

Impact of Pine looper Defoliation in Scots pine

**Secondary attack by pine shoot beetles, Tree mortality,
Top-kill, Growth losses, and Foliage recovery**

Jan Cedervind
Department of Entomology
Uppsala

Doctoral thesis
Swedish University of Agricultural Sciences
Uppsala 2003

Acta Universitatis Agriculturae Sueciae
Silvestria 297

ISSN 1401-6230
ISBN 91-576-6531-1
© 2003 Jan Cedervind, Uppsala
Tryck: SLU Service/Repro, Uppsala 2003

Abstract

Cedervind, J. 2003. *Impact of pine looper defoliation in Scots pine: secondary attack by pine shoot beetles, tree mortality, top-kill, growth losses, and foliage recovery.*

Doctor's dissertation.
ISSN 1401-6230, ISBN 91-576-6531-1

Widespread defoliation of forests caused by insects or fungi cause economic losses throughout the world. Successful outbreak management involves cost/benefit estimation and requires knowledge of potential yield losses. Currently, such knowledge is scarce. This thesis evaluates the significance of single-year defoliation by the pine looper moth (*Bupalus piniaria* L.) (Lepidoptera: Geometridae) and secondary attack by the pine shoot beetle (*Tomicus piniperda* L.) (Coleoptera: Scolytinae) for yield losses in Scots pine (*Pinus sylvestris* L.). In a seven-year study, tree mortality and growth losses were quantified after a *B. piniaria* outbreak with a subsequent *T. piniperda* infestation at Hökensås in 1996. Secondary attack by *T. piniperda* was also studied in a Scots pine stand at Fredriksberg, infested by *Gremmeniella abietina* (Lagerberg) Morelet. in 2001.

Tree mortality at Hökensås mainly occurred in areas with an average defoliation intensity of 90-100%. Tree mortality averaged 25%, and the "defoliation threshold" for tree survival was found to be $\leq 90\%$ defoliation. Tree mortality peaked two years after the defoliation event, which coincided with high levels of pine shoot beetles. Involvement of *T. piniperda* in tree mortality increased with time since defoliation, and tree susceptibility to beetle attack increased with increasing defoliation intensity and decreasing dominance status of trees. As foliage of trees recovered, fewer trees were susceptible to beetle attack, and ultimately, beetle attacks ended as breeding substrate was depleted. Tree susceptibility to beetle attack was a function of tree vigour and beetle density.

Growth losses at the Hökensås site were a combined effect of pine looper defoliation and shoot pruning by *T. piniperda*. Radial, height and volume growth losses were proportional to defoliation intensity. Whereas radial growth was little affected by beetle-induced shoot pruning, height growth was severely affected by beetle-induced damage to leading shoots. Growth losses alone, excluding tree mortality, were large enough to economically justify control of the pine looper outbreak had the outbreak been prevented in 1996.

At Fredriksberg, *T. piniperda* colonised trees that would have survived the damage caused by *G. abietina*. However, trees with 90-100% foliage losses died because of the damage caused by *G. abietina* alone, and tree survival seemed to require that trees retained at least 20% of full foliage.

Keywords: *Bupalus piniaria*, defoliation, *Gremmeniella abietina*, *Tomicus piniperda*

Author's address: Jan Cedervind, Department of Entomology, Swedish University of Agricultural Sciences, P.O. Box 7044, S-750 07 Uppsala, Sweden. E-mail: jan.cedervind@entom.slu.se

Contents

Introduction, 7

Aims and hypotheses, 9

Study system and methods, 10

Study organisms, 10

Pinus sylvestris, 10

Bupalus piniaria, 11

Gremmeniella abietina, 11

Tomicus piniperda, 11

Outbreak descriptions, 12

The Bupalus piniaria outbreak, 12

The Gremmeniella abietina outbreak, 13

Study sites, 13

Field procedures, 13

Hökensås (papers I, II, III, and V), 13

Fredriksberg (paper IV), 16

Results and Discussion, 17

Comparison of defoliation estimation methods (*paper I*), 17

Tree mortality and top-kill (*paper II*), 17

The role of *Tomicus piniperda* in tree mortality (*paper III*), 21

Experimental evidence for *T. piniperda* aggressiveness (*paper IV*), 26

Growth losses and Foliage recovery (*paper V*), 27

Economic consequences of the pine looper outbreak, 33

Conclusions, 35

References, 36

Acknowledgements, 43

Appendix

Papers I-V

This thesis is based on the following papers, which in the text are referred to by the Roman numerals I-V.

- I. Långström, B., Hellqvist, C. & Cedervind, J. 2004. Comparison of methods for estimation of needle losses in Scots pine following defoliation by *Bupalus piniaria*. *Silva fennica* 38, 00-00. (In press)
- II. Cedervind, J. & Långström, B. 2003. Tree mortality, foliage recovery and top-kill in stands of Scots pine (*Pinus sylvestris*) subsequent to defoliation by the pine looper (*Bupalus piniaria*). *Scandinavian Journal of Forest Research* 18, 505-513.
- III. Cedervind, J. & Pettersson, M. & Långström, B. 2003. Attack dynamics of the pine shoot beetle, *Tomicus piniperda* (Col.; Scolytinae) in Scots pine stands defoliated by *Bupalus piniaria* (Lep.; Geometridae). *Agricultural and forest entomology* 5, 253-261.
- IV. Cedervind, J. & Lindelöw, Å. Scots pine (*Pinus sylvestris*, L.) mortality caused by the fungus *Gremmeniella abietina* (Lagerb.) Morelet. and the pine shoot beetle (*Tomicus piniperda* L.). *Scandinavian Journal of Forest Research* 0, 00-00. (Accepted)
- V. Cedervind, J. & Långström, B. Growth losses and foliage recovery in Scots pine exposed to different levels of defoliation after a single-year outbreak of the pine looper *Bupalus piniaria* and subsequent pine shoot beetle attacks. (Manuscript)

Paper I, II, and III and selected figures therein are reproduced with the kind permission of the publishers.

Introduction

Forest insect herbivores occur in forest ecosystems all over the world (Berryman 1988). Normally, during endemic conditions (non-outbreak conditions), insect herbivory does not exceed 10% of the annual leaf biomass production (Larsson & Tenow 1980), and relatively few species ever reach population densities high enough to cause notable damage to forest stands. From the long-term perspective of a forest ecosystem, insect herbivory can act as a regulator of forest primary production. By maintaining optimal rates of nutrient cycling in forest ecosystems, insect herbivory may sometimes actually lead to accelerated growth (Mattson & Addy 1975). Mattson & Addy (1975) suggested that insect herbivory can increase the light penetration through the foliage canopy, reduce competition among plants, increase the rate of fall of nutrient-rich litter, stimulate the redistribution of nutrients within plants, and stimulate decomposing activity. Field observations where initial growth reduction in defoliated trees is followed by increased growth support this hypothesis (see Alfaro & Shepherd 1991 and references therein).

However, some forest insect herbivores reach outbreak levels, and these insect pests can cause extensive damage (eg. Kulman 1971; Shepherd 1994; Day & Leather 1997). From the short-term perspective of the forest manager, tree mortality and growth losses caused by herbivory are rarely acceptable. Due to severe economic losses caused by forest insect herbivores, much attention has been devoted towards understanding the impact of important defoliators on commercially important conifers in North America (Wickman 1980; Alfaro et al. 1982, 1999; Piene 1989; Ostaff & MacLean 1995; Piene & MacLean 1999; Alfaro 1991 and references therein). In Europe, there is scattered information available on growth losses caused by conifer defoliators from different parts of Europe (Pschorn-Walcher 1982; Laurent-Hervouet 1986; Austarå et al. 1987; Britton 1988; Baronio 1989), but until recently few attempts have been made to grasp the whole series of events from recording pest densities or foliage losses to impact studies and analyses of economic consequences in terms of lost yield. Recent work has, however, increased the understanding of the impact of defoliators on intensively managed forest stands, and forestry (Straw 1996; Straw et al. 2000, 2002; Långström et al 2001; Armour et al. 2003; Lyytikäinen-Saarenmaa & Tomppo 2002).

The impact of defoliation, such as tree mortality and growth losses, is affected by a variety of different factors. It varies depending on which defoliator species and host trees that are studied (eg. Shepherd 1994), defoliation history and intensity (eg. Långström et al. 2001),

as well as the timing of defoliation, which can be related to the quality of foliage removed (Ericsson et al. 1980a). For example, the European pine sawfly (*Neodiprion sertifer*, Geoffr.) (Hymenoptera, Diprionidae), the most common outbreak defoliator in Fennoscandia (Lekander 1950), is an early-season defoliator, which leaves the current year needles intact. Thus, the impact is usually limited to growth losses (Austarå et al. 1987), whereas *Diprion pini* (L.) (Hymenoptera, Diprionidae), a late-season defoliator, which removes all foliage and in addition to growth losses may cause tree mortality, at least if defoliation occurs in two consecutive years (Långström et al. 2001).

Forest insect pest populations can fluctuate tremendously over time, sometimes in cyclical patterns related to density-dependent processes, but also due to stochastic events (Berryman 1986; Speight et al. 1999). Populations are often cited to be controlled by top-down factors (natural enemies) and/or, bottom-up factors (food supply, or host plant quality which is related to soil nutrients and water availability) (see eg. Berryman 1988; Perry 1994; Speight et al. 1999). The pine looper moth (*Bupalus piniaria* L.) (Lepidoptera, Geometridae) (Barbour 1988), and *N. sertifer* (Björkman 1991), for example are reported to be affected by both top-down and bottom-up factors. Herbivore outbreaks are often considered to occur as a result of some kind of stress on host plants, because stressed plants become more suitable as food for insect herbivores, due to increased levels of available nitrogen (White 1974, 1984, but see Kytö et al. 1996). Furthermore, secondary compounds (allelochemicals) act as a defence against insect defoliators, making plants less palatable or even toxic (eg. Haukioja 1991; Björkman 1991; Lyytikäinen 1993; McMillin & Wagner 1997; Speight et al. 1999), and stressed plants may also synthesize less defensive chemicals (Rhoades 1979, but see Koricheva et al. 1998; Huberty & Denno 2004). Larsson (1989) pointed out that factors that induce stress in trees are frequently correlated with direct effects on insect herbivore population density. However, severe defoliation by pine insects, such as *B. piniaria* and *N. sertifer*, indeed often occur after periods of drought, and seems to be associated with forest stands on poor soils (Trägårdh 1939; Kulman 1971; Schwenke 1978; Larsson & Tenow 1984; Brokenhuizen et al. 1993).

Defoliation by insect herbivores is a form of stress on trees in itself, which reduces tree vigour. If carbohydrate reserves required for regrowth of foliage (Kozlowski et al. 1991) and resistance processes (Christiansen et al. 1987; Raffa & Berryman 1987) are depleted due to defoliation, tree mortality may occur due to the defoliation itself or by subsequent stem attacks by secondary insect species, for example bark beetles. Tree susceptibility to bark beetle attack is known to increase with reduced host tree vigour (Larsson et al. 1983; Wright et al. 1984; Waring & Pitman 1985; Christiansen et

al. 1987; Långström et al. 1992; Christiansen & Fjone 1993; Schroeder & Eidmann 1993; Annila et al. 1999).

The pine shoot beetle (*Tomicus piniperda*, L.) (Coleoptera: Scolytinae) is a common species in the Scots pine (*Pinus sylvestris* L.) ecosystem and a key species in the current thesis. It hosts aggressive blue-stain fungi that can kill host trees if inoculated by a sufficient amount (Solheim et al. 1992). *T. piniperda*, however, does not have aggregation pheromones (Byers et al. 1985), a trait common for aggressive bark beetles such as *Ips typographus* in Europe (Christiansen & Bakke 1988), and *Dendroctonus frontalis* (Flamm et al. 1988), and *D. ponderosae* (Raffa 1988) in North America, which are able to kill healthy trees by mass attack. Instead, *T. piniperda* is guided by host odours emitted by weakened trees, and if aggregated in sufficient numbers they may colonise the trees (Schroeder & Eidmann 1987; Långström & Hellqvist 1993; Annila et al. 1999). Thus, *T. piniperda* is considered a moderately aggressive bark beetle species, and it is known to colonise weakened trees, for instance, after defoliation (Lekander 1953; Annila et al. 1999; Långström et al. 2001). It is often stated that the risk for *T. piniperda*-induced mortality is increased after only one year of defoliation in Scots pine (eg. Butovitsch 1946; Lekander 1953; Straw 1996), but little is known about the beetle-attack dynamics subsequent to defoliation. Furthermore, the capacity of *T. piniperda* to actually kill trees is not well established, and it is unclear if colonised weakened trees would have survived without beetle colonisation.

Secondary attack by bark beetles, tree mortality, top-kill and growth losses are likely consequences of defoliation, and substantial tree mortality following defoliation could be disastrous for a private landowner who is dependent on forest yield for an annual income. Therefore, a good decision basis is needed for successful defoliator-outbreak management, which involves knowledge of potential yield losses. Currently, such knowledge is scarce for defoliation of Scots pine in general, and for *B. piniaria* defoliation, and foliage losses caused by *Gremmeniella abietina* (Lagerberg) Morelet. in particular.

Aims and hypotheses

The general aim of the present thesis is to improve the knowledge of the consequences of foliage losses in Scots pine, in terms of lost yield, and thereby improve the decision basis for management of future insect defoliator outbreaks and *G. abietina* epidemics. How tree mortality, secondary attack by *T. piniperda*, top-kill, growth losses, and needle-biomass recovery vary with defoliation intensity, time since defoliation and tree dominance status is described. Growth losses and tree mortality are quantified as a function of pine looper moth defoliation intensity. Of special interest is whether defoliation thresholds for tree mortality, top-kill, and growth losses

can be detected. The significance of secondary attack by *T. piniperda* for yield losses in Scots pine after defoliation events by *B. piniaria* and *G. abietina* is evaluated. To achieve improved knowledge on defoliation impact in Scots pine, four key-hypotheses were formulated.

1. There is a defoliation-threshold for growth losses.
2. Growth losses are proportional to defoliation intensity.
3. There is a defoliation-threshold for tree mortality.
4. *Tomicus piniperda* can cause tree mortality.

Study system and methods

Study organisms

Pinus sylvestris

Forests of Scots pine (*Pinus sylvestris* L.) are an integral part of the boreal ecosystem in the Palearctic region (Richardsson & Rundel 1998). The geographical distribution of Scots pine is large as it grows from the Atlantic coast in the west far into Siberia in the east, and far beyond the Arctic Circle in the north down to the Mediterranean area in southern Europe. It is also grown and used as a Christmas tree in North-America (Haack et al. 1997). In Fennoscandia, Scots pine is the only native pine species, and often dominates the landscape in the northern parts of the area where it forms natural monocultures in dry infertile sites. Scots pine also grows well on fertile sites in stands mixed with hardwoods or spruce. Scots pine is a commercially important coniferous tree species within its entire geographical range.

Fennoscandian pine forests are generally intensively managed and healthy, but pests and diseases can cause substantial damage (for review see Eidmann & Klingström 1990). Pine weevils (*Hylobius abietis*) and snow-blight (*Phacidium infestans*) for example, cause damage to seedling stands. Browsing by moose (*Alces alces*), and shoot insects like (*Rhyacionia buoliana*) and needle-twist-rust (*Melampsora pinitorqua*) cause damage to sapling stands. Compared to root rot (*Heterobasidion annosum*), the spruce bark beetle (*Ips typographus*) attacking Norway spruce (*Picea abies*), and pine weevil damage, bark beetles (*T. piniperda*, and *T. minor*) on Scots pine are of less economic significance. Older stands of Scots pine mainly suffer from fungal epidemics like the recent one by *Gremmiella abietina*, or defoliator outbreaks. The European pine sawfly (*Neodiprion sertifer*) is the most frequent defoliator of Scots pine, but not as destructive as the less frequently occurring pine looper moth (*Bupalus piniaria*).

Bupalus piniaria

The pine looper moth (*Bupalus piniaria* L.) (Lepidoptera: Geometridae) is a serious forest pest in Europe (Escherich 1923; Butovitsch 1946; Varley 1949; Crooke 1959; Barbour 1988). It is widely distributed in Sweden, but its outbreak range is confined to areas in southern Sweden, which receive the least precipitation (< 550 mm/year) and experience the warmest summer temperatures (Trägårdh 1939). The pine looper is univoltine and feeds primarily on Scots pine, its native host, but it has also been found feeding on other species of pine (Barbour 1988). Adults fly in mid-summer, and after mating, females preferably deposit their eggs on one year-old needles (Šmits & Larsson 1999). Larvae hatch in July and feed on needles until late autumn in early November when most foliage damage occurs (Broekhuizen et al. 1993). According to (Trägårdh 1939) the larvae feed at first in the top part of tree crowns, which is defoliated first, and thereafter move downwards. Larvae pupate and over-winter in the duff (Barbour 1988). The recent pine looper outbreak at Hökensås in 1996 is described below.

Gremmeniella abietina

The fungal pathogen *Gremmeniella abietina* (Lagerb.) Morelet. is known to occur in forests and nurseries world-wide. It infests and causes damage to a variety of coniferous tree species in Europe, North America, and Asia (Yokota 1975; Setliff et al. 1975; Laflamme & Lachance 1987; Barklund & Rowe 1981; Hansson 1998; Senn 1999; Laflamme & Blais 2000; Karlman 2001). Outbreaks of *G. abietina* have often been preceded by extreme weather conditions (Manion 1991; Venier et al. 1998; Karlman 2001). *G. abietina* infects shoots, which may die if conditions are favourable for growth of the fungus. Infection is initiated in late summer and most fungus growth occurs in late autumn and winter, but symptoms are not visible until the following summer (Patton et al. 1984; Barklund & Hellgren 1992). When locally prevalent, *G. abietina* is commonly found in the lower branches of larger trees (Barklund & Hellgren 1992), but under certain conditions, all living shoots may be killed and the whole tree crown may become infected by the fungus (eg. Manion 1991).

Tomicus piniperda

The geographical range of the pine shoot beetle (*Tomicus piniperda*, L.) (Coleoptera: Curculionidae, Scolytinae) stretches from Europe in the west (eg. Långström & Hellqvist 1993) across Eurasia to China (eg. Hui 1991; Långström et al. 2002) in the east. It has recently been established in North America as well (Haack et al. 1997). Pine shoot beetles (*T. piniperda*, and *T. minor*, Hart.) are insect pests in Swedish

forestry, and the damage they do is threefold: (i) they feed in pine shoots causing growth losses and top damage (Långström 1980, 1983; Långström & Hellqvist 1991) (ii) they colonise weakened trees (Lekander 1953; Långström et al. 2001), and (iii) they introduce associated blue-stain fungi (Solheim et al. 2001) that degrade the quality of timber (eg. Nylinder et al. 2000). Pine shoot beetles are monogamous, univoltine, and monophagous on Scots pine in Sweden. *T. minor* is considered less important of the two pine shoot beetle species, as it is less common and seldom occurs alone in colonised trees (Långström & Hellqvist 1993). The blue-stain fungus associated with *T. minor* is also less pathogenic than those associated with *T. piniperda* (Solheim et al. 2001). Thus, this thesis mainly concerns *T. piniperda*, which flies early in the spring (Lekander 1984), and is guided to host trees by volatiles, such as monoterpenes and ethanol, emitted from host trees (Schroeder & Eidmann 1987). *T. piniperda* prefers to colonise the lower part of pine stems (Saarenmaa 1983; Långström 1983), and in May or June, the parent beetles re-emerge and begin to feed in the pith of pine shoots. After mid-summer, emerging young beetles start to feed on pine shoots. Attacked shoots fall off the tree during the autumn and the following winter, which can result in substantial foliage losses (Långström & Hellqvist 1991, 1992). Although not common, some parent beetles may establish a second sister-brood. *T. piniperda* overwinter in the thick outer bark at the base of living pine trees (Långström 1983).

Outbreak descriptions

The Bupalus piniaria outbreak

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, and an initial aerial survey indicated that roughly 2000 ha were severely defoliated, 2000 ha were intermediately defoliated, and 3000 ha were slightly 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 aimed to represent the classes 10%, 30%, 50%, 70% and 90% defoliation. These damage classes were then related to estimates on the density of pine looper pupae obtained from ground surveys. As high densities of pine looper pupae indicated a risk for continued defoliation in 1997, permission was given 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 and the reference areas were selected to remain unsprayed in order to facilitate evaluations of the

control efficiency. In early August, approximately 4000 ha were sprayed from helicopter using Foray 48B® at an ultra-low volume rate of 3.5 litres per hectare containing 10600 IU per mg of the above mentioned strain of BT. The control operation was successful but probably redundant as no additional defoliation occurred in unsprayed reference areas either. Hence, all pine looper-infested stands suffered only one year of defoliation and the study was redirected towards assessing needle and growth losses following varying levels of defoliation during that one-year.

The Gremmeniella abietina outbreak

In 2001, an estimated area of 200 000 – 300 000 hectares of Scots pine forest in the central area of Sweden was discovered to suffer from damage caused by *G. abietina* (Wulff & Walheim 2002). The outbreak was preceded by wet summers in 1998 and 2000, which may have favoured spore dispersal, followed by mild winters in 1999 and 2000, which may have been favourable for growth of the fungus (Barklund & Unestam 1988 and references therein). There were no reports of new infections in 2002 and the main epidemic seems to have occurred in one year only.

Study sites

The Hökensås area (58° 05' N lat.; 14° 06' E long.) is an esker made up by glaciofluvial deposits dominated by fine sand, and most of the area is 220-280 m above sea level. Annual precipitation is low (550-600 mm), and the water holding capacity of the soil is low resulting in 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 of wood is low (3.8 m³ 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 120-140 years.

The Fredriksberg stand (60° 06' N. lat.; 14° 29' E. long.) was about three hectares in size and contained even-aged, pure 40-year-old Scots pine with varying severity of damage caused by *G. abietina*. The Fredriksberg site was located in the centre of the *G. abietina*-infested area.

Field procedures

Hökensås (papers I, II, III, and V)

In August 1997, information from CIR-images was used to identify 47 stands in different parts of the pine looper outbreak area. The aim was to find similar stands in the areas classified as undefoliated,

moderately, severely and totally defoliated in the aerial survey. In general, the intensity of defoliation increased from west to east within the outbreak area. Therefore, the chosen stands of different damage and age classes were situated along main roads running in east-west direction across the outbreak area (see map in Långström et al. 1999). Some of the stands were situated in the unsprayed reference areas but the majority of plots were allocated to BT-sprayed areas. Since no additional defoliation occurred in 1997, these stands were not kept separate in later analyses. Within the chosen stands, plot sites were located by walking 20 to 30 metres from the edge into the stand to avoid edge effects. Each plot consisted of about 20 trees so plot size depended on stand age and density, and ranged from 50 to 300 m². We mainly used younger stands, approximately 40-years of age, since they were common in the area and frequently severely damaged, but we also included some older and mature stands. Altogether, 47 plots were laid out and 30 of these were in 40-year-old stands.

For each stand plot, the defoliation level was assessed visually as a "stand damage class" by inspecting three to five dominant trees with binoculars. The classification used was the same as the one mentioned above for the CIR-images, 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. To compare this visual inspection of "stand damage class" with CIR interpretation of defoliation levels, the stand plots were marked on the CIR-images (scale 1:8000). The defoliation class (0 - 6) was thereafter interpreted in the CIR-images by the contractor (Nordpointer AB). For both classifications, some stand plots were rated as intermediate, eg. class 4-5, when they could not be assigned to either category.

For a verification of that visually estimated differences in "stand damage classes" and CIR-interpreted damage classes were reflected in the remaining foliage of individual trees, one 40-year-old tree was felled in 13 of the young stands which represented different damage classes. Each of the 40-year-old sample trees was felled in the vicinity of each of the 13 plots. The chosen trees were representative for the defoliation intensity in the stand, and were taken at 10 metres distance from the plot periphery. Suppressed or dominant trees were avoided. After felling, these trees were analysed whorl by whorl from the top down to the last living whorl. For each branch the base diameter was measured and the remaining foliage was estimated for each age class of needles (current, last-year, two-year-old and three-year-old needles, in paper I 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% defoliation. Finally, height and diameter at 1.3 metres height (dbh) was recorded for the tree. For each of these

13 trees, one randomly selected branch in whorls 1996, 1991, 1986 and 1981 (if present) was sampled for additional analysis, 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 oven-dried. Needles were separated from twigs, and thereafter re-dried and weighed.

To quantify tree mortality, top-kill, and growth losses as a function of defoliation intensity, the remaining foliage present on each tree within each plot in the 47 stands, was visually estimated using the above-mentioned classes: 0%, 10%, 30%, 50%, 70%, 90% and 100% defoliation. Using binoculars, we reconstructed the defoliation intensity in 1996 by disregarding the 1997 age class of needles. In papers II and III, the 47 plots were regrouped into four damage classes based on the plot-average defoliation intensity, as estimated for individual trees. Based on these calculated average plot-defoliation intensities, we grouped the plots into four main damage classes, 1: 91-100%, 2: 41-90%, 3: 11-40%, 4: 0-10% remaining foliage. Furthermore, the diameter (dbh) was recorded for each tree, and trees within each plot were grouped into three numerically equally large social status classes based on stem diameter at 1.3-metres height. The smallest group of trees was referred to as suppressed (S), the middle group as intermediate (I), and the largest group of trees was dominant (D). For each tree within the 47 plots we also recorded top damage using the classes: T0 = top-kill (with at least the leader shoot and the branches in the uppermost whorl dead), T1 = damaged living top (no current shoots), T2 = damaged living top (few healthy current shoots), and T3 = healthy top (normal current shoots). The visual estimates of needle biomass present in trees, tree vitality and top-damage were repeated for all trees on plots in early June 1998, early June 1999, late September 1999, in mid May 2001, and in late September 2001.

In each year after the outbreak beginning in autumn 1997, dead trees on plots were inspected. Attacks by *T. piniperda* on trees within the 47 plots were recorded as successful if trees were beetle-colonised and dead. Living trees with beetle attacks were classified as unsuccessfully attacked, since tree death is a prerequisite for beetle colonisation. Trees attacked in 1996 were separated from trees attacked in 1997 by their general appearance (stage of decomposition). In autumn 1997, 1998, 1999, and in spring 2001 we counted exit holes, counted and measured egg gallery lengths in beetle-attacked dead trees.

To obtain an estimate of the abundance of pine shoot beetles in the area, fallen shoots that had been tunnelled by pine shoot beetles (it was impossible to separate shoots tunnelled by *T. piniperda* and *T. minor*) were counted and removed at a 10 m² circular subplot,

centred at the centre stake of each of our 47 plots. The shoot count was done in spring 1998, 1999, 2000, 2001, 2002, and 2003. Based on needle colour and general appearance, the fallen shoots found in spring 1998 were grouped in old and new shoots to try to separate shoots fallen during the autumn-winter 1996-1997 from shoots fallen in 1997-1998.

In 2002, we selected trees of similar size and age (40 years) from 21 of the 47 plots in order to quantify growth losses resulting from the pine looper outbreak. In total, 40 trees were felled and thereafter de-limbed, whorl-by-whorl, and remaining foliage for each branch was estimated using the above-mentioned classes (0 – 100% defoliation). Shoot feeding by pine shoot beetles on branches was visible as tunnelled shoots or hollow shoot-stumps, and these were counted for each branch. Thereafter, tree height, and stem diameter (dbh) was measured. Tree height was measured for the years 1993-2002. In severely defoliated trees where top-kill was frequent, tree height was measured on the main stem up to the dead top, but also along the new top (uppermost living branch), up to the new leader shoot. Finally, a stem disc was cut at 1.3 metres height for tree-ring analysis. Stem discs were kept frozen until analysed.

Fredriksberg (paper IV)

To investigate the capability of *T. piniperda* to cause tree mortality in trees weakened by heavy infestation by *G. abietina* an even-aged, pure 40-year-old Scots pine stand, containing a mixture of trees with varying levels of foliage loss, caused by *G. abietina* was selected for a field trial in the autumn of 2001. Two persons visually estimated the degree of damage, expressed as the amount of foliage loss in the uppermost two-thirds of the crown on each of the trees selected (n=244). The estimates were thereafter compared, and an average of the two estimates was recorded for each tree. The following damage classes were used: (1) = 50-69%, (2) = 70-79%, (3) = 80-89%, (4) = $\geq 90\%$ foliage loss. Trees estimated to have less than 50% foliage loss were not included. Selected trees were numbered and measured for diameter (dbh), and on 28 March 2002, prior to beetle flight, 20 trees in each damage class were baited (B) with alpha-pinene to induce attack, sprayed with an insecticide (S) to deter attack, or left untreated, as control (C) trees. On 5 August 2002, all trees were inspected. On each tree (living and dead), we checked for signs of beetle attack by peeling away the furrowed bark on the lower part of the stem (from root to about 2.5-m height. Trees were recorded as dead, if no green foliage or living shoots were observed. Each tree was classified as: (i) colonised: dead tree in which *T. piniperda* produced offspring (egg galleries completed and exit holes observed), (ii) attacked but not colonised: tree survived or died after attack by *T. piniperda*, but no offspring was produced (egg galleries were initiated but incomplete and no exit holes were observed), (iii)

not attacked: dead or living tree, in which no egg galleries were initiated by *T. piniperda*.

Results and Discussion

Comparison of defoliation estimation methods (paper I)

To secure data on the pine looper defoliation intensity in 1996, and to confirm that visual estimates correlated with measured defoliation intensity, we made a comparison of foliage estimation methods. The field estimate correlated well ($r^2=0.93$) with plot means derived from tree-wise estimates; they also correlated well with the calculated needle biomasses per tree ($r^2=0.90$). However, the attempt to quantify defoliation on a landscape level using CIR-images was less successful. The defoliation intensity, as estimated by damage classes in the CIR-pictures only agreed with the field-damage estimates at the higher end of the damage scale. Others have used CIR-images more successfully (Ekstrand 1994; Stanley et al. 1996). In these studies defoliation of individual trees were made possible by interpretation keys for the objects studied, which may be obtained by verification of interpretation results in the field and subsequent calibration. Ciesla et al. (1984) successfully assessed fewer defoliation classes for larger blocks of defoliated trees as compared with the present study. In addition, in all of these studies CIR-images used had a larger scale. Visual estimates of defoliation have frequently been used for assessing insect damage (Alfaro 1991; Ostaff & MacLean 1995; MacLean & Ebert 1999; Långström et al. 2001), fungal diseases (Nevalainen & Yli-Kojola 1990), or forest decline symptoms (Aamlid 1997). However, the accuracy of these estimates and of visual estimates of defoliation in the present study is unknown. How well our different ways of estimating the foliage of differently defoliated trees represent the true foliage on those trees is therefore not known. However, the visual estimation of the stand damage class was well enough correlated with an objective way to assess defoliation level, and should at least depict relative differences between trees in the range from 0% to 100% defoliation. Thus, the field damage classification formed a relevant basis for later, tree mortality and growth loss studies.

Tree mortality and top-kill (paper II)

The pine looper defoliation in 1996 caused tree mortality and extensive top-kill in the years following the defoliation. Tree mortality peaked two years after defoliation, and amounted to a plot-average of 25% in stands suffering from $\geq 90\%$ defoliation (Fig. 1). Tree mortality occurred also in less defoliated stands, primarily as

self-thinning of suppressed trees, but did not exceed an average of 3% in plots suffering $\leq 70\%$ defoliation. Thus, the single year of defoliation only caused significant tree mortality in plots with $\geq 90\%$ defoliation.

It is often stated that Scots pine in Europe survives one year of severe defoliation, which is supported by field studies (Butovitsch 1946; Austarå et al. 1987; Långström et al. 2001). However, if defoliation occurs in two consecutive years then the risk for tree mortality is substantially increased. Långström et al. (2001) observed 50-75% mortality in large and small Scots pine after two consecutive years of complete sawfly (*Diprion pini*) defoliation, whereas trees defoliated in a single year all survived.

In general, the risk for tree mortality increases with increasing defoliation intensity, and numbers of seasons of defoliation. Similar to *Diprion pini*, outbreaks of pine loopers are usually not sustained (Berryman 1986, Barbour 1988), as in the case of the spruce budworm (*Choristoneura fumiferana*) (MacLean & Ostaff 1989; Shepherd 1994; Maclean & Piene 1995), which can cause even more extensive tree mortality due to sustained outbreaks.

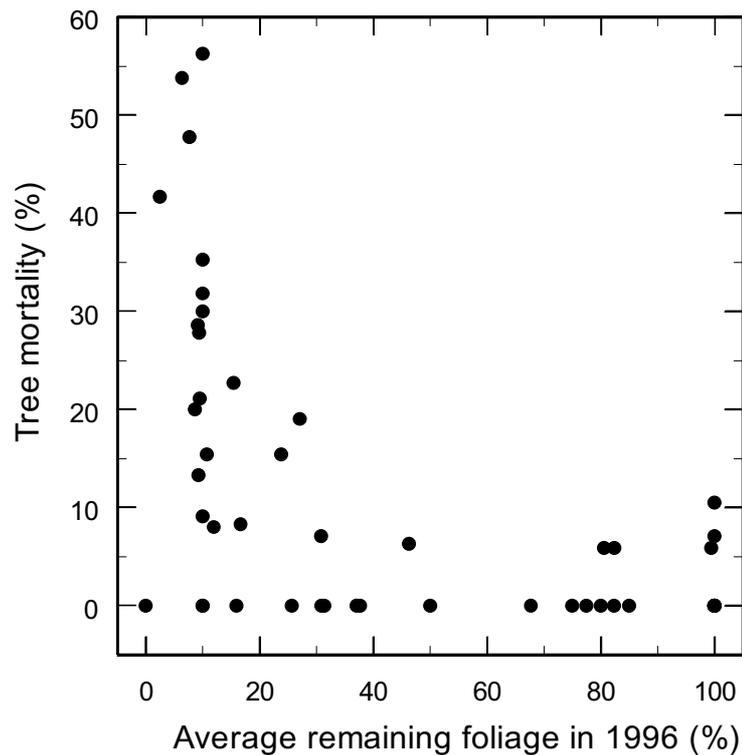


Fig. 1. Tree mortality during 1996-2000, in each of 47 plots in relation to the plot-mean foliage carried by trees after defoliation in 1996. (paper II).

For instance, spruce budworm defoliation during several consecutive years resulted in 87% mortality of the merchantable balsam fir (MacLean & Ostaff 1989), and 94-100% tree mortality in severely defoliated spaced plots (Maclean & Piene 1995).

Three years of defoliation by the Douglas-fir tussock moth (*Orygia pseudotsugata*) resulted in Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) mortality amounting to 51% (Alfaro et al. 1987). Tree mortality mainly occurred in trees with $\geq 90\%$ defoliation. In contrast, a single year of moderate defoliation only resulted in growth losses (Alfaro & Sheperd 1991). Douglas-fir mortality amounting to 40% after five years of moderate spruce budworm defoliation mainly occurred among trees suffering a cumulative defoliation of 200% or more, which equals about two years of complete defoliation (Alfaro et al. 1982). Thus, lower annual defoliation intensity during several consecutive years could potentially equal higher defoliation intensity during fewer years in terms of resulting mortality. However, Alfaro et al. (1987) concluded that defoliation intensity had a much greater impact on tree survival than the number of seasons of defoliation, and further that $< 80\%$ defoliation was a survival-threshold for defoliated Douglas-fir. Wickman (1978) also observed that 90% of the Douglas-fir mortality occurred in stands with $> 90\%$ defoliation. Similarly, the “survival threshold” found in our study for Scots pine after a single year of pine looper defoliation requires that trees retain at least 10% of full foliage.

Tree mortality in the present study, however, varied with tree size, and suppressed trees suffered higher mortality than intermediate and dominant trees, and only suppressed trees died in plots with $< 90\%$ defoliation. Tree mortality was frequent in severely defoliated stands but varied from 0% to 60% within the most severely defoliated plots in the outbreak area. The percentage of tree mortality decreased with increasing tree diameter classes, seen over the whole sampled population of trees, suggesting that the oldest and more widely spaced stands, where trees were large, suffered less mortality than the denser and younger stands (Fig. 2). However, it must here be emphasized that data merely indicates such a trend, and more plots in old severely defoliated stands would have been required to determine the validity of the trend. Similarly, Douglas-fir mortality primarily occurs among the smaller and suppressed trees (Wickman 1978; Alfaro et al. 1982). However, Maclean & Piene (1995) reported little difference in balsam fir (*Abies balsamea*) mortality between spaced and unspaced stands after spruce budworm defoliation, and concluded that defoliation intensity would override any possible impact of spacing on tree mortality. Small trees within stands suffered the highest tree mortality. Maclean & Piene (1995) further concluded that varying tree mortality among plots was not related to

stand characteristics. Thus, the variation in between-plot mortality observed here, apparently related to stand structure, is seemingly contradictory to the above-mentioned studies.

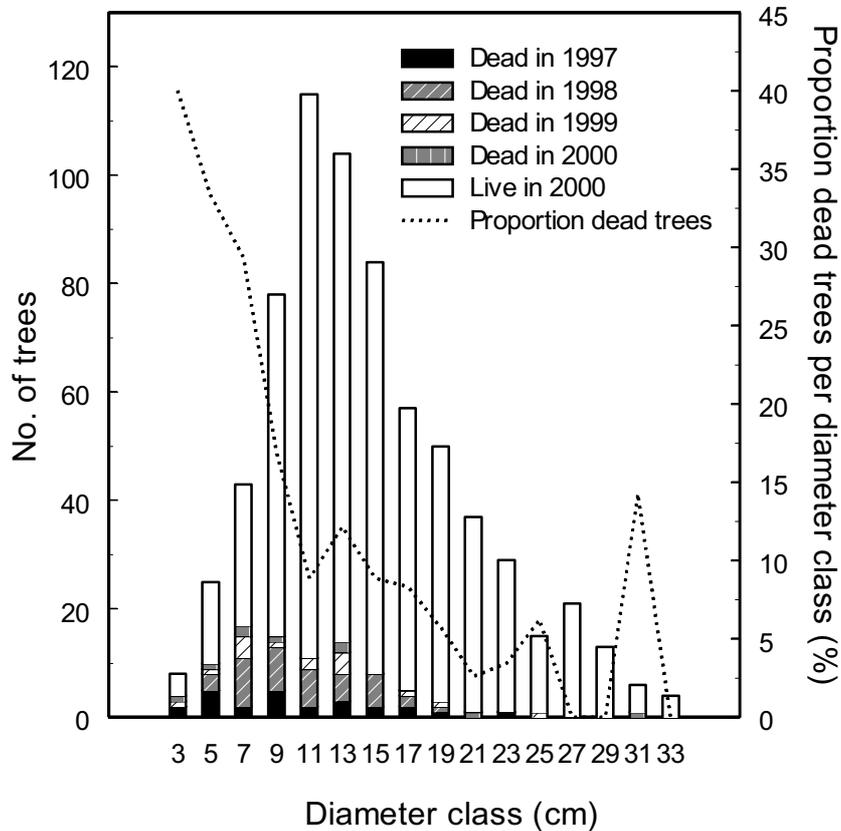


Figure 2. The diameter distribution of 755 trees in 47 plots. Stacked bars summarise the number of dead trees in each year, and living trees in year 2000. The dotted line represents per cent mortality in each diameter class. (paper II).

Another consequence of defoliation is top-kill in severely defoliated trees. Top-kill was most frequent in trees on plots with $\geq 90\%$ defoliation, and 50% of all trees in these stands suffered from top-kill at the end of the study period in spring 2001. The observation that top-kill occurred already in 1997 indicates a direct effect of the defoliation. Besides stunted height growth, top-kill in trees may result in undesirable stem deformations. Browsing damage to young Scots pine caused by moose (Bergqvist et al. 2001) and leader damage to young trees caused by insect feeding (Kletecka 1992) results in undesirable stem deformations (Nylinder et al. 2000), when a lateral branch takes over as a new leader. We suggest that the top-kill observed in the present study will result in similar stem

deformations, but the severity of top-kill depends on the height at which it occurs (Alfaro et al. 1987; Nylinder et al. 2000), i.e. if it will affect the most valuable butt-log or not. Straw (1996) only found a few trees with stem deformations after final harvest, but the defoliation episodes were never visibly detected during the 70-year-long rotation period of the trees, and defoliation intensity was therefore modest. Top-kill after defoliation has been observed in Douglas-fir (Alfaro et al. 1987), Jack pine (McCullouch et al. 1996), Grand fir (Wickman 1978), and in hybrid poplars (Kosola et al. 2001). Generally, the frequency of top-kill increased with the severity of defoliation. Top-kill in Douglas-fir increased with increasing tree size (Wickman 1978; Alfaro et al. 1987), which is in contrast to the present study where there was no difference in top-kill with tree size.

The role of *Tomicus piniperda* in tree mortality (paper III)

The between-plot variation in tree mortality observed in the present study, as potentially dependent on tree size or stand structure and seemingly contradictory to for instance MacLean & Piene (1995) as discussed above, is not contradictory if one scrutinizes the reasons for the between-plot variations in tree mortality. MacLean & Piene (1995) concluded that the plot-to-plot variability in tree mortality did not depend on stand structure, but was an effect of spruce budworm pressure (abundance), and that the spruce budworm created “holes” of dead trees in stands where the budworm pressure is high. Similarly, in the present study, tree mortality was clustered to certain stands, or parts of stands where the secondary pest *T. piniperda* frequently colonised weakened trees. The occurrence of *T. piniperda* could potentially be linked to stand structure characteristics. The larger trees in older stands could have escaped beetle-induced tree mortality because they could tolerate more attacks, or because they were more widely spaced and therefore had higher vigour than younger trees in more dense stands, or both. For *Ips typographus* it is known that a sufficient number of beetle-attacks per square unit of bark surface are required for successful colonisation (Mulock & Christiansen 1986). Thus, in 1997 when the numbers of *T. piniperda* were low, only smaller trees were subjected to a sufficient number of beetle-attacks required for colonisation. Possibly therefore, *T. piniperda* got a “foothold” in younger more dense stands where trees generally were smaller than in older stands. However, there were also variations in tree mortality between plots within the youngest most severely defoliated age class, suggesting that factors other than tree size also were involved.

In total, 82% of all dead trees had been colonised by *T. piniperda*, and although it is often stated that Scots pine survives one year of complete defoliation, it is equally often stated that the risk for pine

shoot beetle attack increases following a single year of defoliation. An early example of this is the reported results of a pine looper outbreak in a Scots pine stand in southern Sweden during 1917 (Trägårdh 1939). The pine looper had been sighted already in 1916 but apparently not caused any noticeable damage until 1917 when pines were severely defoliated. One year after the defoliation event, in 1918, only a few (4%) of the trees, all suppressed, were dying as a result of attack by *T. piniperda*. However, an appraisal of the stand 10 years later showed that tree mortality amounted to 28.4% of the total number of trees, which is close to the 27% mortality of the sampled population of trees recorded after the recent pine looper outbreak (II). In contrast, Butovitsch (1946) estimated tree mortality caused by *T. piniperda* after a 2000 hectares large pine looper outbreak of two years duration (1943-1944) to 1%. However, Butovitsch (1946) claimed that those areas where *T. piniperda* had caused severe mortality were missed in his study, and that the abundance of the beetles was concentrated to a number of “hotspots”, and not evenly dispersed in the defoliated area.

An important conclusion to be drawn from the above-cited studies, however, is that *T. piniperda* is likely responsible for a great deal of the tree mortality observed after a single year of pine looper defoliation. Similar to *T. piniperda*, fir engraver beetles (*Scolytus ventralis*) (Wickman 1978; Wright et al. 1984), and Douglas-fir beetles (*Dendroctonus pseudotsugae*) (Wickman 1978; Wright et al. 1984, Alfaro et al. 1987) colonise Grand fir (*Abies grandis*) and Douglas-fir with > 90% defoliation. However, *T. piniperda* appears to be more important for mortality in Scots pine after defoliation compared to secondary bark beetles attacking defoliated Douglas-fir (Alfaro et al. 1982, 1987, Wickman 1978), which is surprising since both the fir-engraver beetle and the Douglas-fir beetle been reported to cause extensive tree mortality elsewhere (eg. Schmits & Gibson 1996; Ferrell 1991). However, severe outbreaks of both species have often coincided with droughts (Schmits & Gibson 1996; Ferrell 1991) and drought in combination with insect defoliation may have aggravated outbreaks by the fir engraver beetle (Berryman 1973). As already mentioned, 82% of all dead trees had been colonised by *T. piniperda* and the percentage of dead trees colonised by *T. piniperda* in each year increased with time since initial defoliation. The significance of *T. piniperda* as a causal agent for tree mortality probably increased with time since defoliation, but also with increasing tree size since the few large trees that died were colonised. The few trees that died without colonisation by *T. piniperda* were the very smallest, and most of the very smallest trees died early, in 1997, when the abundance of *T. piniperda* was low (Fig. 3).

Slow growing and suppressed trees are generally considered to have an inferior defensive capacity in comparison to larger, faster growing neighbours, i.e. they have reduced tree vigour. Tree vigour

of coniferous trees is often measured as a function of leaf area and stem growth, and Waring & Pitman (1985) showed that lodgepole pine (*Pinus contorta*) resistance to mountain pine beetle (*Dendroctonus ponderosae*) attack increased for remaining pines after thinning. Stand thinning reduces competition for nutrients and allows for more light into the canopy which increases photosynthesis and thus growth. Similarly, Larsson et al. (1983) showed that suppressed ponderosa pines are more susceptible to attack by mountain pine beetles. However, no clear difference in tree vigour was found between Tomicus-killed and surviving pine trees (Långström & Hellqvist 1993).

Reduced tree vigour due to snow-breaks (Schroeder&Eidmann 1993, pruning (Långström et al. 1992) forest fire (Långström et al. 1999b), defoliation (Långström et al. 2001, **III**), or foliar damage caused by pathogens (**IV**) have been demonstrated to increase host susceptibility to pine shoot beetle attacks. Hence, not only dominance status, but also defoliation intensity, among other factors, plays a vital role for the production of secondary metabolites, used as defence against phloem feeding insects and their associated blue stain fungi.

In the present study, we suggest that the population density of *T. piniperda* built up in the first year after defoliation when tree vigour was low. In 1998, there was still an abundance of low-vigour trees and the beetle population reached its maximum as indicated by the shoot-count (Fig. 3). In 1999, most trees had already recovered beyond the risk of attack, and few susceptible trees remained; and consequently beetle numbers declined. Thereafter, the population increased in numbers again as a result of snow damage, which occurred in the area during the winter 2000-2001. Similar patterns of bark beetle-attack over time after defoliation have been observed elsewhere for *T. piniperda* (Lekander 1953; Långström et al. 2001), and for *Scolytus ventralis* and *Dendroctonus pseudotsugae* (Wright et al. 1984).

Långström et al. (2001) found no mortality in Scots pine stands after a single year of complete sawfly-defoliation, whereas adjacent stands defoliated in two consecutive years suffered heavy mortality. The difference between that study and the present may be explained by differences in foliage recovery. The foliage recovery, as estimated by Långström et al. (2001) was comparatively faster than the estimated foliage recovery at Hökensås (**II**), and trees quickly regained enough foliage to become resistant to attack by *T. piniperda*.

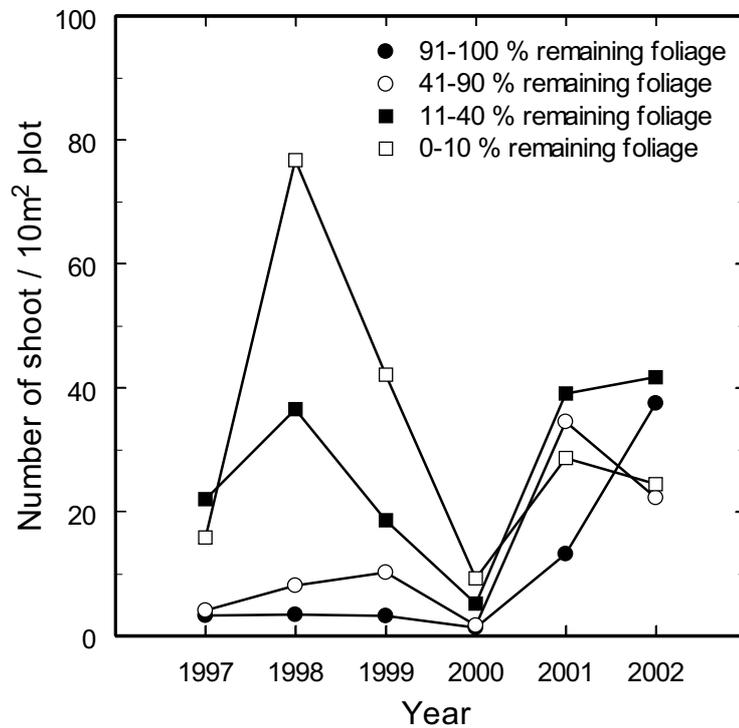


Fig. 3. Beetle-pruned pine shoots/10m² plot in relation to defoliation class. (paper III).

The single-year defoliated trees also grew more vigorously prior to the defoliation than the trees defoliated in two consecutive years, possibly as a result of differences in stand structure or site fertility, which could have facilitated a speedy foliage recovery (Långström et al. 2001). A second possible explanation may be that the abundance of *T. piniperda* was low in the sawfly study, and since there were plenty of susceptible pines adjacent to the single-year defoliated ones, pine shoot beetles reproduced in the most severely damaged trees. However, the shoot count made by Långström et al. (2001) indicated no major difference in beetle abundance between the single-year defoliated area and the adjacent two-year defoliated area, which were similar to severely defoliated areas in the present study. Thus the former explanation of a speedy foliage recovery seems the most likely in explaining the absence of tree mortality in single-year completely defoliated stands observed by Långström et al. (2001).

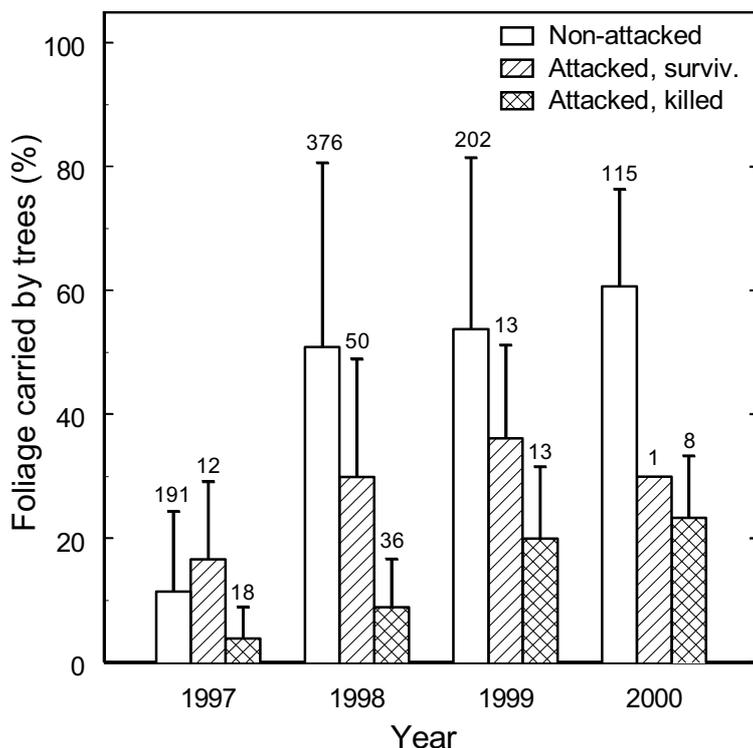


Fig. 4. Average amount of foliage prior to attack by *T. piniperda*, of trees that were not attacked, trees that were attacked but survived, and trees that were attacked and killed in different years. Non-attacked trees only include trees that were standing on plots where other trees were attacked in that year. Error bars indicate SD, and n = number of trees. (paper III).

The significance of a speedy foliage recovery to avoid susceptibility to *T. piniperda* attack was evident also in the Hökensås area, as the amount of foliage in both colonised trees, and in trees where colonisation failed, were higher in each year after defoliation (Fig. 4). Inspection of dead trees in every year revealed that trees that died following the attack carried less foliage at the time of attack than those that survived attack. Among trees colonised, and presumably killed by *T. piniperda*, the attack density increased with increasing amount of foliage in trees. As already noted, most tree mortality occurred among suppressed trees in plots with 90-100% defoliation. Not only was the percentage of attacked trees higher in the suppressed tree category, 28% compared to 14% and 9% in intermediate and dominant trees, but also the percentage of successful attacks (i.e. trees died following the attack) was higher in suppressed trees. Few intermediate and dominant trees died without being colonised by *T. piniperda*.

Since *T. piniperda* is dependent on host trees with reduced vigour for successful reproduction (Schroeder & Eidmann 1987; Långström & Hellqvist 1993), the beetle will have increased difficulties in locating suitable host trees when host tree vigour increases. Consequently, the density of egg galleries steadily increased from 1997 to 2000, as a result of a larger beetle population searching for a decreasing number of suitable trees to colonise. Eidmann & Nuorteva (1968), and Saarenmaa (1983) found intraspecific competition to reduce the rate of reproduction of *T. piniperda* at attack densities between 50-100 egg galleries/m² and increased intraspecific competition in the later years most likely occurred in the present study since the rate of reproduction decreased during the study period. This may have contributed to the observed decline in number of trees attacked by *T. piniperda* in 1999 and in 2000. However, attacks by *T. piniperda* most likely ended as a result of a lack of susceptible host trees.

Experimental evidence for *T. piniperda* aggressiveness (paper IV)

Our results indicate that *T. piniperda* was responsible for most of the tree mortality observed after the pine looper moth defoliation event (II, III). Colonised dead trees were considered to be “beetle-killed”. However, in reality it is impossible to know if these “beetle killed” trees would have survived or died if not attacked. To investigate whether *T. piniperda* had the potential to actually cause tree mortality, Scots pines with varying degree of foliar damage caused by the fungal pathogen *Gremmeniella abietina* were subjected to one of three treatments. The trees were either: 1. baited with alpha-pinene to induce beetle attack, 2. sprayed with an insecticide to deter beetle attack, or 3. left untreated as control. Most trees with < 90% foliage loss survived, unless heavily attacked by *T. piniperda*. Since 70% tree mortality occurred in each of the treatments in trees with ≥ 90% foliage loss, these trees died from the damage caused by *G. abietina* alone, in spite of the fact that many of these baited and control trees were colonised by *T. piniperda*. Thus, the conclusion is that, yes, *T. piniperda* can cause tree mortality in trees that would have survived unless attacked.

Furthermore, an interesting result of the *G. abietina*-experiment at Fredriksberg was that 70% tree mortality occurred in trees with ≥90% foliage loss, which was far greater than the average of 25% observed after the pine looper outbreak (II). In addition, the 70% tree mortality was entirely caused by the fungus, whereas the primary cause for 25% tree mortality after the pine looper outbreak was *T. piniperda*. The fungal-induced foliage losses are thus much more serious “per unit of foliage lost” in terms of tree mortality than insect defoliation. It is possible that defence against the pathogen adds to the stress caused by the defoliation itself.

The defence deployed by Scots pine against the fungal pathogen *Gremmeniella abietina* is not well known. However, formation of necrosis, twig and stem cankers, resinous filled cavities under the bark, and changes in xylem colour observed in lodgepole pine (*Pinus contorta*, var. *latifolia*) and in Scots pine, indicates that a constitutive as well as an induced defence reaction occurs in response to infection by *G. abietina* (Witzell 2001 and references therein). The defence reaction against *G. abietina* has been described in more detail for saplings of jack pine (*Pinus banksiana*), where intense resin exudation and formation of lingo-suberized tissue is induced in pine shoots in response to infection (Simard et al. 2001). Induced defence reaction in response to insect defoliation is not known to occur in Scots pine (Lyytikäinen 1993). Assuming that the induced defence reaction in response to *G. abietina* is costly, in terms of carbohydrates needed for both regrowth of foliage (Kozłowski 1991), and defence against the pathogen, then defoliation by insects may be less severe (per unit of foliage lost) since available carbohydrate reserves are only required for regrowth of foliage. Furthermore, insect defoliation in Scots pine normally does not kill entire crown sections of trees, as observed after the recent infestation by *G. abietina*. Thus, needle biomass recovery after *G. abietina* infestation may entirely depend on a few surviving branches in the top of trees, which may be crucial for tree survival in the long-term (i.e. ability to resist secondary attack by *T. piniperda*).

Growth losses and Foliage recovery (paper V)

In the absence of a monitoring program (eg. Straw 1996) defoliator outbreaks may not be discovered until after they have caused visible damage, which was the case in the pine looper outbreak at Hökensås in 1996. Even if tree mortality can be avoided by controlling an outbreak, foliage losses may already have occurred and surviving trees will suffer growth losses (Alfaro & Shepherd 1991). To evaluate the costs of a defoliator outbreak, both potential tree mortality and growth losses must be quantified.

In addition to tree mortality and top-kill, height, diameter, and volume growth losses occurred as a result of the pine looper defoliation in 1996. In general, growth losses increased with degree of defoliation and trees with 90 to 100% defoliation lost 56% and 59% of the volume growth respectively during the six years following the defoliation (Fig. 5). Undeveloped trees also grew less than predicted by pre-outbreak tree-ring width. Potentially, undeveloped trees could have been slightly defoliated although undetected, but this is highly unlikely based on the field observations (I). Intact 1997 needle year-classes in branches from felled sample trees added increased support for field observations (I). Most likely natural fluctuations in tree-ring width caused the reduction in radial

growth in undefoliated trees. However, a comparatively large reduction in radial growth in completely defoliated trees from 1995 to 1996 indicated that this group of trees could have been slightly defoliated in 1995. Thus, subtracting the growth losses attributed to natural fluctuations, radial and volume growth losses amounted to approximately 50% during six years in $\geq 90\%$ defoliated trees, which corresponds to a loss of three years of annual growth. However, since the trees with 70% defoliation, or more, still only had about half of normal shoot lengths six years after defoliation, both volume growth losses and height losses of 70%, 71%, and 57% in trees with 100%, 90%, and 70% defoliation respectively will increase. However, the estimated height growth losses are more insensitive than both volume and radial growth loss estimates since the predicted height loss was based on the average leader length of only three years preceding the outbreak.

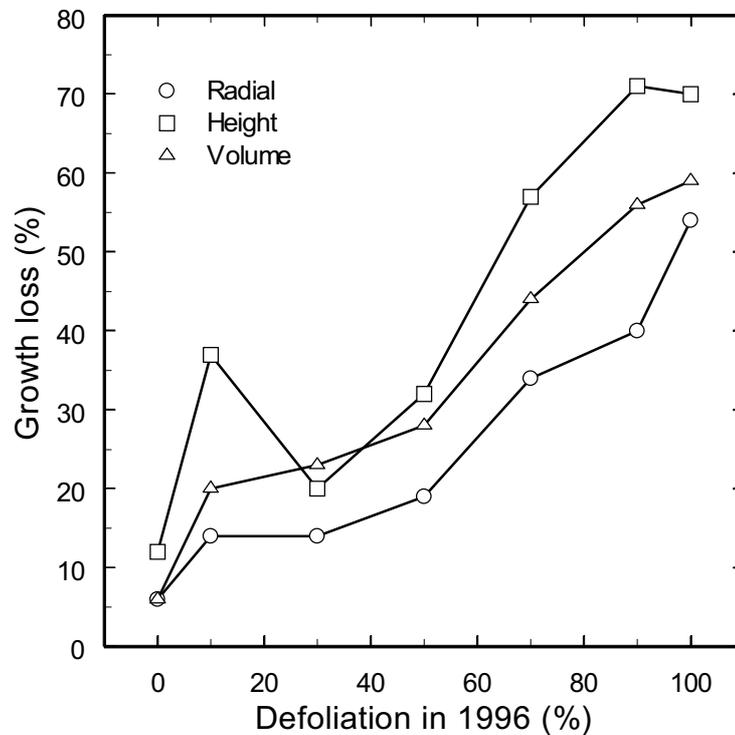


Fig. 5. Radial, height, and volume growth losses in relation to defoliation in 1996. (paper V).

Numerous studies have quantified growth losses in coniferous tree after defoliation by various insect pests (Kulman 1971; Alfaro et al. 1982; Austarå et al. 1987; Piene 1989; Alfaro & Shepherd 1991; Ostaff & MacLean 1995; Straw 1996; Piene & MacLean 1999;

Långström et al. 2001). In general, growth losses increase with the severity of defoliation (Ericsson et al 1980a; Alfaro & Shepherd 1991) and numbers of years of defoliation (Långström et al. 2001). Although quite a few studies on growth losses in Scots pine exists (eg. Eklund 1964; Austarå et al. 1987; Straw 1996; Långström et al. 2001; Glynn & Lindelöw 2002) differences in site conditions, methods used (see Baldwin 1990) and species involved makes comparisons more difficult. Older studies may sometimes suffer from insensitive growth and defoliation measurements (for review see Kulman 1971).

For Scots pine, radial growth losses of completely defoliated trees in the present study correspond well to that recorded for 40-year-old Scots pine after a nine-year recovery period (Austarå et al. 1987). However, the trees were defoliated in two consecutive years by *Neodiprion sertifer*, suffered 78% defoliation in each year, and the stand had a stocking level far below normal levels. Långström et al. (2001) reported that a single-year of complete defoliation of Scots pine incurred a total loss in annual tree ring growth of about 35% during 4 years. These figures are slightly lower than the 48% loss during six years observed in the present study but could be a result of the comparatively faster foliage recovery estimated by Långström et al. (2001). The trees severely defoliated in two consecutive years suffered substantially higher radial growth losses (Långström et al. 2001). Glynn & Lindelöw (2002) found no differences in growth between low defoliation levels (26% of current-year needles lost) and moderate levels of defoliation (70% of current-year needles lost) after defoliation by the needle-shortening pine gall midge (*Thecodiplosis brachyntera*) in Scots pine. The 70% loss of current-year needles probably corresponded to no more than a total defoliation of 20-25% depending on the number of needle-year-classes pines in the area carried. Straw (1996) found significant growth losses although the related pine looper moth pupal densities were far from what is considered to cause damage, and visible defoliation was never detected. Although growth losses in the present study appear to be linear over the whole range of defoliation intensity, we could actually only show significant annual radial growth losses in trees with > 70% defoliation. In conclusion, to determine whether growth losses occurred at low or moderate defoliation intensities would have required a much higher number of replicates to statistically significantly distinguish effects of low defoliation intensities from random variation.

However, the roughly proportional increase in radial growth loss (Fig. 5) with increasing defoliation intensity is consistent with findings elsewhere (Kulman 1971), but Ericsson et al. (1980a) showed that early season defoliation, as related to the quality of foliage removed, has less impact on growth than late season defoliation at similar defoliation intensities. In general, older foliage

contribute less to growth because of their lower photosynthetic capacity, which stems from physiological changes in needles as they age (Kozłowski & Pallardy 1997), but possibly also partly because of an inferior position in relation to current year needles (Stenberg et al. 1994). Ericsson et al. (1980a) concluded that the more severe impact on growth of late season defoliation versus early season defoliation was the lack of 1-year old foliage, the most important source for carbohydrates for growth in the year following defoliation. The accumulation of carbohydrates in preformed buds may also have been disrupted by the late season defoliation. Thus, the impact of defoliation intensity on growth can depend on the timing of defoliation, as related to the quality of foliage removed. Furthermore, the timing of defoliation is related to the defoliator species involved, which makes defoliation-induced growth losses caused by different defoliator species more difficult to generalise.

In coniferous trees there is a relatively stable relationship between photosynthetic leaf area, stem diameter, sapwood cross-sectional area, and root biomass (Waring & Schlesinger 1985), sometimes termed homeostasis (Kozłowski et al. 1991). A loss of needle biomass due to defoliation reduces the sapwood cross-sectional area (Långström & Hellqvist 1991), root growth (Sanchez-Martinez & Wagner 1999), and stem diameter growth (Austarå et al 1987), since production of new foliage may be a stronger sink for available carbohydrates than stem growth (Ericsson et al. 1980a; Piene 1989). The production of new foliage after defoliation in evergreen trees is a slow process compared with deciduous tree species, where partial replacement of lost foliage occurs within the same season (Kosola et al. 2001; Krause & Raffa 1996).

Possibly, the architectural plasticity possessed by deciduous trees (Krause & Raffa 1996, Millard et al. 2001) or improved photosynthesis in remaining foliage (Hoogesteger & Karlsson 1992) reduces the impact of low or moderate levels of defoliation on growth. Piene (1989) concluded that the production of epicormic shoots combined with increased retention of older foliage contributed to rapid growth recovery rates in spruce budworm-defoliated balsam fir. Thus, the ability to quickly replace lost foliage reduces growth losses. In our study, all trees had similar foliage levels in 2002, but heavily defoliated trees had a longer recovery period than less defoliated ones (Fig. 6). This pattern is similar to that observed by Långström et al. (2001) after one year of severe defoliation, whereas trees suffering two years of defoliation had far from recovered after six years.

Compensatory growth after foliage losses in evergreen trees has been hypothesized to occur through enhanced photosynthesis in remaining needles, intensified use of starch reserves, or improved water balance (Ericsson et al. 1980b). The empirical evidence for

compensatory growth in evergreen trees is variable (eg. Krause & Raffa 1996; Puettman & Saunders 2001; Clancy 2002) and results are inconclusive.

Radial growth losses in the present study were a combined effect of pine looper defoliation and shoot pruning by pine shoot beetles. Removing more than 40% of the live crown in Scots pine by pruning of the lower branches has a significant negative effect on radial growth (Uotila & Mustonen 1994).

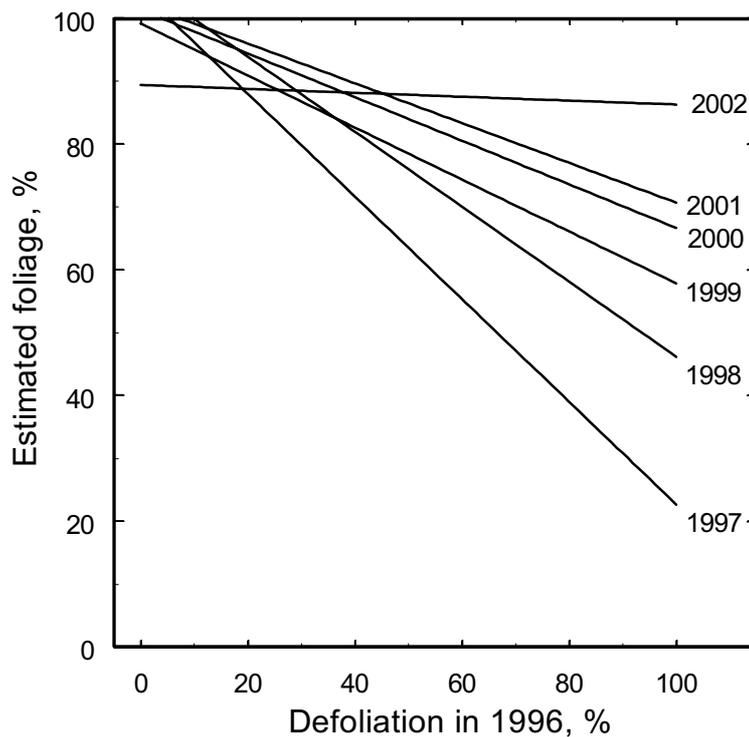


Fig. 6. Foliage recovery of 40 sample trees with varying initial defoliation in 1996. (paper V)

Pruning of shoots from the top of the tree and downwards simulates shoot pruning by pine shoot beetles (*T. piniperda*, and *T. minor*), and pruning in this manner at defoliation levels of 25-30% caused 18% and 40% growth loss for artificially-pruned, and beetle-pruned trees respectively during two to three years (Ericsson et al. 1985).

Similarly, shoot pruning caused volume growth losses of up to 30% during three years in 25-year-old beetle-pruned Scots pine, and 12% if hand pruned (Långström et al. 1990). About 200 shoots were removed, which was estimated to correspond to 20% and 30% of the total foliage in hand-pruned and beetle pruned treatments

respectively. Trees in the present study were of similar size to those studied by Långström et al. (1990), and most trees suffered a loss of 100 shoots or less, but during a period of several years, not during one single year as in the above mentioned studies. The defoliation caused by pine shoot beetles therefore probably only amounted to maximally 10% foliage removal. However, pine shoot beetles caused shoot losses in all defoliation classes, and even undefoliated trees had about 10% foliage reduction at the end of the study period (Fig. 6). Conclusively, the growth impact of beetle-induced shoot pruning was primarily restricted to an impact on height growth.

In the present study, height growth losses were approximately proportional to defoliation intensity, and were also a combination of defoliation and beetle-induced damage to leading shoots, as the effects of defoliation could not be separated from that of beetle-induced leader damage. Pine shoot beetle attack to the leading shoot was frequent and increased with degree of defoliation, and height growth in trees with 70-100% defoliation was still 40-60% below normal levels, six years after the defoliation. Height growth depends on carbohydrates and hormones produced in the upper crown; green pruning up to 70% live crown from below has very little effect on height growth in red pine (Kozłowski et al. 1991). In controlled experiments it has been shown that defoliation (Ericsson et al. 1980a) reduces height growth more than shoot pruning (Ericsson et al. 1985), and shoot pruning has little effect on height growth unless it involves the leader (Långström & Hellqvist 1991, 1992). After a 9-year recovery period, Austarå et al. (1987) found a 47% height loss in 90-year-old stands and 18% height loss in a 40-year-old stand, which on the average suffered 73% defoliation in two consecutive years. They did not report any beetle-induced leader damage, and height losses of 70% defoliated trees in the present study were more than twice that reported by Austarå et al. (1987). Thus, leader damage caused by pine shoot beetles can decrease height growth by at least twice that of defoliation alone.

By contrast to height growth, which probably was more severely affected by beetle-induced leader damage than by defoliation, radial growth returned to normal when trees had regained about 80% of full foliage, which is consistent with Långström et al. (2001). Wickman (1980) found that defoliated trees, 36 years after defoliation grew better than undefoliated trees in an adjacent stand. Increased nutrient cycling and a “thinning effect” as a result of 30% tree mortality were hypothesised as the probable cause for the increased growth in defoliated trees. Similarly, Alfaro & Shepherd (1991) found that after radial growth had returned to normal levels, radial growth increased above the predicted normal growth. He proposed that in the absence of tree mortality, increased nutrient cycling could explain the increase in growth. Långström et al. (2001) observed no such increase in growth after recovery of normal radial growth levels

in single-year completely defoliated trees, perhaps a result of that a “thinning effect” did not occur in the absence of tree mortality. In the present study there were no such clear effects of improved growth after growth recovery, with the exception of undefoliated trees and trees with 10% defoliation. In this case, the improved growth resulted from a “thinning effect” caused by the snow damage, and subsequent tree mortality during the winter 2000-2001. Possibly, there also was such a tendency of enhanced growth in surviving trees with 70% initial defoliation. However, in most plots with severe defoliation where such an enhanced radial growth could be expected due to tree mortality, radial growth had just returned to normal at the end of the study period. It is possible that an increase in growth will occur once trees have restored full foliage.

Hypothetically, if tree mortality leads to an initial loss in volume, with an enhanced growth later in the surviving trees, then 25% tree mortality could be beneficial for the development of the stand – a “thinning without associated costs”. The problem with this line of speculation, however, is that the average 25% tree mortality does not occur evenly over the whole defoliated area, but instead is aggregated and linked to the hot spots where *T. piniperda* occurs. The resulting empty gaps created in the stands leads to less timber yield in the final harvest. So, where moderate tree mortality may be beneficial for forests not intensively managed through maintaining optimal rates of nutrient cycling and tree growth (Mattson & Addy 1975), it is not part of the current management practices in Swedish forestry.

Economic consequences of the pine looper outbreak

The primary issue of the current thesis has been to provide decision makers with a better base of knowledge of the impact of one-year defoliations in Scots pine, in terms of yield losses. Here, I will go one step further and provide a rough calculation of defoliation costs. Tree mortality occurred unevenly between severely defoliated plots, and an economic evaluation of yield losses including average tree mortality would require a more comprehensive analysis, since the actual costs of tree mortality will differ widely between individual stands. Therefore, I will here only consider volume growth losses.

I assume that the rotation period is extended according to growth losses observed, i.e. 50% volume growth loss (in trees with 90-100% defoliation) over a period of six years will extend the rotation period by three years, and 40% volume growth loss (in trees with 70% defoliation) over 6 years will extend the rotation period by 2.4 years. I further assume a rate of interest of 3.0%, which has been used by others (Austarå et al. 1987; Straw et al. 2002). Based on information from Ingvar Johansson (retired manager of the defoliated area), I assume the following: (i) a rotation period of 130 years, (ii) stands

contain on the average 350 m³/hectare of wood at final felling, (iii) a net revenue of 350 SEK/m³ (corresponding to about 39 Euro and 44 \$US), which yield an approximate net revenue of 122500 SEK/hectare (including the costs of harvesting).

Three years of accumulated 3%-interest on the net revenue 122500 SEK/hectare, yield an approximate increase of 11500 SEK/hectare, which can be considered as the future cost of growth losses in trees with 90-100% defoliation. The value of the future cost at the time of defoliation can be calculated by discounting the future cost back 93 years in time, since the defoliation occurred at 40 years of age, the rotation period was 130 years, and the rotation period was extended by three years. This gives a cost of 730 SEK/hectare in volume growth losses at the time of defoliation. In trees with an average of 70%, and 50% defoliation, the corresponding cost would be 580 SEK/hectare, 370 SEK/hectare respectively. These results can be compared with the cost of the control operation estimated at 440 SEK/hectare (Långström et al. 1999b).

Considering the omission of costs of tree mortality, the use of current-day values of revenue for expected revenue in future, that growth had not reached normal levels at the end of the study period, and the fact that prices are deliberately set at a low level, the above-calculation is an underestimation of the real costs of the pine looper outbreak in terms of yield losses. However, since the control operation most likely was redundant in the absence of further defoliation in 1997, as observed in untreated areas and as indicated in paper I, the 440 SEK/hectare cost of the control operation only added to the cost of tree mortality and growth losses. However, if the control operation had not been undertaken, and if a second year of defoliation had resulted thereof, then substantial tree mortality, as observed by Långström et al. (2001) most likely would have occurred. Thus, the cost of the control operation could be viewed as a reasonable insurance to avoid a second year of defoliation and substantial tree mortality. Conclusively, had the pine looper outbreak been controlled in 1996, growth losses and tree mortality could have been avoided, and the control operation would have been economically justified in terms of prevention of yield losses. If this had been the case, and considering the deliberate underestimations made in above calculations, the control operation would have been economically justified in areas with an average of 50% defoliation or more. These were also the areas that actually were sprayed in autumn 1997.

Conclusions

A single-year defoliation of Scots pine by the pine looper moth resulted in tree mortality, top-kill and growth losses as a combined effect of the defoliation itself and subsequent secondary attack by pine shoot beetles. Tree mortality and top-kill occurred mainly in trees with 90-100% defoliation, and $\geq 90\%$ defoliation seemed to be a defoliation threshold for tree mortality resulting from the single-year pine looper moth defoliation. Since *T. piniperda* after a few years of population build-up was able to colonise trees having more than 10% of full foliage, the defoliation threshold for tree mortality and tree susceptibility to attack by *T. piniperda* was a function of tree vigour related to foliage recovery and dominance status, and beetle density. At the Fredriksberg site, *T. piniperda* was also found to colonise and kill trees that would have survived the foliage loss caused by *G. abietina*. It is thus likely that *T. piniperda* was the main cause for the tree mortality recorded after the pine looper defoliation at Hökensås. In addition, the results indicate that the foliage loss caused by *G. abietina* is a more serious type of stress than insect defoliation per unit of lost foliage. The “defoliation threshold” for tree survival may thus be $\leq 80\%$ defoliation for trees infested by *G. abietina*. Growth losses quantified after pine looper defoliation were proportional to defoliation intensity but the hypothesis of a “defoliation threshold” below which growth losses do not occur could not be rejected. The involvement of *T. piniperda* in growth losses was mainly restricted to a heavy impact on height growth.

Conclusively, the results presented here have implications for practical management of defoliator outbreaks and fungal epidemics. The use of a monitoring program for early detection of insect outbreaks of fungal epidemics could facilitate application of timely control measures and prevent yield losses. In the absence of such possibilities, salvage operations should be focused to trees or areas with foliage losses as estimated by the above defoliation thresholds for tree mortality. Thereby, prevention of local *T. piniperda* population build-up, optimisation of use of manpower and machinery, and salvaged timber value could be achieved.

Several prospects for future research exist. Improving and calibration of the CIR-technique would be valuable for damage detection and operational planning. Separation of the weather, *Tomicus*- and *Bupalus*-effect in the observed growth losses, requires deeper analyses of the data. Additional studies on the patterns of growth loss in older stands are required before the total effects of the pine looper outbreak at Hökensås in 1996 can be fully evaluated. Relating the four known outbreaks at Hökensås to climatic factors preceding the outbreaks could yield information on why the outbreaks developed with a possible predictive value.

References

- Aamlid, D. 1997. Crown condition assessment in the Nordic countries. Proceedings from an intercalibration course for northern Europe on crown condition assessment, 24-25 June 1997, Norway. *Aktuelt fra Skogforsk* 10, 1-38.
- Alfaro, R.I. 1991. Damage assessment and integrated pest management of forest defoliators. *Forest Ecology and Management* 39, 275-281.
- Alfaro, R. I. & Shepherd, R. F. 1991. Tree-ring growth of interior Douglas-fir after one year's defoliation by Douglas-fir tussock moth, *Forest Science* 37, 959-964.
- Alfaro, R. I., van Sickle, G. A., Thomson, A. J. & Wegwitz, E. 1982. Tree mortality and radial growth losses caused by the western spruce budworm in a Douglas-fir stand in British Columbia. *Canadian Journal of Forest Research* 12, 780-787.
- Alfaro, R. I., Taylor, S. P., Wegwitz, E. & Brown, R.G. 1987. Douglas-fir tussock moth damage in British Columbia. *Forestry Chronicle* 63, 351-355.
- Alfaro, R. I., Taylor, S., Brown, G. & Wegwitz, E. 1999. Tree mortality caused by the western hemlock looper in landscapes of central British Columbia. *Forest Ecology and Management* 124, 285-291.
- Annala, E., Långström, B., Varama, M., Hiukka, R. & Niemelä, P. 1999. Susceptibility of defoliated Scots pine to spontaneous and induced attack by *Tomicus piniperda* and *Tomicus minor*. *Silva Fennica* 33, 93-106.
- Armour, H., Straw, N. & Day, K. 2003. Interactions between growth, herbivory and long-term foliar dynamics of Scots pine. *Trees* 17, 70-80.
- Austarå Ø., Orlund A., Svendsrud A., Veidahl A. 1987. Growth loss and economic consequences following two years defoliation of *Pinus sylvestris* by the Pine sawfly *Neodiprion sertifer* in West Norway. *Scandinavian Journal of Forest Research* 2, 111-119
- Baldwin, I. T. 1990. Herbivory simulations in ecological research. *Trends in Ecology and Evolution* 3, 91-93.
- Barbour, D. A. 1988. The pine looper in Britain and Europe, In: *Dynamics of Forest Insect Populations* (ed. A. A. Berryman), p. 291-308. Plenum Press, New York.
- Barklund, P. & Rowe, J. 1981. *Gremmeniella abietina* (*Scleroderma lagerbergii*), a primary parasite in a Norway spruce die-back. *European Journal of Forest Pathology* 11, 97-108.
- Barklund, P. & Unestam, T. 1988. Infection experiments with *Gremmeniella abietina* on seedlings of Norway spruce and Scots pine. *European Journal of Forest Pathology* 18, 409-420.
- Barklund, P. & Hellgren, M. 1992. Skadesvampen *Gremmeniella abietina* på tall och gran. *Swed. Univ. of Agri. Sciences, Uppsala. Skogsfakta*. 16. 6 pp. ISSN: 1101-8305. (In Swedish)
- Baronio, P., Faccioli, G. & Butturini, 1989. A study of the influence of defoliation by *Neodiprion sertifer* (Geoffr.) (Hym., Diprionidae) on the growth of *Pinus sylvestris* in Romagna. *Bolletino dell'Instituto di Entomologia 'Guido Grande' della Universita degli studi Bologna* 43, 17-24.
- Bergqvist, G., Bergström, R. & Edenius, L. 2001. Patterns of stem damage by moose (*Alces alces*) in young *Pinus sylvestris* stands in Sweden. *Scandinavian Journal of Forest Research* 16, 363-370.
- Berryman, A. A. 1973. Population dynamics of the fir engraver, *Scolytus ventralis* (Coleoptera: Scolytidae). *The Canadian Entomologist* 105, 1465-1488.
- Berryman, A. A. 1986. *Forest insects*. Plenum Press, New York and London. 279 pp.
- Berryman, A. A. 1988. *Dynamics of forest insect populations: Patterns, causes and implications*. Plenum Press, New York and London. 603 pp.
- Björkman, C. 1991. *Interactions between a pine sawfly, its host and natural enemies as mediated by plant chemicals*. Doctoral thesis, Swedish University of Agricultural Sciences. ISBN: 91-576-4504-3.
- Britton, R. J., 1988. Physiological effects of natural and artificial defoliation on the growth of young crops of lodgepole pine. *Forestry* 61, 165-175.

- Brokenhuizen N., Evans H. F. & Hassel M. P. 1993. Site characteristics and the population dynamics of the pine looper moth. *Journal of Animal Ecology* 62, 511-518.
- Butovitsch V. 1946. Redogörelse för flygbekämpnings-kampanjen mot tallmätaren under åren 1944-1945, *Meddelanden från Statens Skogsforskningsinstitut* 35, 108 pp. (in Swedish)
- Byers, J. A., Lanne, B. S., Löfqvist, J., Schlyter, F. & Bergström, G. 1985. Olfactory recognition of host-tree susceptibility by pine shoot beetles. *Naturwissenschaften* 6, 324-326.
- Christiansen, E. & Bakke, A. 1988. The spruce bark beetle in Eurasia. In: *Dynamics of Forest Insects Populations* (ed. A. A. Berryman). p. 479-503. Plenum Press, New York.
- Christiansen, E. & Fjone, G. 1993. Pruning enhances the susceptibility of *Picea abies* to infection by the bark beetle-transmitted blue-stain fungus, *Ophiostoma polonicum*. *Scandinavian Journal of Forest Research* 8, 235-245.
- Christiansen, E., Waring, R. H. & Berryman, A. A. 1987. Resistance of conifers to bark beetle attack: Searching for general relationships. *Forest ecology management* 22, 89-106.
- Ciesla, W. M., Bennett, D. D. & Caylor, J. A. 1984. Mapping effectiveness of insecticide treatments against pandora moth with color-IR photoes. *Photogrammetric Engineering and Remote Sensing* 50, 73-79.
- Clancy, K. M. 2002. Mechanisms of resistance in trees to defoliators. In: *Mechanisms and deployment of resistance in trees to insects*. (eds. M. R. Wagner, K. M. Clancy, F. Lieutier & T. D. Paine). p. 79-103. Kluwer Academic Publishers, Dordrecht.
- Crooke, M. 1959. Insecticidal control of the pine looper in Great Britain. I. Aerial spraying. *Forestry* 32, 166-196.
- Day, K. R., & Leather, S.R. 1997. Threats to forestry by insect pests in Europe. In: *Forests and insects*. (eds. A. D. Watt, N. E. Stork, & M. D. Hunter). p. 177-206. Chapman & Hall.
- Eidmann, H. H. & Nuorteva, M. 1968. Der einfluss der siedlungsdichte und anderer faktoren auf die anzahl der nachkommen von *Blastophagus piniperda* L. (Col., Scolytidae). *Annales Entomologica Fennica* 34, 135-148.
- Eidmann H. & Klingström A. 1990. *Skadegörare i skogen*. LTs förlag. 355 pp. (in Swedish).
- Eklund, B. 1964. Om återverkningarna av den röda tallstekelns skadegörelse på tallens diametertillväxt vid brösthöjd. *Norrlands Skogsvårdsförbunds Tidskrift* 16, 205-218. (In Swedish).
- Ekstrand, S. 1994. Close range forest defoliation effects of traffic emissions assessed using aerial photography. *The Science of the Total Environment* 146/147, 149-155.
- Ericsson A., Larsson S., Tenow O. 1980a. Effects of early and late season defoliation on growth and carbohydrate dynamics in Scots pine. *Journal of Applied Ecology* 17, 747-769.
- Ericsson A., Hellkvist J., Hillerdal-Hagströmer K., Larsson S., Mattson-Djos E., Tenow O. 1980b. Consumption and pine growth-hypotheses on effects on growth processes by needle-eating insects. *Ecological Bulletins* 32, 537-546.
- Ericsson A., Hellkvist 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.
- Escherich, K. 1923. *Die Forstinsekten Mitteleuropas II*. Verlag Paul Parey, Berlin. 663 pp.
- Ferrell, G. T. 1991. Fir engraver. *U.S. Department of Agriculture, Forest Service. Pacific Southwest Forest and Range Experiment Station, Berkley, CA. Forest Insect and Disease Leaflet* 13. 8 pp.
- Flamm, R. O., Coulson, R. N. & Payne, T. L. 1988. The southern pine beetle. In: *Dynamics of Forest Insects Populations* (ed. A. A. Berryman). p. 531-553. Plenum Press, New York.
- Glynn, C. & Lindelöw, Å. 2002. Defoliation by the needle-shortening pine gall midge, *Thecodiplosis brachyntera*, on pines in central Sweden. *Scandinavian Journal of Forest Research* 17, 150-157.

- Hägglund, B. & Lundmark, J.-E. 1977. Site index estimation by means of site properties. Scots pine and Norway spruce in Sweden. *Studia Forestalia Suecica* 131, 1-38.
- Haack, R.A., Lawrence, R.K., McCullough, D.G. & Sadof, C.S. 1997. *Tomicus piniperda* in North America: Integrated response to a new exotic scolytid. In: *Proceedings: Integrating cultural tactics into the management of bark beetles and reforestation pests.* (eds. J. C. Gregoire, F. M. Liebhold, F. M. Stephen, K. R. Day & S. Salom). p. 62-72. *USDA Forest Service, General Technical Report NE-236.* 243 pp.
- Hansson, P. 1998. Susceptibility of different provenances of *Pinus sylvestris*, *Pinus contorta* and *Picea abies* to *Gremmeniella abietina*. *European Journal of Forest Pathology* 28, 21-32.
- Haukioja, E. 1990. Induction of defenses in trees. *Annual Review of Entomology* 36, 25-42.
- Hoogesteger, J. & Karlsson P. S. 1992. Effects of defoliation on radial stem growth and photosynthesis in the mountain birch (*Betula pubescens* ssp. *tortuosa*). *Functional Ecology* 6, 317-323.
- Huberty, A. F. & Denno, R. F. 2004. Plant water stress and its consequences for herbivorous insects: a new synthesis. *Ecology* (In press).
- Hui, Y. 1991. On the bionomy of *Tomicus piniperda* (L.) (Col., Scolytidae) in the Kunming region of China. *Journal of Applied Entomology* 112, 366-369.
- Karlman, M. 2001. Risks associated with the introduction of *Pinus contorta* in northern Sweden with respect to pathogens. *Forest Ecology and Management* 141, 97-105.
- Kletecka, Z. 1992. Distribution of damage by *Rhyacionia*, *Blastesthia* and *Retinia* tip moths (Lep., Tortricidae) depending on the exposure of planted and naturally seeded pine stands. *Journal of Applied Entomology* 113, 334-341.
- Koricheva, J., Larsson, S. & Haukioja, E. 1998. Insect performance on experimentally stressed woody plants: a meta-analysis. *Annual Review of Entomology* 43, 195-216.
- Kosola, K. R., Dickman, D. I., Paul, E. A. & Parry, D. 2001. Repeated defoliation effects on growth, nitrogen acquisition, carbohydrates, and root demography of poplars. *Oecologia* 129, 65-74.
- Kozlowski, T. T. & Pallardy, S. G. 1997. *Physiology of woody plants*. Academic press, San Diego, California. 411 pp.
- Kozlowski, T. T., Kramer, P. J. & Pallardy, S. G. 1991. *The physiological ecology of woody plants*. Academic press, San Diego, California. 657 pp.
- Krause, S. C. & Raffa, K. F. 1996. Differential growth and recovery rates following defoliation in related deciduous and evergreen trees. *Trees Structure and Function* 10, 308-316.
- Kulman H.M. 1971. Effects of insect defoliation on growth and mortality of trees. *Annual Review of Entomology* 16, 289-324.
- Kytö, M., Niemelä, P. & Larsson, S. 1996. Insects on trees: population and individual response to fertilization. *Oikos* 75, 148-159.
- Långström B. 1980. Distribution of pine shoot beetle attacks within the crown of Scots pine. *Studia Forestalia Suecica* 154, 25 pp.
- Långström B. 1983. Life cycles and shoot-feeding of the pine shoot beetles. *Studia Forestalia Suecica* 163, 1-29.
- Långström B. & Hellqvist C. 1991. Shoot damage and growth losses following three years of *Tomicus*-attacks in Scots pine stands close to a timber storage site. *Silva Fennica* 25, 133-145.
- Långström B. & Hellqvist C. 1992. Height growth recovery and crown development in top-damaged *Pinus sylvestris* trees. *Scandinavian Journal of Forest Research* 7, 237-247.
- Långström B. & Hellqvist C. 1993. Induced and spontaneous attacks by pine shoot beetles on young Scots pine trees: tree mortality and beetle performance. *Journal of Applied Entomology* 115, 25-36.
- 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.
- Långström B., Hellqvist C., Ericsson A., Gref R. 1992. Induced defence reaction in Scots pine following stem attacks by *Tomicus piniperda*. *Ecography* 15, 318-327.

- Långström B., Olofsson E., Lindelöw Å., Larsson S. 1999a. Bt mot tallmätaren på Hökensås. *Skog & Forskning* 4, 28-34. (In Swedish).
- Långström B., Hellqvist C., Ehnström B. 1999b. Susceptibility of fire-damaged Scots pine (*Pinus sylvestris* L.) trees to attack by *Tomicus piniperda* L. *Physiologie and genetics of tree-phytophage interactions; INRA, Les Colloques et* 90, 299-311.
- Långström B., 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* and subsequent attack by *Tomicus piniperda*. *Scandinavian Journal of Forest Research* 16, 342-353.
- Långström, B., Lisha, L., Hongpin, L., Peng, C., Haoran, L., Hellqvist, C. & Lieutier, F. 2002. Shoot feeding ecology of *Tomicus piniperda* and *T. minor* (Col., Scolytidae) in southern China. *Journal of Applied Entomology* 126, 333-342.
- Laflamme, G. & Lachance, D. 1987. Large infection center of *Scleroderris* cancer (European race) in Quebec province. *Plant Disease* 71, 1041-1043.
- Laflamme, G. & Blais, R. 2000. Resistance of *Pinus banksiana* to the European race of *Gremmeniella abietina*. *Phytoprotection* 81, 49-55.
- Larsson, S. 1989. Stressful times for the plant stress-insect performance hypothesis. *Oikos* 56, 277-283.
- Larsson S. & Tenow O. 1980. Needle-eating insects and grazing dynamics in a mature Scots pine forest in central Sweden. *Ecological Bulletins* 32, 269-306.
- Larsson S. & Tenow O. 1984. Areal distribution of a *Neodiprion sertifer* (Hym., Diprionidae) outbreak on Scots pine as related to stand condition. *Holarctic Ecology* 7, 81-90.
- Larsson, S., Oren, R., Waring, R. H. & Barrett, J. W. 1983. Attacks of mountain pine beetle as related to tree vigor of Ponderosa pine. *Forest Science* 29, 395-402.
- Laurent-Hervouët, N. 1986. Mesure des pertes de croissance radiale sur quelques espèces de *Pinus* dues deux défoliateurs forestiers. II. Cas du Lophyre du pin dans le Bassin parisien. *Annales des Sciences Forestières* 43, 419-440.
- Lekander, B. 1953. Über das Auftreten von *Blastophagus piniperda* und *Pissodes pini* im Wald vorher befallen von *Panolis*- und *Bupalus*- Raupen. *Meddelanden från Statens Skogsforskningsinstitut* 44, 31 pp.
- Lekander, M. 1950. Skogsinsekternas uppträdande i Sverige under tiden 1741-1945. *Meddelanden från Statens Skogsforskningsinstitut* 39, 207 pp.
- Lekander, B. 1984. Tidpunkten för större mörghorrens svärmning i olika delar av Sverige under åren 1970-79 (Date of flight commencement of *Tomicus piniperda* in Sweden during 1970-79). *Sveriges Skogsvårdsförbunds Tidskrift* 1, 7-21.
- Lyytikäinen, P. 1993. *The performance of diprionid sawflies in relation to the origin, defoliation and foliar chemistry*. Doctoral thesis, University of Helsinki, Reports 19. ISBN: 951-45-6553-3.
- Lyytikäinen-Saarenmaa, P. & Tomppo, E. 2002. Impact of sawfly defoliation on growth of Scots pine *Pinus sylvestris* (Pinaceae) and associated economic losses. *Bulletin for Entomological Research* 92, 137-140.
- MacLean D.A. & Ostaff, D. P. 1989. Patterns of balsam fir mortality caused by an uncontrolled spruce budworm outbreak. *Canadian Journal of Forest Research* 19, 1087-1095.
- MacLean D.A. & Ebert, P. 1995. The impact of hemlock looper (*Lambdina fiscellaria fiscellaria* (Guen.)) on balsam fir and spruce in New Brunswick, Canada. *Forest Ecology and Management* 120, 77-87.
- MacLean D.A. & Piene H. 1995. Spatial and temporal patterns of balsam fir mortality in spaced and unspaced stands caused by spruce budworm defoliation. *Canadian Journal of Forest Research* 25, 902-911.
- Manion, P. D. 1991. *Tree disease concepts*. 2nd edn. Englewood Cliffs, New Jersey, Prentice Hall, Inc. p. 182-206.
- Mattson W.J. & Addy N.D. 1975. Phytophagous insects as regulators of forest primary production. *Science* 190, 515-522.

- McCullouch, D. G., Marshall, L. D., Buss, L. J. & Kouki, J. 1996. Relating jack pine budworm damage to stand inventory variables in northern Michigan. *Canadian Journal of Forest Research* 26, 2180-2190.
- McMillin, J. D. & Wagner, M. R. 1997. Chronic defoliation impacts pine sawfly (Hymenoptera: diprionidae) performance and host plant quality. *Oikos* 79, 357-362.
- Millard, P., Hester, A., Wendler, R. & Baillie, G. 2001. Interspecific defoliation responses of trees depend on sites of winter nitrogen storage. *Functional Ecology* 15, 535-543.
- Mulock, P. & Christiansen, E. 1986. The threshold of successful attack by *Ips typographus* on *Picea abies*: a field experiment. *Forest Ecology and Management* 14, 125-132.
- Nevalainen, S. & Yli-Kojola, H. 1990. The occurrence of abiotic and biotic damage and its relation defoliation (needle loss) of conifers in Finland. In: *Acidification in Finland*. (eds. P. Kauppi, P. Anttila & K. Kenttämies). p. 561-582. Springer Verlag Berlin.
- Nylinder, M., Lundström, H. & Fryk, H. 2000. *Skador och fel på tall- och grantimmer*. Tierps tryckeri. 103 pp.
- Ostaf, D. P. & MacLean, D. A. 1995. Patterns of balsam fir foliar production and growth in relation to defoliation by spruce budworm. *Canadian Journal of Forest Research* 25, 1128-1136.
- Patton, R. F., Spear, R. N. & Blenis, P. V. 1984. The mode of infection and early stages of colonization of pines by *Gremmeniella abietina*. *European Journal of Forest Pathology* 14, 193-202.
- Perry, D. A. 1994. *Forest ecosystems*. The John Hopkins University Press, Baltimore or London. pp. 649.
- Piene, H. 1989. Spruce budworm defoliation and growth loss in young balsam fir: defoliation in spaced and unspaced stands and individual tree survival. *Canadian journal for forest research* 19, 1211-1217.
- Piene, H., & MacLean, D.A. 1999. Spruce budworm defoliation and growth loss in young balsam fir: patterns of shoot, needle and foliage weight production over a nine-year outbreak cycle. *Forest Ecology and Management* 123, 115-133.
- Pschorn-Walcher, H. 1982. Unterordnung Symphyta, Pflanzenwespen. In: *Die Forstschädlinge Europas, 4 Band, Hautflügler und Zweiflügler*. (ed. W. Schwenke). p. 4-196. Paul Parey, Hamburg Berlin.
- Puettmann, K. J. & Saunders, M. R., Patterns of compensation in eastern white pine (*Pinus strobus* L.): the influence of herbivory intensity and competitive environments. *Oecologica* 129, 376-384.
- Raffa, K. F. 1988. The mountain pine beetle in western North America. In: *Dynamics of Forest Insect Populations* (ed. A. A. Berryman). p. 507-530. Plenum Press, New York.
- Raffa, K. F. & Berryman, A. A. 1987. Interacting selective pressures in conifer-bark beetle systems: a basis for reciprocal adaptations? *The American Naturalist* 129, 234-262.
- Reeve J.D., Matthew P., Ayres P. & Lorio P.L. 1995. Host suitability, predation, and bark beetle population dynamics. In: *Population dynamics: New approaches and synthesis*. (eds. N. Cappuccino & P. W. Price). p. 339-357. Academic Press Inc.
- Rhoades, D. F. 1979. Evolution of plant chemical defence against herbivores. In: *Herbivores: Their interaction with secondary plant metabolites*. (eds. G. A. Rosenthal. & D. H. Janzen). p. 3-54. Academic Press, New York.
- Richardson, D.M., & Rundel, O.W. 1998. Ecology and biogeography of Pinus: an introduction. In: *Ecology and biogeography of Pinus*. (ed. D. M. Richardson). p. 3-46. Cambridge University Press.
- Saarenmaa, H. 1983. Modelling the spatial pattern and intraspecific competition in *Tomicus piniperda* (Coleoptera, Scolytidae). *Communicationes Instituti Forestalis Fenniae* 188, 1-38.
- Sanchez-Martinez, G. & Wagner, M. R. 1999. Short-term effects of defoliation by sawflies (Hymenoptera: Diprionidae) on above- and below-ground growth of three ponderosa pine genotypes. *Environmental Entomology* 28, 38-43.
- Schroeder, L. M. & Eidmann, H. H. 1987. Gallery initiation by *Tomicus piniperda* (Coleoptera: Scolytidae) on Scots pine trees baited with host volatiles. *Journal of Chemical Ecology* 13, 1591-1599.

- Schroeder, L. M. & Eidmann, H. H. 1993. Attacks of bark-and wood-boring Coleoptera on snow-broken conifers over a two-year period. *Scandinavian Journal of Forest Research* 8, 257-265.
- Schmitz, R. F. & Gibson, K. E. 1996. Douglas-fir beetle. *USDA, Forest Service, Forest insect and disease leaflet* 5, 1-8.
- Schwenke, W. 1978. *Die Forstschädlinge Europas, 3 Band Schmetterlinge*. Paul Parey Hamburg und Berlin. 467 pp.
- Senn, J. 1999. Tree mortality caused by *Gremmeniella abietina* in a subalpine afforestation in the central Alps and its relationship with duration of snow cover. *European Journal of Forest Pathology* 29, 65-74.
- Setliff, E. C., Sullivan, J. A. & Thompson, J. H. 1975. *Scleroderris lagerbergii* in large Red and Scots pine trees in New York. *Plant Disease Reporter* 59, 380-381.
- Shepherd, R. F. 1994. Management strategies for forest insect defoliators in British Columbia. *Forest Ecology and Management* 68, 303-324.
- Simard, M., Rioux, D. & Laflamme, G. 2001. Formation of lingo-suberized tissues in jack pine resistant to the European race of *Gremmeniella abietina*. *Phytopathology* 91, 1128-1140.
- Solheim, H., Långström, B. & Hellqvist C. 1992. Pathogenicity of the blue-stain fungi *Leptographium wingfieldii* and *Ophiostoma minus* to Scots pine: effect of tree pruning and inoculum density. *Canadian Journal of Forest Research* 23, 1438-1443.
- Solheim, H., Krokene, P. & Långström, B. 2001. Effects of growth and virulence of associated blue-stain fungi on host colonization behaviour of the pine shoot beetles *Tomicus minor* and *T. piniperda*. *Plant Pathology* 50, 111-116.
- Šmits, A. & Larsson, S. 1999. Effects of previous defoliation on pine looper larval performance. *Agricultural and Forest Entomology* 1, 19-26.
- Speight, M. R., Hunter, M. D. & Watt, A. D. 1999. *Ecology of insects concepts and applications*. Blackwell Science Ltd., Oxford. 350 pp.
- Stanley, B., Dunne, S. & Keane, M. 1996. Forest condition assessments and other applications of colour infrared (CIR) aerial photography in Ireland. *Irish Forestry* 53, 19-27.
- Stenberg, P., Kuuluvainen, T., Kellomäki, S., Grace, J. C., Jokela, E. J. & Gholz, H. L. 1994. Crown structure, light interception and productivity of pine trees and stands. *Ecological Bulletins* 43, 20-34.
- Straw, N. A. 1996. The impact of pine looper moth, *Bupalus piniaria* L. (Lepidoptera; Geometridae) on the growth of Scots pine in Tentsmuir forest, Scotland. *Forest Ecology and Management* 87, 209-232.
- Straw, N. A., Fielding, N. J., Green, G. & Price, J. 2000. The impact of green spruce aphid, *Elatobium abietinum* (Walker) and root aphids on the growth of young Sitka spruce in Hafren Forest, Wales: effects on height, diameter and volume. *Forest Ecology and Management* 134, 97-109.
- Straw, N. A., Armour, H. L. & Day, K. R. 2002. The financial costs of defoliation of Scots pine (*Pinus sylvestris*) by pine looper moth (*Bupalus piniaria*). *Forestry* 75, 525-536.
- Trägårdh, I. 1939. *Sveriges skogsinsekter*. Hugo Gerbers Förlag, Stockholm. 508 pp.
- Uotila, A. & Mustonen, S. 1994. The effect of different levels of green pruning on the diameter growth of *Pinus sylvestris* L. *Scandinavian Journal of Forest Research* 9, 226-232.
- Varley, G. C. 1949. Population changes in German forest pests. *Journal of Animal Ecology* 18, 117-122.
- Venier, L. A., Hopkin, A. A., McKenny, D. W. & Wang, Y. 1998. A spatial, climate-determined risk rating for *Scleroderris* disease of pines in Ontario. *Canadian Journal of Forest Research* 28, 1398-1404.
- Waring, R. H. & Pitman, G. B. 1985. Modifying lodgepole pine stands to change susceptibility to mountain pine beetle attack. *Ecology* 66, 889-897.
- Waring, R. H. & Schlesinger, W. H. 1985. *Forest Ecosystems: Concepts and Management*. Academic press, Orlando, Florida. 389 pp.

- White, T. C. R. 1974. A hypothesis to explain outbreaks of looper caterpillars, with special reference to populations of *Selidosema suavis* in a plantation of *Pinus radiata* in New Zealand. *Oecologica (Berlin)* 22, 119-134.
- White, T. C. R. 1984. The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed plants. *Oecologica (Berlin)* 63, 90-105.
- Wickman, B. E. 1978. Tree mortality and top-kill related to defoliation by the Douglas-fir tussock moth in the Blue Mountains outbreak. *USDA, Forest Service Research Paper. PNW-233*. 47 pp.
- Wickman, B.E. 1980. Increased growth of white fir after a Douglas-fir tussock moth outbreak. *Journal of Forestry* 78, 31-33.
- Witzell, J. 2001. Formation and growth of stem cankers caused by *Gremmeniella abietina* on young *Pinus contorta*. *Forest Pathology* 31, 115-127.
- Wright, L. C., Berryman, A. A. & Wickman, B. E. 1984. Abundance of the fir engraver, *Scolytus ventralis*, and the Douglas-fir beetle, *Dendroctonus pseudotsugae*, following tree defoliation by the Douglas-fir tussock moth, *Orygia pseudotsugata*. *Canadian Entomologist* 116, 293-305.
- Wulff, S. & Walheim, M. 2002. *Gremmeniella abietina*: uppträdande i Sverige 2001. Resultat från riksskogstaxeringen och skogsskadeinventeringen. *Swedish University of Agricultural Sciences, Department of Forest Resource Management and Geomatics*. <http://www.resgeom.slu.se/stax/projekt/skogskad/gremmeniella.pdf>; (accessed 27-Oct-2003).
- Yokota, S. 1975. Scleroderris cancer of Todo-fir in Hokkaido, northern Japan. *European Journal of Forest Pathology* 5, 7-12.

Acknowledgements

The most difficult part of the thesis to write is likely the acknowledgements section, since so many people, at the department and elsewhere, has made life as a PhD-student easier, and more enjoyable. I must not forget to mention any of them. But if I do (and I will), please consider the fact that these lines are written at 03:00 o'clock in the morning and there is no more coffee left.

Bo Långström, my main supervisor, who dared to hire me, was an excellent guide through the various stages of my work. In my mind we have always had an excellent working relation in spite of occasionally different opinions on how to interpret data, and how to write scientific papers. We had lots of fun during extremely long field days, and I doubt I will ever have a better boss than you. Secondly, both of my assistant supervisors have meant a lot to me, and it is hard to express that in a few lines. Åke Lindelöv, you introduced me to the world of wood living Coleoptera – well Lepidoptera are fun too, and that is something I will cherish for the rest of my life. Carolyn Glynn, you saved me during difficult times and I always felt better just by talking to you. Your positive attitude and creativity is really appreciated!

Without the help of Claes Hellqvist (and daughters) little field/lab work would have been accomplished. You were also an excellent field-work companion who taught me the meaning of Knapsu. Helena Bylund seems to always have time for me and my statistical issues. I don't know what I would have done without your help. There are countless other people at the Department of Entomology, and other departments who have helped me from time to time in various ways with field work, lab work, or practical issues, for which I am truly grateful. Solveig and Karin, my neighbours always offered a friendly face, Martin sometimes volunteered for defeat playing the hockey game in the basement (during coffee breaks).

I got a spiritual boost from the IUFRO-conference in Nancy, and I have really appreciated the possibilities for international exchange, abroad and at the department. Persons I have met whom have widened my horizons are Blas Lavandero, Susanne Kunholtz, Thao Tao, Chen Peng, Sigrid Netherer, Agnis Smits, and last but not the least Anke Herrmann.

What would the Department of Entomology be without its formidable PhD students? Creation of spexes, outings, parties, and everyday chit chat has made life easier and a lot more fun. P.O., I hope we will get to go fishing again!

Finally, my dear wife Holly has put up with me during the intense working-months required to finish this thesis, and it hasn't been easy, but now life will return to normal again!
