relationship between needle biomass per branch and branch basal area at the branch base for the 15 sample trees representing different damage classes (DC), felled in autumn 1997. There were 5, 3, 3 and 4 trees in damage classes 0–1, 3, 5 and 6, respectively. One live branch was sampled from each of whorls 1996, 1991 1986 and 1981 (if present) for each sample tree.

one third of the older needles as compared with damage class 0–1, indicating a 70% defoliation in 1996. All needle age classes differed significantly between damage classes (ANOVA: $F_{1996} = 13.84$, $p = 0.0008$, df = 2,14; $F_{1995} = 21.39$, $p = 0.0001$, df = 2,14; $F_{1994} = 21.76$, $p = 0.0001$, df = 2,14).

We have no data on the number of needles per needle age class, but the average current needle length was similar for defoliated and undefoliated trees in 1997 (Fig. 4a; ANOVA: $F = 0.28$, $p = 0.75$, df = 2,14) although it differed in 1996 (ANOVA: $F = 10.71$, $p = 0.002$, df = 2,14). There was no difference in current leader shoot lenght in 1996 (ANOVA: $F = 2.33$, $p = 0.13$, df = 2,14), whereas undamaged branches had significantly longer leader shoots in 1997 than branches of damage class 6 (Fig. 4b: ANOVA: $F = 12.66$, $p = 0.001$, df = 2,14). Thus, the smaller shoots (i.e. fewer rather than smaller needles) explain the lower current needle biomass observed above in the highest damage class 6.

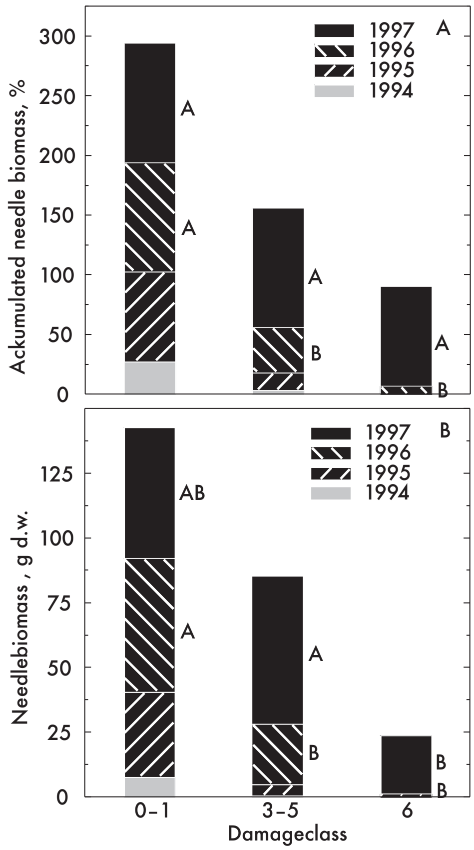

Fig. 3. Relative (A) and total (B) needle biomass of sample branches from trees of different damage classes (the intermediate classes in figure 2 were pooled into class 3–5, now containing 6 trees). Data for all sample branches from each tree were pooled. Different letters beside bars indicate significant differences ($p < 0.05$) between damage classes and age classes (ANOVA followed by Tukey´s test for multiple comparisons; percentages were arcsin-transformed prior to anlysis; Zar 1999).

3.3 Needle Biomass of Felled Sample Trees

In Fig. 1d, we already expressed the relationship between stand defoliation class and the accumulated foliage of the felled sample trees. How does this relate to the quantitative needle biomass estimates? Knowing the total BBA per tree, we simply converted the needle weight of the sample branches using the quotient method

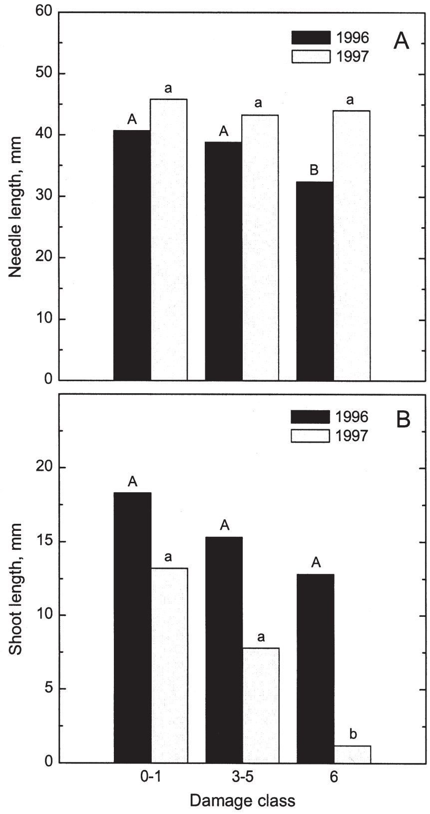

Fig. 4. Mean needle (A) and leader shoot length (B) along the main branch axis in 1996 and 1997 on sample branches from trees of different damage classes. For further details, see legend to Fig. 3.

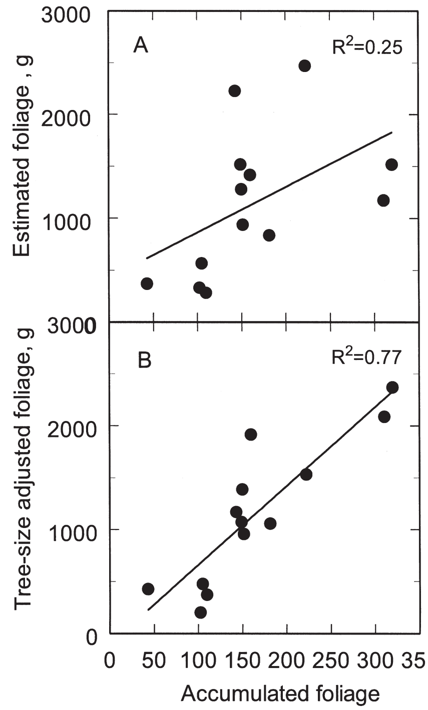

Fig. 5. Relationships between relative foliage estimates (accumulated foliage per tree; cf Fig. 1d) and needle biomass of sample trees derived from sample branches and total branch basal areas per tree (A), and the same after correction for tree-size differences (B). For further information, see the text.

that was described under materials and methods, and plotted it against the mean accumulated percentage of needle biomass for each tree (Fig. 5a). Differences in tree size, however, blurred the relationship ($R^2 = 0.25$), but when the tree size was normalized by relating the needle biomass to a standardized tree with dbh 10 cm, the pattern substantially improved (Fig. 5b), and the correlation between the two ways of describing the tree foliage increased to $R^2 = 0.77$.

4 Discussion and Conclusions

Scots pine is normally carrying four age classes of needles during the summer and three in the winter. The current (C) needles develop in early summer, and the fourth age class (C+3) is shed in the autumn (Flower-Ellis et al. 1976, Ericsson et al. 1980). Needles may, however, drop prematurely due to eg. water stress, or may sometimes be retained longer than for three years, especially in old trees in the north (Albrektson 1988, Kurkela and Jalkanen 1990).

Our sample branches show that undamaged trees at Hökensås had two full age classes (C and C+1) and two incomplete age classes (C+2 and C+3) amounting to an accumulated total of ca 300%. As the sampling was done in early September when the C+3 needles were turning yellow and ready to drop, part of these may have been lost during the handling of the branches. Thus, our figures may underestimate this neeedle age class, and hence the difference between undefoliated and defoliated branches should rather be higher than our figures indicate. Our data also showed that very slight, if any, larval feeding occurred in 1997, regardless of whether the trees were sprayed with BT or not. This result agrees with the observation mentioned above that much less larvae were found on the sample branches than could be expected from the pupal survey. The observed lack of further defoliation by the pine looper larvae is difficult to explain, but it is probably linked to the oviposition behaviour and non-preference for current needles of the pine looper (Šmits 2001).

Assuming that the sample branches represent the trees, we conclude that one year after the defoliation the most defoliated trees carried ca one fifth of the foliage compared to the undefoliated ones (cf. Fig. 3). Our figures also indicate that they carried less than 5% of full foliage after the defoliation in 1996. We do, however, not know how much of the 1993 needles (i.e. C+3 in 1996) were left on any of the trees in the autumn 1996, but one can assume that the needle age class distribution for undefoliated trees was was fairly similar between years. Hence, trees of damage classes 5 and 6 really lost more than 90% of their needles. As the branches of the intermediate damage classes were pooled, the means only indicate that this heterogeous group on an average carried ca 40 and 60% of full foliage in autumn 1996 and 1997, respectively. It is more interesting to note that the weight of the current needles of lightly defoliated trees was similar to that of undefoliated trees, which should indicate a potential for rapid foliage recovery. It is also noteworthy that the most defoliated trees produced significantly less foliage and smaller shoots in 1997 as compared to less defoliated trees. As the needle length in 1997 was unaffected by the defoliation in the previous year, this reduction in needle biomass was probably due to reduced shoot length and shoot mortality.

It is obvious that the needle biomass of a given tree or branch is related to its size, and consequently branch length and diameter have been found to correlate with the needle biomass (Långström et al. 1998, Grote 2002). According to the ”pipe model theory” the leaf area or biomass of any plant is intimately linked to the water transporting capacity in the stem (Shinozaki et al. 1964). A strong correlation between needle biomass and stem sapwood area has also been found in Scots pine (Whitehead 1978, Albrektson 1984), and Loomis et al. (1966) demonstrated that the argument holds for individual pine branches, too. This relationship is, however, only valid for ”normal” undamaged branches, whereas defoliated branches would require correction terms accounting for the needle loss, and the time lag in basal area response to a reduced foliage (cf. Långström and Hellqvist 1991b). Despite this, we tried a simple approach with separate equations for different damage classes, and found, as was expected, different slopes between the regression lines for undefoliated and defoliated branches (cf. Fig. 2). Correlation coefficients were, however, variable and particularly poor for the most defoliated branches. Hence, we abandoned the idea of using the equations for estimating tree needle biomass, and instead derived it from the needle biomass of the sample branches by the quotient method described above. That method should reflect the situation of the individual tree in a better way, but suffers from the small sample size (3–4 branches out of 50 or more live branches per tree).

Visual estimation of needle losses on standing trees have frequently been used for assessing insect damage (Alfaro 1991, Ostaff and MacLean 1995, Långström et al. 2001), fungal diseases (Nevalainen and Yli-Kojola 1990), or forest decline symptoms (Aamlid 1997), but the accuracy of these estimates is largely unknown. During a calibration course, trained observers rated defoliation levels of individual trees very similarly (SD < 10%) but the true defoliation levels were not known (Aamlid and Horntvedt 1997). Horntvedt (1997) demonstrated a clear relationship between foliage density (i.e. foliage weight per branch basal area unit) and crown density class, that is similar to our Fig. 5b, but he gives no accuracy estimate. In those cases, when defoliation levels have been determined with greater effort either on standing trees (Piene 1989a) or on felled trees (Långström and Hellqvist 1991a) no visual classification was done in advance that could have been compared to the more precise assessment. Thus, we do not really know how well our different ways of estimating the foliage of differently defoliated trees represent the true needle biomass on those trees, but at least we know that our estimates are strongly correlated, and should hence at least depict relative differences between trees in the range from intact to totally defoliated ones. All the above-mentioned techniques require that the needle losses are estimated when they occur. Until recently, there has been no way to reconstruct past needle losses, but now the very laborious ”needle trace method” offers some possibilities in this direction (Kurkela and Jalkanen 1990)

Colour infrared aerial photographs have frequently been used for different forest health assessments including insect damage (Ciesla et al. 1984, Ackermann 1993). Ciesla et al. (l984) found a 74% agreement between defoliation classification from CIR-photographs and independent ground classifications of defoliated ponderosa pine stands. Similarly, individual Scots pine trees as well as stands suffering different levels of sawfly defoliation could be correctly grouped in 20% defoliation classes from CIR-pictures at the scale 1:6000 (Ackermann 1993). Compared to these two studies, our results were less satisfying, as the lower damage classes were systematically overestimated from the CIR-pictures as compared to the field classification. As the CIR-pictures, however, were taken in early summer during the shoot elongation period, whereas the ground assessments were made after the growing season in September, these two estimates were not fully comparable. We cannot explain this discrepancy, but we are confident that the ground classification gives a more correct picture of the damage levels, as this correlated well with the other ways of assessing the foliage of individual trees in the stands.

In conclusion, we found that a visual estimation of the stand damage class was well enough correlated with more objective ways to assess the defoliation level, and hence that this kind of damage classification can be a useful tool in planning forest protection operations. We also conclude that severely defoliated stands can be correctly identified from CIR-pictures, whereas more work would be needed to calibrate the technique for identifying low and moderate defoliation. For operational planning of countermeasures such as aerial sprayings, it would be essential also to detect low–moderate defoliation levels although the main target for countermeasures would be the severely damaged areas. These are also the areas where tree mortality is most likely to occur as a result of the defoliation itself, or due to secondary beetle attacks. Moderate needle losses may, however, cause growth losses that probably are more or less proportional to defoliation levels, but these relationships are poorly known. The growth reduction itself can often be properly measured, but the underlying needle losses have seldom been quantified, and without knowing both aspects defoliation episodes can neither be compared nor generalised. There is hence a great need for improved tools to assess low to intermediate foliage losses.

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