Dead Wood Retention and the Risk of Bark Beetle Attack

Per Olof Hedgren
Department of Entomology
Uppsala

Doctoral thesis
Swedish University of Agricultural Sciences
Uppsala 2002

Acta Universitatis Agriculturae Sueciae
Silvestria 247

ISSN 1401-6230
ISBN 91-576-6331-9

Tryck: SLU Service/Repro, Uppsala 2002

ABSTRACT

Hedgren, P. O. 2002. *Dead wood retention and the risk of bark beetle attack.*

Doctor's dissertation.
ISSN 1401-6230, ISBN 91-576-6331-9

Wind-felled Norway spruce trees left for conservation purposes and spruce stems stored as forest fuel may be colonised by the bark beetles *Ips typographus* and *Pityogenes chalcographus* (Coleoptera: Scolytidae). The risk of nearby living trees being attacked and killed by these species was experimentally investigated at stand edges bordering fresh clearcuts. Attack by *I. typographus* was studied at edges of mature spruce with one, five or no cut trees. Attack by *P. chalcographus* was studied within plots on edges of young spruce. The plots contained piles of cut young trees, or no piles.

Number of trees killed by *I. typographus* did not differ between edges with and without cut trees, or between edges with one and five cut trees. Tree-killing was more frequent close (<20 m) to felled trees than elsewhere on the edges, suggesting that felled trees provide focal points for attacks within edges. The piles increased the risk of *P. chalcographus* attack, but almost no attacked tree was killed. Attacks were associated with pile colonisation, whereas emergence by the new generation beetles did not increase the risk of attack.

Previous studies have shown a high reproductive success of *I. typographus* in felled trees after storms and a low success in standing trees killed during outbreaks. Here, the success was compared in pairs of colonised cut trees and standing killed trees at a time with no outbreak and relatively few felled trees available in the landscape. The success in killed standing trees was (a) significantly higher than in cut trees, and (b) high enough to suggest that killed standing trees can contribute substantially to the area-wide production of beetles.

The ability of *P. chalcographus* to kill trees and reproduce in them has previously been little studied. Here, attacks on living trees were induced by baiting trees with pheromone dispensers. The tree-killing ability was low. Reproductive success in killed trees was generally low, but was significantly higher in trees also attacked by *I. typographus*.

Keywords: Ips typographus, *Pityogenes chalcographus*, Scolytidae, *Picea abies*, stand edges, wind-felled trees, GROT, reproductive success

Author's address: Per Olof Hedgren, Department of Entomology, SLU, Box 7044, S-750 07 UPPSALA, Sweden. E-mail: per.olof.hedgren@entom.slu.se

Contents

Appendix

Papers I-IV

This thesis is based on the following papers, which will be referred to in the text by their respective Roman numerals.

I. Hedgren, P. O., Schroeder, L. M. & Weslien, J. 2002. Tree killing by *Ips typographus* (Coleoptera: Scolytidae) at stand edges with and without colonised felled spruce trees. *Agricultural and Forest Entomology*, in press.

II. Hedgren, P. O. & Schroeder, L. M. Reproductive success of the spruce bark beetle *Ips typographus* (L.)(Col.: Scolytidae) in killed standing trees and cut trees. Manuscript.

III. Hedgren, P. O., Weslien, J. & Schroeder, L. M. Risk of attack by the bark beetle *Pityogenes chalcographus* (L.) on living trees close to colonised felled spruce trees. Accepted for publication in *Scandinavian Journal of Forest Research*.

IV. Hedgren, P. O. The bark beetle *Pityogenes chalcographus* (L.) in standing trees - reproductive success, tree mortality and interaction with *Ips typographus*. Manuscript.

Papers I and III are reproduced with due permission from the publishers.

Introduction

In managed forests there is often a conflict between maintaining biodiversity and controlling certain insect pests. Dead trees constitute the habitat for a large number of species (Esseen *et al.* 1997, Jonsell *et al.* 1998, Siitonen 2001). In managed forests in Europe, the amount of dead wood has been seriously reduced (Fridman & Walheim 2000, Siitonen 2001). Thus, more dead wood must be retained to improve the conditions for species that depend on dead wood. However, recently dead trees may harbour a few species that are regarded as forest pests, *e.g.* the bark beetles *Ips typographus* (L.) and *Pityogenes chalcographus* (L.) (Coleoptera: Scolytidae)(Thalenhorst 1958, Eidmann 1992). These two species reproduce in Norway Spruce *Picea abies* (L.) Karst. During so-called "outbreaks" *I. typographus* can kill large numbers of mature trees over vast areas (Worrell 1983). *P. chalcographus* occasionally cause high tree mortality in young stands (Trägårdh & Butovitsch 1935, Thomsen 1939, Klauser 1954, Eidmann 1992). It is unclear, however, to what extent *P. chalcographus* can kill standing trees. Population management of these two species involves traditional "clean management" practices, and in Sweden this is required by law. The Forestry Act sets upper limits on the amount of logging waste and recently windfelled coniferous trees allowed, as well as time periods for timber storage in the forest (Anon. 1993). Since Norway spruce is a common tree species in parts of Europe, removal of *e.g.* windfelled spruce trees affect the general level of dead wood in the landscape. Moreover, in Sweden, dead wood from logging operations (mostly tops and branches) is currently used as an energy source on an industrial scale. In practice, fresh logging waste collected in piles may remain on the clearcut over summer to dry out. During that time the piles can attract, and produce, bark beetles, which may inflict damage on nearby stands. These two kinds of dead wood retention (for biodiversity purposes or short-term storage) may be associated with bark beetle damage on nearby standing trees, and this forms the background for the present study.

Most bark beetle species are restricted to dead trees (Wood 1982), but *I. typographus* and *P. chalcographus* can colonise dead trees as well as living standing trees Knowledge of their reproductive success in the two kinds of breeding substrate is important for understanding the population dynamics, *e.g.* how much the population can increase by breeding in a given substrate. This knowledge is also important for understanding how large part of the area wide production of beetles that takes place in the two kinds of substrates. Conditions for reproduction are different in these two sorts of tree because living trees have defences whereas dead trees have little or no defence. Living spruce trees defend themselves against bark beetle attack by means of a pre-formed system of resin-filled ducts in bark and wood, and by mobilising an inducible defence, which surrounds the infected site with dead resin-rich cells, thereby preventing the intruders from advancing (see Franceschi *et al.* 2000 and references therein). When *I. typographus* (L.) attacks living trees, mass attacks are required to overcome tree defences, resulting in high breeding density, severe intraspecific competition and low reproductive success (Thalenhorst 1958, Lekander 1972b, Ogibin 1974). In contrast, windfelled trees can be colonised at low densities, which releases the beetles from intraspecific competition, resulting in high reproductive success (Lekander 1955, Inouye 1963, Butovitsch 1971, Furuta 1989). Previous studies have analysed the two sorts of tree separately, *i.e.* felled trees after storm fellings, and killed standing trees during outbreaks, but here the aim was to compare them directly in the normal, "non-outbreak" situation when the level of windfall was relatively low (II). There are few studies on the reproduction in *P. chalcographus*; it is, *e.g.*, unclear how well the species can reproduce in standing trees.

Aims and outline of this thesis

This thesis focuses on the risk of bark beetle attack close to recently felled spruce trees. As long as the bark is fresh, such trees constitute a suitable breeding material for *I. typographus* and *P. chalcographus*. When a windfelled tree is colonised, nearby standing trees may be attacked through the process of "switching" (*cf.* Geizler & Gara 1978, Schlyter 1985): when the first attacked tree is "filled up" by beetles, the attack gradually switch to another, neighbouring tree. There is also a risk of attack during emergence by the new generation beetles. In this situation, any beetle that emits aggregation pheromone may recruit many conspecifics from the locally produced new generation beetles. In Sweden, the generation time of both species is usually one year, and the new generation will disperse from the development site the following summer.

The studies on *I. typographus* were performed at edges of mature spruce stands, which bordered fresh clearcuts. There were several reasons for this choice of study site. Firstly, these edges have trees large enough to be colonised by *I. typographus*. Secondly, wind fellings often occur at such edges because the newly exposed trees are sensitive to strong wind (Esseen 1994, Peltonen 1999). Thirdly, logging waste from clearcut harvesting is currently a widely used energy source in Sweden (so-called "forest fuel"). Tops, branches and large-diameter stem parts are collected in large piles, which often remain on the clearcut during summer to dry out. The chosen sites, therefore, constitute sites with high risk of *I. typographus* attack. Mature spruce trees at the edge were cut to simulate *e.g.* windfelled trees. In contrast, attacks by *P. chalcographus* were recorded at the edges of young spruce stands adjacent to fresh clearcuts, because this species occasionally attacks such stands. Piles of suitable breeding material were established at such edges. Moreover, standing trees were baited with pheromone dispensers to investigate the species' capacity to kill trees. The main questions addressed were as follows:

1a) Do stand edges with low numbers (1 or 5) of felled trees colonised by *I. typographus* have higher tree mortality compared with stand edges without felled trees? (I)
1b) Do such trees influence the spatial distribution of killed standing trees along the edges? (I)
2) How does the reproductive success of *I. typographus* in killed standing trees compare with its success in felled trees? (II)
3a) Are young spruce trees close to piles of suitable breeding material for *P. chalcographus* attacked more than similar trees at places without such piles? (III)

3b) When is the risk of *P. chalcographus* attacks highest - during colonisation of the piles, or during emergence of the new generation the following year? (III)
4a) How capable is *P. chalcographus* of killing apparently healthy standing trees? (III, IV)
4b) How successful is *P. chalcographus* reproduction in such trees? (IV)

Study organisms

Ips typographus

In the Nordic countries, the flight period in *I. typographus* generally starts in May or June (Annila 1977), and flights may extend tens of km (Forsse & Solbreck 1985). They search for spruce trees, or parts of trees, with a diameter exceeding *ca.* 10 cm. *I. typographus* reproduces in, *e.g.*, windfelled trees, large-diameter logging waste, and also in living trees. To be able to reproduce in living trees, the number of attacking beetles must be high enough to overcome the trees defensive systems (Thalenhorst 1958, Mulock & Christiansen 1986). Tree-killing is facilitated by a mass attack co-ordinated by an aggregation pheromone (Bakke 1976, Bakke *et al.* 1977b). The beetles also infect the attacked tree with pathogenic fungi, of which one, *Ceratocystis polonica* (Siem.) C. Moreau can kill healthy spruce trees when artificially inoculated into the bark in sufficiently high doses (Horntvedt *et al.* 1983). Thus, the risk of trees being killed by *I. typographus* increases as population levels rise (Weslien *et al.* 1989). Each male excavates a nuptial chamber in the bark, releases aggregation pheromone and is joined by several females (usually 1-3). After mating, the females excavate one egg gallery each in the phloem and lay their eggs in niches in the walls of the gallery. The larvae feed on the phloem. A large proportion of the parent beetles may re-emerge to establish a second brood in another tree (Bakke *et al.* 1977a). In Sweden, the next generation of beetles usually starts to emerge from the brood tree in August (Weslien 1992) to hibernate in the forest litter below, but some remain under bark (Christiansen & Bakke 1988). The sex ratio is nearly 1:1 at emergence (Annila 1971).

Occasionally, large numbers of living trees are attacked and killed. Such outbreaks are associated with storm fellings (Bombosch 1954, Inouye 1963, Lekander 1972b, Furuta 1989) or periods of severe drought (Christiansen & Bakke 1988). The connection with storm fellings is straightforward. Storms produce a surplus of breeding material with weak or no defences, *i.e.* broken or uprooted trees, and the beetle population can spread and reproduce successfully without being adversely affected by intraspecific competition. The inverse relationship between intraspecific competition and offspring survival is well established in laboratory studies by Anderbrant *et al.* (1985). Later, as the felled trees become unsuitable for further use, the enlarged population has to breed in standing trees. The effects of weather are unclear (Christiansen & Bakke 1988). Swarming and aggregation on suitable hosts is probably favoured by warm, sunny conditions. The same kind of weather should also induce water stress in the host trees and reduce their resistance. However, artificial inoculation experiments suggest that moderate water-stress may in fact enhance resistance against the pathogenic fungi spread by the beetle (Christiansen & Bakke 1997).

The reproductive success in *I. typographus* has mostly been studied in combination with storm fellings and outbreaks. With a surplus of broken or uprooted stormfelled trees the success can be high, and may exceed 10 daughters per mother beetle (Lekander 1955, Inouye 1963, Butovitsch 1941, 1971, Furuta 1989). In contrast, the success in standing trees is often low, as the high attack density needed to overcome the defence causes intense intraspecific competition. In such trees the mother beetles may produce on average 2 daughter beetles (Weslien & Regnander 1990), and the success is sometimes below 1.0 (Lekander 1972b, Furuta 1989). This may partly be compensated for by a second brood in another tree, but there is always a mortality rate during *e.g.* dispersal, hibernation and colonisation to consider as well.

Pityogenes chalcographus

P. chalcographus occasionally cause high tree mortality in young stands of Norway spruce (Trägårdh & Butovitsch 1935, Thomsen 1939, Klauser 1954, Eidmann 1992). Between 1970 and 1971, for instance, young spruce trees were attacked and killed at many locations in southern Sweden (Lekander 1972a, Ehnström *et al.* 1974, Eidmann 1992). The suggested cause of this outbreak was low tree vigour due to water stress in combination with high population levels after storm fellings (Lekander 1972a, Ehnström *et al.* 1974). Otherwise, the species is normally confined to windfelled trees, broken tops and logging waste. It is also often found on mature standing trees attacked by *I. typographus*. Colonisation of breeding material is facilitated by an aggregation pheromone released by the males (Francke 1977, Byers *et al.* 1988). Each male initiates a nuptial chamber in the bark, and is joined by three to nine females, each of which excavates an egg gallery in the phloem (Klauser 1954). In Scandinavia, there is usually one generation per year, and the new generation hibernates as adults or larvae. The flight period usually lasts from May to August (Eidmann 1974, Annila 1977, Harding *et al.* 1986). *P. chalcographus* does not seem to be consistently associated with aggressive pathogenic fungi (Krokene & Solheim 1996).

This species has been less extensively studied than *I. typographus* and it is, for example, unclear how successfully the beetle can overcome the defences of living, standing trees and reproduce in them. Reproductive success is influenced by both intra- and interspecific competition under bark (Thalenhorst 1958). *P. chalcographus* often co-occurs with *I. typographus* in large killed trees, and since *P. chalcographus* (2 mm long) is much smaller than *I. typographus* (5 mm long) it may be hypothesized that the coexistence should be negative for reproductive success in *P. chalcographus* (*cf.* Denno *et al.* 1995).

Materials and methods

Dead wood retention and risk of attack by *I. typographus* (I)

In total, 76 stand edges of mature spruce were included in this experiment. Each edge bordered on a fresh clearcut, logged the previous winter. At 19 edges a single tree was cut, whereas a group of 5 trees was cut at 17 edges (all cut trees were left at the site). In total, 40 edges were left without cut trees to be used as controls. Stand edge was spatially defined as a 10-m-wide strip at the outermost part of each stand (Fig. 1 in (I)), and was visually inspected by walking along the edge. In May and June, standing trees within 20 m of the cut trees were assessed for signs of *I. typographus* attack, whereas the entire edges and the control edges were assessed in the autumn. All edges were also assessed in June and September the following year. The rationale of the study required the cut trees be colonised by *I. typographus*, and the first assessment confirmed that 99% of the cut trees had met this requirement.

Reproductive success of *I. typographus* in killed standing trees and cut trees (II)

Both cut trees and killed standing trees were sampled in a pairwise manner to compare the beetle's reproductive success in them on 6 of the 76 above-mentioned sites. On each site the sampled cut and standing trees occurred close (<8 m) to each other. Stem sections were cut from one cut tree and from one killed standing tree at five sites, and from two cut and two standing trees at one site. The stem sections were cut at the beginning of autumn when *I. typographus* offspring generation had completed development, but had not yet started to emerge. All insects that emerged from the sections until the following spring were collected in emergence traps. Finally, the bark was peeled off to count egg galleries, and reproductive success, defined as the number of daughters per mother beetle, was calculated.

Natural enemies of *I. typographus* can reduce brood survival by >80 % (Weslien 1992); therefore it was of interest to estimate their abundance. A large set of associated species were collected, including beetles, predatory flies (*Medetera* spp.) and parasitic Hymenoptera, and they were determined to species or genus level. Their abundance was estimated as number of emerged individuals/m^2 bark.

Dead wood retention and risk of attack and tree-killing by *P. chalcographus* (III, IV)

Risk of attack by *P. chalcographus* was studied by establishing a pile of suitable breeding material in front of a young stand. A total of 58 stands (mean diameter=7 cm, range=3-15 cm), bordering on fresh or one-year-old clearcuts, were included. At the edge of each of these stands one plot was established, consisting of a 30 x 2-m strip of the stand edge. At 31 of these plots, 30 young spruce trees growing at the centre of the plot were cut in spring, prior to the flight period of *P.*

chalcographus, and put together in a pile situated less than 1 m from the stand edge. The remaining 27 plots were left untreated (*i.e.* with no pile) as controls. The experiment was repeated during three years (1998: 26 edges, 1999: 13 edges, 2000: 19 edges, see Table 1 in III). Bark beetle attacks on living trees within the plots were assessed at regular intervals until the autumn of the following year. Thus, attacks associated with both colonisation of the piles and emergence by the new generation were included. In these assessments, number of entrance holes on attacked standing trees within the plots was counted. Tree survival, as well as distance to the pile, was noted.

The ability to kill trees was studied by baiting standing trees with pheromone dispensers (containing synthetic aggregation pheromone). These trees were then continuously attacked for several weeks. In 1998, 41 trees were baited in this way, their diameter at breast height ranged from 4-21cm, whereas 22 trees were baited in 2000 (diameter range=14-25 cm). Tree survival was recorded, and attack density close to the dispensers was estimated (for details, see (IV)).

Reproductive success of *P. chalcographus* in standing trees (IV)

Stem sections were cut from baited trees (see above) that were killed, and also from killed, unbaited neighbouring trees (in total 28 trees). The sections were kept in emergence traps to collect all emerging insects. Emergence had started at the time of sampling, and already existing exit holes on the sections were marked and counted before enclosure. Afterwards, the bark was peeled off from the sections and bark beetle egg galleries were counted. The brood systems of *P. chalcographus* are characteristic, and cannot be confused with *e.g. I. typographus* brood systems. Reproductive success was estimated as ((number of emerged beetles + number of pre-existing exit holes) x female proportion) / (number of egg galleries) for each tree. Here, the emerged beetles made one exit hole each; this was assumed to be valid also for the beetles that emerged before enclosure. The female proportion was determined in a sample of 1688 emerged individuals.

Results and discussion

Dead wood retention and risk of attack by *I. typographus* (I)

The tree mortality was not significantly different at stand edges with and without colonised felled trees (Table 1). This is in line with a previous study (Peltonen 1999). In fact, the average number of killed trees per edge was four times higher in control edges than in edges with cut trees in the first summer, even though the difference was not significant (Table 1). Moreover, within stand edges, tree killing was directed to the vicinity of colonised felled trees, suggesting that the felled trees provided focal points for attacks on living trees, and hence influenced the spatial distribution of killed trees within the edges. Such a pattern may erroneously lead to the conclusion that the presence of felled trees in general increases tree mortality

Table 1 Tree mortality due to *Ips typographus* at spruce stand edges with cut trees (n=24 edges) or without cut trees (n=30 edges) in the first and second summer after cutting (standard error within parentheses). Difference in proportions were analysed with Chi-2 test (using absolute numbers), whereas Mann-Whitney U-test were used for the remaining comparisons. Edges with additional, naturally windfelled trees were not included in this analysis.

Variable	Treatment		*p*
	1 or 5 cut trees	no cut trees	
First summer:			
Proportion of stand edges with killed trees	33%	43%	0.45
No. of killed trees per stand edge	1.0 (0.4)	4.1 (1.2)	0.14
No. of killed trees per km of stand edge	6.9 (2.9)	16.6 (4.5)	0.32
Second summer:			
Proportion of stand edges with killed trees	31%	31%	0.97
No. of killed trees per stand edge	1.3 (0.7)	1.2 (0.5)	0.91
No. of killed trees per km of stand edge	8.5 (4.5)	6.6 (2.4)	1.00

in spruce stand edges, but the results clearly showed that total tree mortality at edge level did not increase.

There are at least two reasons why trees at edges are at risk of being attacked. Firstly, large quantities of host volatiles are released from *e.g.* stumps and logging waste on fresh clearcuts (Strömvall & Petersson 1991). *I. typographus* is weakly attracted to fresh spruce wood (Lindelöw *et al.* 1992), and attraction to its aggregation pheromone increases when combined with host volatiles (Bakke 1985, Austarå *et al.* 1986, Franklin *et al.* 2000). Secondly, *I. typographus* prefers to colonise sun-exposed trees, as demonstrated by the fact that wind-felled trees are more likely to be colonised at stand edges, or in gaps formed by storm fellings, than in forest interiors (Peltonen 1999, Göthlin *et al.* 2000).

Reproductive success of *I. typographus* in killed standing trees and cut trees (II)

The reproductive success of *I. typographus* was significantly higher in standing killed trees than in cut trees. The average number of daughters per mother beetle was 3.4 in killed standing trees and 1.7 in cut trees. Although based on a small sample, this result may have important implications as it indicates that killed standing trees may contribute substantially to the area-wide production of *I. typographus* in the normal, non-outbreak situation. There are no estimates of the abundance of colonised standing and felled trees at the landscape level. But the stand edges in paper I contained about 20 killed standing trees and 9 colonised windfelled trees per km of edge. Killed standing trees may serve to maintain the population level in the landscape, and the view that such trees constitute populations sinks may not be correct in all situations.

The high reproductive success in the killed standing trees is not in accordance with previous studies. One reason may be that several of these studies included standing trees killed at the end of an outbreak. These trees could have escaped earlier attacks, *e.g.*, because they were the most resistant ones. It also possible that natural enemies increase in numbers and thereby inflict a higher mortality towards the end of an outbreak. The success in cut trees, on the other hand, was lower than previously has been found in felled trees after storm fellings. The conditions are, however, different when felled trees are abundant, and when they are few (*i.e.* this case), since a surplus of breeding material can reduce intraspecific competition and result in high reproductive success.

It is unclear why the reproductive success was higher in killed standing trees than in cut trees. Egg galleries were 20% longer in killed standing trees than in cut trees (on average 6 and 5 cm long, respectively), which may partly explain the difference. The difference in egg gallery density was not statistically significant between the two kinds of tree, but the density was in fact higher in cut trees than in standing trees at five of the six sites. The relative impact of natural enemies is unclear; they emerged abundantly from both sorts of tree.

It should be noted that the forest protection regulations in Sweden on bark beetle breeding material include fallen or cut coniferous trees with fresh bark (max level of 5 m^3/ha), but not standing colonised trees. On the other hand, the current upper limit is the result of negotiations and is not based on specific studies. Further studies, preferably experimental ones, are needed to establish critical thresholds of breeding material. The results in paper I give some indications of a possible threshold for the amount of colonised trees within an edge and the risk of continued attacks.

Dead wood retention and risk of attack and tree-killing by *P. chalcographus* (III, IV)

Piles of suitable breeding material increased the risk of *P. chalcographus* attacks on the nearest standing trees, but almost all attacks failed and the trees survived (III). Nearly all attacks occurred during the colonisation phase of the piles, suggesting that aggregation pheromones released at the piles induced some beetles to attack nearby standing trees. Hardly any attacks occurred in connection with emergence of the new generation the following year. Comparisons between different years are generally complicated by differences in weather conditions, but this particular experiment was repeated three times to compensate for this problem, and they also partly overlapped in time (*i.e.* the second summer of one experiment was the first summer of another experiment).

The results (III, IV) indicate that the ability of *P. chalcographus* to kill apparently healthy standing trees is low. Many trees (226 in total) close to the piles were attacked, but only one tree attacked by *P. chalcographus* alone was killed (III). In study IV, 37 pheromone-baited trees were attacked by *P. chalcographus* alone, but only three were killed (=8%). There was no lack of beetles in the study areas as demonstrated by the catch in pheromone-baited traps (III, IV).

Many of the trees >10 cm in diameter baited with *P. chalcographus* pheromone were also attacked by *I. typographus*. The mortality rate of these trees (64%) was much higher than of the trees attacked by *P. chalcographus* alone, which suggests that *I. typographus* killed these trees. Furthermore, the *I. typographus* attack rate was higher on killed trees than on surviving trees. In contrast, neither the attack rate nor the attack density (number of entrance holes/m^2) of *P. chalcographus* differed between trees that died and those that survived. One reason for this outcome could be that *P. chalcographus* has a weaker association with pathogenic fungi than *I. typographus* (Krokene & Solheim 1996).

Reproductive success of *P. chalcographus* in standing trees (IV)

The reproductive success in *P. chalcographus* was low in the killed trees. On average only 0.9 daughters emerged per mother beetle. The success decreased with increasing egg gallery density, a pattern previously demonstrated for other bark beetles, such as *I. typographus* (*e.g.* Anderbrant *et al* 1985). It is likely that the low success found here was caused by the high level of intraspecific competition. Perhaps, one may argue that the baiting with pheromone dispensers caused abnormally high egg gallery densities, and, therefore, unusually intense intraspecific competition. However, the density in baited trees partly overlaps with the density previously found in logs (pulp wood) stored in the forest (Ehnström 1976), which suggests that the baiting resulted in realistic levels of competition.

Interestingly, the reproductive success was significantly better in trees also colonised by *I. typographus*. In trees colonised by *P. chalcographus* alone 0.75 daughters emerged per mother beetle (SE=0.14, n=19 trees), compared to 1.20 (SE=0.22, n=9 trees) in trees colonised by both species. There was no association between success and tree diameter or bark thickness. It is unclear why *P. chalcographus* would succeed better in the presence of *I. typographus*. Nevertheless, this result suggests that tree killing by *I. typographus* can be favourable for *P. chalcographus*. Possibly, the success can be higher in such trees in parts not included here, such as tree top and branches.

Management implications

Moderate numbers of logs or windfelled trees colonised by *I. typographus* do not increase the number of bark beetle killed trees at stand edges (I). Piles of forest fuel that contain a few spruce logs can therefore be kept in the forest over summer without undue risk of damage to nearby trees by *I. typographus*. Even though the Forestry Act allows 5 m^3 (Anon. 1993) of fresh coniferous wood per ha, many forest owners associate dead trees with bark beetle damage, and therefore remove most or all dead trees. However, at least 5 colonised felled trees can be retained at a stand edge without an increased risk. The risk for increased damage in the surrounding landscape is probably small as long as a moderate number of windfelled trees are retained at fresh stand edges, because such edges constitute only a small part of the managed forest landscape. Within edges, the position of colonised logs or windfelled trees is important as they act as foci of attacks on standing trees. This influence seems sufficiently strong to be used practically in forest management. Within a stand edge, for instance, it may be feasible and desirable to direct attacks towards economically less important positions (*e.g.* a group of retained trees), or an adjacent reserve.

P. chalcographus represents little or no threat to healthy standing trees (III, IV). Storage of suitable breeding material does not seem to cause any serious damage to nearby young stands, even though it is unclear what may happen during periods of severe drought. The Forestry Act of Sweden includes regulations directed specifically against *P. chalcographus* (Anon. 1993). The amount of small-diameter logging waste that can be left after cuttings is limited, and thinnings are not allowed during certain times of the year. These regulations impose constraints on forest management, and their value can be questioned as the ability of this species to kill healthy trees seems to be low.

The results indicate that standing trees may contribute substantially to the production of *I. typographus* at the landscape level under normal "non-outbreak" situations (II). Thus, the removal of small amounts of recently felled trees without considering killed standing trees is a doubtful practise. Moreover, windfelled spruce trees are not always colonised by *I. typographus* (Annila & Petäistö 1978, Schroeder & Lindelöw 2002), and salvage of small quantities may not be economically sound. Finally, small amounts of windfelled trees are not associated with increased damages by *I. typographus* on nearby trees (paper I, Peltonen 1999).

In Sweden, an increased level of dead wood in the forest landscape is a national goal (Prop. 2000/01-130). *I. typographus* produces large dead trees in a natural way, even though its activity is difficult to control. This species is directly associated with several other species (*e.g.* parasitoids)(II), and the dead wood can benefit a large number of wood-living species (Jonsell *et al.* 1998, Gärdenfors 2000). Possibly, beetle-killed trees have qualities that are lacking in some forms of artificially created dead wood, such as machine-made high stumps of spruce on clearcuts. Thus, *I. typographus* should be recognised as an ecologically important species in the boreal forest landscape.

References

Anderbrant, O., Schlyter, F. & Birgersson, G. 1985. Intraspecific competition affecting parents and offspring in the bark beetle *Ips typographus*. *Oikos* 45:89-98.

Annila, E. 1971. Sex ratio in *Ips typographus* L. (Col., Scolytidae). *Annales Entomologici Fennici* 37:7-14.

Annila, E. 1977. Seasonal flight patterns of spruce bark beetles. *Annales Entomologici Fennici* 43: 31-35.

Annila, E. & Petäistö, R. J. 1978. Insect attack on windthrown trees after the December 1975 storm on western Finland. *Communicationes Instituti Forestalis Fenniae* 94.2.

Anonymous 1993. Skogsvårdslagen 1993:553. (In Swedish.)

Austarå, Ø., Bakke, A. & Midtgaard, F. 1986. Response in *Ips typographus* to logging waste odours and synthetic pheromones. *Journal of Applied Entomology* 101:194-198.

Bakke, A. 1976. Spruce Bark Beetle, *Ips typographus*: Pheromone production and field response to synthetic pheromones. *Naturwissenschaften* 63:92.

Bakke, A., Austarå, Ø., & Pettersen, H. 1977a. Seasonal flight activity and attack pattern of *Ips typographus* in Norway under epidemic conditions. *Meddelelser fra Norsk institutt for skogforskning* 33:253-268.

Bakke, A., Frøyen, P. & Skattebyen, P. & Skattebøl, L. 1977b. Field response to a new pheromonal compound isolated from *Ips typographus*. *Naturwissenschaften* 64:98-99.

Bakke, A. 1985. Deploying pheromone-baited traps for monitoring *Ips typographus* populations. *Zeitschrift für angewandte Entomologie* 99:33-39.

Bombosch, S. 1954. Zur Epidemiologie des Buchdruckers (*Ips typographus* L.). *Die grosse Borkenkäferkalamität in Südwestdeutschland 1944-1951*. Edited by G. Wellenstein, pp. 239-283. Forstschutzstelle Südwest, Ringingen, Ebner, Ulm.

Butovitsch, V. 1941. Studier över granbarkborrens massförökning i de av decemberstormen 1931 härjade skogarna i norra Uppland. *Meddelanden från Statens Skogsförsöksanstalt*, 32:297-360 (in Swedish with German summary).

Butovitsch, V. 1971. Undersökningar över skadeinsekternas uppträdande i de stormhärjade skogarna i mellersta Norrlands kustland åren 1967-69. *Research Notes* 8. Dep. of Forest Zoology, Royal College of Forestry, Stockholm (in Swedish with German summary).

Byers, J. A., Birgersson, G., Löfqvist, J. and Bergström, G. 1988. Synergistic pheromones and monoterpenes enable aggregation and host recognition by a bark beetle. *Naturwissenschaften* 75:153-155.

Christiansen, E. & Bakke, A. 1988. The spruce bark beetle of Eurasia. In: *Dynamics of forest insect populations* (edited by A.A. Berryman), pp. 479-503. Plenum Publishing Corporation.

Christiansen, E. & Bakke, A. 1997. Does drought really enhance *Ips typographus* epidemics? - A Scandinavian perspective. In J. C. Grégoire, A. M. Liebhold, F.M Stephen, K.R. Day & Salom, S.M., editors. Proceedings: *Integrating cultural tactics into the management of bark beetle and reforestation pests*. USDA Forest Service General Technical Report NE-236.

Denno, R. F., McClure, M. S. & Ott, J. R. 1995. Interspecific interactions in phytophagous insects: competition reexamined and resurrected. *Annual Review of Entomology* 40:297-331.

Ehnström, B., Bejer-Petersen, B., Löyttyniemi, K. & Tvermyr, S. 1974. Insect pests in forests of the Nordic countries 1967-1971. *Annales Entomologici Fennici* 40:37-47.

Ehnström, B., 1976. Barkborreangrepp i massavedsvältor. *Skogsvirkesskydd*. Conf. Proceed., Sveriges Skogsvårdsförbund, Stockholm 3-4 Dec 1975. Djursholm. (In Swedish.)

Eidmann, H. 1974. Versuche über den Verlauf des Schwärmens von Borkenkäfers und des Insektenbefalls an Kiefernholz in Mittelschweden. *Studia Forestalica Suecica* 113. Royal College of Forestry, Stockholm. (In German.)

Eidmann, H. 1992. Impact of bark beetles on forests and forestry in Sweden. *Journal of Applied Entomology* 114:193-200.

Esseen, P.A. 1994. Tree mortality patterns after experimental fragmentation of an old-growth conifer forest. *Biological Conservation* 68:19-28.

Esseen, P. A., Ehnström, B., Ericsson, L & Sjöberg, K. 1997. Boreal forests. *Ecological Bulletins* 46:16-47.

Forsse, E., Solbreck, S. 1985. Migration in the bark beetle *Ips typographus* L.: duration, timing and height of flight. *Zeitschrift für angewandte Entomologie* 100:47-57.

Franceschi, V. R., Krokene, P., Krekling, T. & Christiansen, E. 2000. Phloem parenchyma cells are involved in local and distant defence responses to fungal inoculation or bark-beetle attack in Norway spruce (Pinaceae). *American Journal of Botany* 87:314-326.

Francke, W. 1977. 2-ethyl-1,6-dioxaspiro[4.4]nonane, principal aggregation pheromone of *Pityogenes chalcographus* (L.). *Naturwissenschaften* 64:590-591.

Franklin, A.J., Debruyne, C. & Grégoire, J-C. 2000. Recapture of *Ips typographus* L. (Col., Scolytidae) with attractants of low release rates: localized dispersion and environmental influences. *Agricultural and Forest Entomology* 2:259-270.

Fridman, J. & Walheim, M. 2000. Amount, structure and dynamics of dead wood on managed forestland in Sweden. *Forest Ecology and Management* 31:23-36.

Furuta, K. 1989. A comparison of endemic and epidemic populations of the spruce bark beetle (*Ips typographus japonicus* Niijima) in Hokkaido. *Journal of Applied Entomology* 107:289-295.

Geiszler, D.R. & Gara, R.I. 1978. Mountain pine beetle attack dynamics in lodgepole pine. *Theory and practice of mountain pine beetle management in lodgepole pine forests*. Proceedings published by University of Idaho, Moscow, USDA Forest Service, Washington D.C. and the Intermountain Forest and Range Experiment Station, Ogden, Utah.

Gärdenfors, U. (ed.) 2000. *Rödlistade arter i Sverige 2000 - The 2000 Red List of Swedish Species*. ArtDatabanken, SLU, Uppsala.

Göthlin, E., Schroeder, L.M. & Lindelöw, Å. 2000. Attacks by *Ips typographus* and *Pityogenes chalcographus* on windthrown spruces (*Picea abies*) during two years following a storm felling. *Scandinavian Journal of Forest Research* 15:542-549.

Harding, S., Lapis, E. B. & Bejer, B. 1986. Observations on the activity and development of *Pityogenes chalcographus* L. (Col., Scolytidae) in stands of Norway spruce in Denmark. *Journal of Applied Entomology* 102:237-244.

Horntvedt, R., Christiansen, E., Solheim, H. & Wang, S. 1983. Artificial inoculation with *Ips typographus*-associated blue-stain fungi can kill healthy Norway spruce trees. *Meddelelser fra Norsk institutt for skogforskning* 38:1-20.

Inouye, M. 1963. Details of bark beetle control in the storm-swept areas in the natural forest of Hokkaido, Japan. *Zeitschrift für angewandte Entomologie* 51:160-164.

Jonsell, M., Weslien, J. & Ehnström, B. 1998. Substrate requirements of red-listed saproxylic invertebrates in Sweden. *Biodiversity and Conservation* 7:749-764.

Klauser, O. 1954. Ein Beitrag zur Kenntnis des Kupferstechers *Pityogenes chalcographus* L. In: Wellenstein, G. (ed.) *Die Grosse Borkenkäferkalamität in Südwestdeutschland 1944-1951*, pp. 285-299. Forstschutzstelle Südwest, Ringingen.

Krokene, P. & Solheim H. 1996. Fungal associates of five bark beetle species colonizing Norway spruce. *Canadian Journal of Forest Research* 26:2115-2122.

Lekander, B. 1955. Skadeinsekternas uppträdande i de av januaristormen 1954 drabbade skogarna. *Meddelanden från Statens Skogsforskningsinstitut*, 45, 35 pp (in Swedish with German summary).

Lekander, B. 1972a. Den sextandade - ytterligare ett bekymmer för svenskt skogsbruk. *Skogen* 59:239-241. (In Swedish.)

Lekander, B. 1972b. A mass outbreak of *Ips typographus* in Gästrikland, central Sweden, in 1945-1952. *Research note 10*. Dept. Forest Zoology, Royal College of Forestry, 39 pp, Stockholm (in Swedish with English summary).

Lindelöw, Å. Risberg, B. & Sjödin, K. 1992. Attraction during flight of scolytids and other bark- and wood-dwelling beetles to volatiles from fresh and stored spruce wood. *Canadian Journal of Forest Research* 22:224-228.

Mulock, P. & Christiansen, E. 1986. The threshold of successful attacks by *Ips typographus* on *Picea abies*: a field experiment. *Forest Ecology and Management* 14:125-132.

Ogibin, B. N. 1974. Effect of population density on fertility in *Ips typographus* L. *Sovjet Journal of Ecology* 4:420-425.

Peltonen, M. 1999. Windthrows and dead-standing trees as bark beetle breeding material at forest-clearcut edges. *Scandinavian Journal of Forest Research* 14:505-511.

Schlyter, F. 1985. Aggregation pheromone system in the spruce bark beetle *Ips typographus*. Doctoral Thesis, Dept. of Animal Ecology, University of Lund, Sweden.

Schroeder, L. M. & Lindelöw, Å. 2002. Attacks on living spruce trees by the bark beetle *Ips typographus* (Col.: Scolytidae) following a storm-felling: a comparison between stands with and without removal of wind-felled trees. *Agricultural and Forest Entomology* 4:47-56.

Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecological Bulletins* 49:11-41.

Strömvall, A.-M. & Petersson, G. 1991. Conifer monoterpenes emitted to air by logging operations. *Scandinavian Journal of Forest Research* 6:253-258.

Thalenhorst, W. 1958. *Grundzüge der Populationsdynamik des grossen Fichtenborkenkäfers Ips typographus L.* Schriftenreihe der Forstlichen Fakultät der Universitet Göttingen 21:1-126.

Thomsen, M. 1939. Angreb af *Tomicus chalcographus* paa unge Sitkagraner, rødgraner og Douglasgraner. Det forstlige Forsøgsvæsen i Danmark XV, 136, København. (In Danish.)

Trägårdh, I. & Butovitsch, V. 1935. Bericht über die Bekämpfungsaktion gegen Borkenkäfer nach den Sturmverheerungen 1931-32. Statens Skogsförsöksanstalt 28, 1, Stockholm. (In Swedish with German summary.)

Weslien, J., Annila, E., Bakke, A., Bejer, B., Eidmann, H., Narvestad, K., Nikula, A. & Ravn, H.P. 1989. Estimating risks for spruce bark beetle (*Ips typographus* (L.)) damage using pheromone-baited traps and trees. *Scandinavian Journal of Forest Research* 4:87-98.

Weslien, J. & Regnander J. 1990. Colonisation densities and offspring production in the bark beetle *Ips typographus* (L.) in standing spruce trees. *Journal of Applied Entomology* 109:358-366.

Weslien, J. 1992. The arthropod complex associated with *Ips typographus* (L.): Species composition, phenology, and impact on bark beetle productivity. *Entomologica Fennica* 3:205-213.

Wood, D. L. 1982. *The bark and ambrosia beetles of North and Central America (Coleoptera : Scolytidae), a taxonomic monograph*. Brigham Young University, USA.

Worrell, R. 1983. Damage by the spruce bark beetle in South Norway 1970-80: A survey, and factors affecting its occurrence. *Meddelelser fra Norsk institutt for skogforskning* 38:1-34.

Acknowledgements

First I would like to thank Åke Lindelöw, because he is the one who once introduced me to the department by giving me a job to survey beetles on a remote, jungle-like island in the summer of 1997. Since then he has taught me more about entomology than anyone else. One thing led to another, and this PhD study started in spring -98.

Martin Schroeder has been an excellent supervisor. I especially appreciate his ability to return manuscripts in no time at all, filled with creative suggestions of improvements. Jan Weslien was my assistant supervisor, and was a great supporter during the whole period.

I enjoyed the friendly and helpful atmosphere at the department, and therefore I would like to express a collective Thank you! My PhD colleagues on the road to here are especially thanked (Jan C, Peter, Velemir, Sanna, Mattias, Olofx2, Mats, Karro, Lina, Örjan, Johanna and all you others). The field trip to Kenya was terrific. There are also many nice happenings to remember, such as "spex" and the Lucia-show.

Among all the courses I attended, I really remember Åke & Martin Chainsaw School because of its refreshingly short span between theory and practise (“hold it here.... that's the choke....OK, cut the trees over there”). It is sad I forgot to include this course among the 40 points.

The dead-wood-and-beetle group was very inspiring (Mats Jonsell, Mattias, Lasse, Anders, Åke, Martin, Erik, Thomas and others). I thank Helena Bylund for help with statistical problems, and how to make SAS work. Hubertus Eidmann gave detailed and valuable comments on several manuscripts. Mats J and Christer Solbreck also gave valuable input on my writings.

Several people gave valuable help with lab and field work: Oskar Kullingsjö (*e.g.* cutting small trees, and sorting insects etc), Peter Dalin (*e.g.* sorting insects), Erik Göthlin (field work) and Bengt Hedgren (*e.g.* cutting numerous big trees). I thank Heino Ounap in Estonia for great help with determinations of a large number of parasitoids and *Medetera* flies. Marc Kenis was a helpful host during my stay at CABI in Delemont in Switzerland, and introduced me to parasitoid determinations. He also helped with many determinations.

Finally, I thank mother and father for all support you gave me during this time!

The study was funded by the Swedish National Energy Administration (Statens Energimyndighet).