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The bark beetle *Ips typographus* (L.)  
on patches of dead or dying host trees:  
Estimating the colonization success  
and the risk of consequential tree deaths

ACADEMIC DISSERTATION

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The European spruce bark beetle (*Ips typographus* L.), a pest species capable of killing living trees, has caused considerable damage in Norway spruce [*Picea abies* (L.) Karst.] forests in Central and Northern Europe. According to the Finnish Forest Insect and Fungal Damage Prevention Act, groups of 20 or more damaged conifers should be removed from managed forests to prevent the accumulation of suitable bark beetle breeding material and to inhibit consequential outbreaks and beetle induced tree deaths. Legislation, along with efficient forest management practices, has drastically lowered the amount of dead wood in the managed forests of Finland. Considering dead wood inhabiting species, we should find ways to increase the amount of dead wood in managed forest without significantly increasing the risk of insect outbreaks. The main objective of this study was to estimate the colonization success of *I. typographus* and the risk of consequential tree deaths on windthrow and forest restoration areas. Under these main questions, the effect of felling technique (naturally formed root connections vs. cutting), burning treatment and recent forest disturbance history on *I. typographus* colonization and consequential tree mortality were also tested.

In contrast to the relatively extensive colonization by *I. typographus* in windthrow and restoration areas, numbers of consequential tree deaths were overall very low. The number and mean diameter ( $d_{1.3}$ ) of damaged trees were the most important characteristics associated with the level of colonization in both windthrow and restoration areas. In addition to these characteristics, the amount of recently dead standing spruce trees was also associated with the level of colonization and the number of tree deaths in windthrow areas. The study also shows that population levels of *I. typographus* varied greatly within the studied areas and that recent forest disturbance history affects the size of local beetle populations significantly. In addition, it seems that the progress of the colonization process of damaged trees is affected by the size of the local *I. typographus* population and its interaction with tree resistance level. The results indicate that in Finland, at endemic *I. typographus* population levels, forest owners can safely leave less than twenty wind-felled spruce trees in managed forests. Retention of even larger quantities of trees does not seem to evoke significant tree mortality. It is, however, clear that the risks of consequential damage increase with increasing amounts of damaged retention trees. The risks are also higher in stands where the natural mortality of trees is high and in cases where consecutive storm damage occurs within one or two years.

**Contents:**

<b>1 Introduction .....</b>	<b>6</b>
1.1 Background .....	6
1.2 Aims of the study .....	7
<b>2 Biology and ecology of the European spruce bark beetle – a review .....</b>	<b>7</b>
<b>3 Materials and methods .....</b>	<b>9</b>
3.1 Natural windthrows .....	9
3.2 Experimental setups .....	10
3.2.1 Restoration experiments .....	10
3.2.2 Windthrow simulations .....	10
3.3 Insect sampling .....	10
3.4 Statistics .....	11
<b>4 Results and discussion .....</b>	<b>11</b>
4.1 Colonization of damaged trees .....	11
4.2 Breeding success .....	13
4.3 Tree mortality .....	14
<b>5 Conclusions and future directions .....</b>	<b>15</b>
<b>Acknowledgements</b>	
<b>References</b>	
<b>Original publications (I-IV)</b>	

**List of original publications:**

- I Eriksson, M., Pouttu, A., Roininen, H., 2005. The influence of windthrow area and timber characteristics on colonization of wind-felled spruces by *Ips typographus* (L.). For. Ecol. Manag. 216: 105-116.
- II Eriksson, M., Lilja, S., Roininen, H., 2006. Dead wood creation and restoration burning: Implications for bark beetles and bark beetle induced tree deaths. For. Ecol. Manag. 231: 205-213.
- III Eriksson, M., Neuvonen, S., Roininen, H. Balancing between biodiversity and forest hygiene: Retention of wind-felled trees and the risk of consequential tree deaths in Finland. Manuscript submitted to Scan. J. For. Res.
- IV Eriksson, M., Neuvonen, S., Roininen, H. *Ips typographus* (L.) attack on patches of felled trees, with or without root connection, and the risk of consequential tree deaths. Manuscript.

I participated the design of studies I, III and IV. I was responsible for the data sampling in all four studies. The field work in studies I and II was conducted as a group of two or three people. For studies III and IV I collected the data alone. I analyzed the data and was responsible for the preparation of all four articles. The processing of articles was conducted together with co-authors.

## 1 Introduction

### 1.1 Background

Spruce bark beetle (*Ips typographus* L.) (Coleoptera: Scolytidae) is considered the most destructive scolytid in the coniferous forests of Europe (Christiansen & Bakke, 1988). Periodic outbreaks of this species have caused large timber losses in Central and Northern Europe (Annala, 1969). Although Finnish forests have not suffered from large outbreaks, the high economic losses in Scandinavian Norway spruce [*Picea abies* (L.) Karst.] forests (Worrel, 1983, Eidman, 1992) have also affected forest legislation in Finland. As in many cases heavy storms have preceded *I. typographus* outbreaks (e.g. Christiansen & Bakke, 1988), the Forest Insect and Fungal Damage Prevention Act (Anon., 1991) was passed to prevent the accumulation of suitable material for bark beetle breeding in managed forests, in order to inhibit bark beetle outbreaks after windthrows or other comparable disturbances.

The Act obligates forest owners to remove wind-felled coniferous trees from the forest if damaged trees account for more than 10% of the number of trees or form groups of at least 20 conifers (Anon., 1991). In practice smaller groups of wind-felled trees have also been removed from the forest due to fear of insect attack. These high standards of forest hygiene and efficient forest management (e.g. thinning and mechanical soil scarification) have drastically lowered the amount of dead wood in the managed forests of Fennoscandia (Siitonen 2001), thus endangering the existence of many dead wood inhabiting species (Samuelsson et al., 1994; Esseen et al., 1997; Jonsell et al., 1998; Siitonen, 2001). Although the spruce bark beetle is a serious forest pest, it also has notable positive effects on forest biodiversity. By colonizing newly dead or dying spruce trees it starts the decomposition of bark

and wood creating new habitats for many species utilizing dead wood (see Weslien, 1992, and references therein). Therefore the challenge of modern forestry is to combine profit-making and biodiversity-sustaining forestry. Considering dead wood inhabiting species we should find ways to increase the amount of dead wood in managed forests without significantly increasing the risk of insect outbreaks.

Storms and snow damage could considerably increase the amount of dead wood in Finnish forests if the prevailing practices of removing almost all damaged trees from managed forests were to change. It has been estimated that over ten million m<sup>3</sup> of trees were damaged, by the seven largest storms, during the years 1975-1985 (Laiho, 1987), and that the autumn storms in 2001 alone felled about seven million m<sup>3</sup> of trees (Ihalainen & Ahola, 2003). If trees felled or damaged by smaller scale local storms and snow were also included the average volume of trees damaged by abiotic factors, could exceed one million m<sup>3</sup> per year. In addition to dead wood creation, wind disturbance, by uprooting trees, contributes significantly to the structural complexity of boreal forest ecosystems (Ulanova, 2000). The retention of wind-felled trees in managed forests would also be a cost-effective measure for increasing the amount of dead wood (Ranius et al., 2005; Jonsson et al., 2006). The retention of damaged trees in managed forests could, however, become expensive, if significant insect damages, such as bark beetle outbreaks, were to follow.

To avoid significant insect damage after wind disturbance, risk estimation regarding wind throws and consequential tree deaths should be developed. Wermelinger (2004) suggested that the risk of attack on living trees seems to be related mainly to the exposition, age, and nutrient and water supply of the trees. In addition to tree susceptibility, local

insect abundance, weather conditions, and forest management also affect the dynamics of outbreaks. Pheromone traps and pheromone-baited trees have been used for monitoring population levels and forecasting damage (Weslien et al., 1989; Hübertz et al., 1991; Weslien, 1992; Lindelöw & Schroeder, 2001; Faccoli & Stergulc, 2004). These results are inconsistent, but monitoring results can at least be used to identify the low risk areas. Tools such as GIS (Wichmann & Ravn, 2001) and regression analyses (Lexer, 1995; Dutilleul et al., 2000) have also been used to assess the susceptibility of spruce stands.

In Finland, where no large-scale outbreaks have been reported, expensive and laborious continuous monitoring would not be economically viable. A better option might be to concentrate efforts on estimating the risks of individual windthrows after extensive storm damage. Schroeder (2001) reviewed six studies from windthrow areas and found a trend indicating that larger areas experienced on average higher tree mortality per hectare, by *I. typographus*, than the smaller areas. Schroeder & Lindelöw (2002) reported an almost perfect correlation between the number of colonized wind-felled trees and the number of trees killed in a 4-year period following the storm disturbance. The datasets used in the reviewed papers (Schroeder, 2001) included only one to five windthrow areas per study. There is therefore still a need for more extensive studies on the influence of windthrow area and timber characteristics on consequential tree deaths.

An excellent field laboratory was created when autumn storms felled about 7 million m<sup>3</sup> of forest in southern Finland in 2001 (Ihalainen & Ahola, 2003). Most of the wind-felled trees (62%) were Norway spruce. This enabled me to study *I. typographus* populations using a large sample of distant, evidently independent, Norway

spruce dominated windthrow areas with varying characteristics. As forest restoration and especially artificial dead wood creation has become more common, also experiments testing the effects of restoration practices on local *I. typographus* populations were also included in this thesis.

## 1.2 Aims of the study

The main objective of this study was to evaluate the risks involved in leaving varying amounts of damaged, wind-felled or cut, spruce trees in managed forests in Finland. The data on this thesis have been collected from both field inventories and experimental studies. Articles I and III are based on inventories made of natural windthrow areas to find out the level of *I. typographus* attack, on both wind-felled (I) and standing trees (III), and the windthrow area and timber characteristics significantly associated with the attacks. Basically, the objectives were the same in articles II and IV, but these studies were experimental, with adjusted levels of felled trees. Further issues studied were the effects of restoration burning (II) and the felling technique (natural with randomly formed root connections vs. cutting) (IV) on *I. typographus* colonization (IV), breeding success (II, IV) and number of consequential tree deaths (II, IV).

## 2 Biology and ecology of the European spruce bark beetle – a review

The distribution of the European spruce bark beetle in Europe covers almost the whole continent (Wood & Bright, 1992). Adults usually hibernate in the litter near the tree where they developed (Christiansen & Bakke, 1988). Some beetles hibernate under the bark of felled or standing trees. Usually the spring flight starts after the air temperature has

reached 20°C and the litter or moss layer temperature is at least 9-12°C (Annala, 1969, and references therein). Male beetles attack host trees, burrow nuptial chambers, and by emitting pheromones, attract 1 to 4 females to mate with them (Christiansen & Bakke, 1988). Each female then excavates her own maternal gallery for egg laying. The optimum temperature for reproduction and juvenile development have been calculated to be 29-30°C and the heat sum for total development ranges from 334 degree-days (Wermelinger & Seifert, 1998, 1999) to 365 degree-days (Wermelinger, 2004). At higher altitudes and in northern parts of Europe *I. typographus* usually produces one generation per year but parent beetles may also produce sister broods (Bakke et al., 1977). In very warm years in Scandinavia (Austarå et al., 1977) and more commonly in the lowlands of Central Europe beetles are able to produce two generations per year (Wild, 1953). However, in Scandinavia the possibilities of the second generation beetles completing their development in standing trees are poor, and therefore the probabilities of their surviving through the winter are also rather small (Austarå et al., 1977).

At endemic (non-outbreak) population levels, the spruce bark beetle typically breeds in weakened (e.g. wind-felled) trees. Therefore the most important factor regulating spruce bark beetle populations may be the competition for low resistant host substrate (Økland & Berryman, 2004), which is sparsely distributed in the managed forests of Fennoscandia (Siitonen, 2001). In densely attacked trees, intraspecific competition decreases breeding success and impedes population increase (Anderbrant, 1990). The resource-depletion model of forest insect outbreaks by Økland & Bjørnstad (2006) involves the accumulation of resources (susceptible standing trees) during endemic periods of bark beetle populations

and depletion during outbreaks. The transition from endemic to outbreak populations is caused by external disturbance events such as extensive windstorms that free the beetle population from intraspecific competition by producing an oversupply of low resistant breeding material. Favorable weather conditions during swarming and breeding may lead to a rapid population increase and a possible outbreak, resulting in consequential deaths of living trees. High numbers of colonizing beetles are a prerequisite for successful colonization of living trees, which defend themselves by volatile resin exudation (e.g. Mulock & Christiansen, 1986). Another important part is played in breaking the host's defenses by mutualistic blue-stain fungi of the genus *Ophiostoma* and *Ceratocystis* (Paine et al., 1997; Lieutier, 2002), which are mainly transported to new hosts on the beetle's pronotum and elytra (Furniss, et al., 1990). The fungi kill trees by drying up the sapwood and preventing water transport to the crown (Christiansen & Bakke, 1988).

Large windfall events, which enable rapid population increase, are probably a major initiator and synchronizer of *I. typographus* outbreaks (Økland & Berryman, 2004). There are also indications that the risk of outbreak is not only dependent on population size, but external factors such as severe and long-lasting drought stress may also be important for triggering outbreaks. However, the effect of drought is not that simple - while severe drought stress makes trees more susceptible to beetle attacks (Berryman, 1982; Worrel, 1983), moderate drought may make them even more resistant to the attacks (Dunn & Lorio, 1993).

The spruce bark beetle probably uses host volatiles to locate susceptible trees (Austarå et al., 1986). At least ethanol and acetaldehyde have been found to attract spruce bark beetles



(Lindelöw & Risberg, 1992). These compounds are emitted from stressed plants (Kimmerer & Kozlowski, 1982) such as injured conifers (Sjödín et al., 1989). It is therefore likely that the attraction effect strengthens as the amount of damaged trees increases. When attacking living trees, a mass attack is needed to overcome the defensive resin exudation from the attacked trees. This mass attack is evoked by emitting aggregation pheromones, mainly methylbutenol and (S) *cis*-verbenol, attracting conspecifics (Bakke et al., 1977). The emission of aggregation pheromones continues until the defenses of the host tree have been defeated (Birgersson, 1989). The duration of this phase therefore depends on the vigor of the host tree. After the females have entered the galleries, the emission of anti-aggregation pheromones, ipsenol and verbenone, begins (Bakke, 1981). Ipsenol is produced by the beetles while associative yeasts in egg galleries are mainly responsible for the production of verbenone (Leufvén et al., 1984). It is supposed that verbenone indicates to beetles that the host is unsuitable for colonization (Byers et al., 1989). Anti-aggregation pheromones seem to regulate egg gallery density and shift the attack to new bark areas or neighboring trees (Bakke, 1981).

The defensive mechanisms of conifers against bark beetles include both constitutive and inducible defenses (reviewed in Franceschi et al., 2005). Constitutive defense includes the excretion of oleoresin from interconnected systems of ducts in the bark and wood. When a duct is severed, e.g. due to the boring of bark beetles, oleoresin is excreted to repel, flush, entrap or otherwise kill the invading organism, due to the toxic nature of resin. Constitutive defense is functional against bark beetles as long as an adequate amount of oleoresin is excreted per each intruder. When the number of attacks per tree increases the

amount of resin excreted per wound rapidly tapers off (Schwerdtfeger, 1955). If resin exudation is insufficient, gallery construction may be initiated. At this stage beetles contaminate the phloem and cambium tissues with a number of microorganisms, including several species of blue-stain fungi (Christiansen & Bakke, 1988). Against these intruders the inducible hypersensitive response occurs locally at the site of infection or attack (Bleiker & Uzunovic, 2004), leading to the production of reactive oxygen species and rapid cell death intended to kill and contain invading organisms (Franceschi et al., 2005). Beyond this localized response, there are also more generalized responses such as the formation of callus tissue, early lignification of fibers and changes in chemical defenses (reviewed in Franceschi et al., 2005).

### 3 Materials and methods

#### 3.1 Natural windthrows

We recorded windthrow area and timber characteristics as well as numbers of standing spruce trees attacked and killed by *I. typographus* in Norway spruce dominated windthrow areas hit by the autumn storms in 2001 (latitude: 60°02'–61°54'N and longitude: 23°06'–26°06'E). Sixty-five windthrow areas with varying numbers of wind-felled spruce trees were originally included (I). However, as a consequence of logging operations during 2003–2005, four of the original 65 windthrow areas were omitted from the article dealing with the number of trees killed by *I. typographus* (III). The studied areas ranged from single tree gaps (individual wind-felled trees) to large gaps with over 3000 wind-felled spruce trees. Continuous areas with a patchwork of gaps (less than 100 m between adjacent gaps) were also included. To be able to compare the standing crop of windthrow areas, the

basal area ( $\text{m}^2 \text{ha}^{-1}$ ) (Philip, M. S., 2002) of spruce trees, pine trees (*Pinus sylvestris* L.), deciduous trees and recently (2000-2001) dead standing Norway spruces was also estimated. The estimate was made with a relascope (Philip, 2002) from three to five points in each windthrow area and mean values were used in the analyses. Most of the fieldwork was done during the year 2003, but the counting of spruce trees killed after the storms by *I. typographus* continued until autumn 2005.

### 3.2 Experimental setups

#### 3.2.1 Restoration experiment

Restoration experiments (II) were conducted in the southern boreal zone (Ahti et al., 1968) in southern Finland ( $61^{\circ}12' - 61^{\circ}25' \text{N}$ ,  $25^{\circ}00' - 25^{\circ}15' \text{E}$ ). Altogether, 18 stands were selected for the experiment. The average age of the stands was 80 years (range from 60 to 100 years). All of the stands were managed. The treatments consisted of three levels of down wood retention (5, 30, and  $60 \text{ m}^3 \text{ha}^{-1}$ ) (DWR = trees, including all tree species, felled and left in the stand) and burning treatment (burn/non-burn) ( $3 \times 2$  factorial). Each treatment combination was repeated three times ( $3 \times 6 = 18$ ). A constant volume of  $50 \text{ m}^3 \text{ha}^{-1}$  of standing retention trees (all tree species included) were left standing dispersed on each experimental stand, which meant that some of the felled trees were transported out of each stand. The restorative cuttings were carried out in February and March 2002 and the burnings during June to August 2002. The burnings were carried out using the traditional Finnish prescribed burning technique (Lemberg & Puttonen, 2003). Trees were sampled in July 2003 and the spruce trees killed, after the restoration treatments, by *I. typographus* on forest edges surrounding restoration areas were

counted, starting from autumn 2003 to autumn 2005.

#### 3.2.2 Windthrow simulations

In this study (IV) groups of 20 spruce trees were felled in 16 stands in November 2003. Half of the experimental stands were situated in Ruotsinkylä research forests in southern Finland (later referred as the southern area) ( $60^{\circ}33' \text{N}$ ,  $24^{\circ}57' \text{E}$ ), in areas where the autumn storms in 2001 felled large amounts of spruce forest (Ihalainen & Ahola, 2003). Consequently it was expected that the population levels of *I. typographus* would be elevated in these southern areas. The other half of the experimental stands were situated in the Punkaharju research forests - in eastern Finland (later referred as the eastern area) ( $61^{\circ}41' \text{N}$ ,  $29^{\circ}24' \text{E}$ ) which did not suffer from recent storms. In both areas trees on half of the stands were felled by cutting and the other half by pulling the trees down (to simulate wind-felling). Trees were pulled down using a tractor winch attached to the tree at the height of about five meters. In some cases some large roots were cut, opposite to the felling direction, to facilitate the felling. However, most of the root connections remained intact in these felled trees. Sampling of the felled trees was conducted in July-August 2005 and the number of spruce trees killed by *I. typographus* in experimental stands, after the trees had been felled, was inspected in autumns of 2004 and 2005.

### 3.3 Insect sampling

The sample size of the inspected trees depended on the number of wind-felled or cut trees (I, II, IV). If a study area had 30 or less damaged trees all accessible trees were inspected. Where a larger number of trees were damaged, a random sample of 30-90 trees was taken. Pieces of bark (15 x 60 cm) were

**Table 1.** Measured response variables in original publications.

	Study			
	I	II	III	IV
Damaged trees colonized	X <sup>(1)</sup>	X <sup>(1)</sup>		X <sup>(2)</sup>
Egg gallery density	X <sup>(3)</sup>	X <sup>(3)</sup>		X <sup>(4)</sup>
Estimated number of egg galleries per study area	X	X		
Breeding success		X <sup>(5)</sup>		X <sup>(6)</sup>
Tree mortality		X	X	X

<sup>(1)</sup> Percentage of damaged trees colonized

<sup>(2)</sup> Number of damaged trees colonized

<sup>(3)</sup> Density per m<sup>2</sup> of attacked bark surface

<sup>(4)</sup> Density per m<sup>2</sup> of bark surface

<sup>(5)</sup> Female offspring per mother beetle

<sup>(6)</sup> Offspring per mother beetle

removed from tree bole and egg galleries (I, II, IV), and exit holes (II, IV) of *I. typographus* were counted at 1.3 m, 4 m, and at intervals of 4 meters until the diameter of tree trunk decreased to less than 10 (I, II) or 15 (IV) cm. *P. chalcographus* mating chambers were counted at the same heights from a smaller area (I, II) (15 x 15 cm). The breeding success of *I. typographus* was calculated as the number of female offspring (II) or offspring (IV) per mother beetle (supposing that one offspring emerged through each exit hole).

### 3.4 Statistics

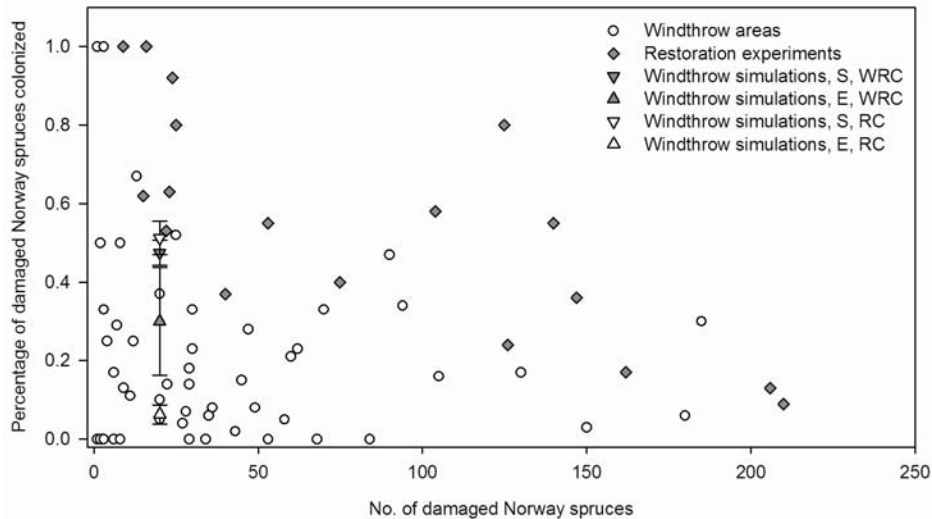
The data on the number of insects on damaged trees (I,II) and spruce trees killed by *I. typographus* (III) in windthrow and restoration areas were highly skewed with non-normal errors. Generalized linear models (GLM) (McCullagh & Nelder, 1989) with different error distributions (binomial, negative binomial) or quasi-likelihood were therefore used, depending on the analysis (see e.g. Crawley, 2003). In experimental settings (II, IV) two-way analysis of variance was also used when testing the effects of experimental treatments. All the analyses were carried out in R (R Development Core Team, 2005).

## 4 Results and discussion

### 4.1 Colonization of damaged trees

The number and mean diameter of wind-felled spruce trees (I) and felled spruce trees (II) and the basal area of recently dead standing spruces (I) were the most important characteristics positively associated with the level of colonization. Earlier results show the preference of *I. typographus* for damaged stems of large diameter (Butovitsch, 1971; Schroeder et al., 1999; Göthlin et al., 2000) and the amount of recently dead wood has been found to explain most of the variation in the number of bark beetle individuals (Martikainen et al., 1999). The number of colonized wind-felled trees has also been found to be positively associated with the number of wind-felled trees (Schroeder & Lindelöw, 2002). These and earlier results indicate that a large number of high volume spruce trees attracts large numbers of *I. typographus* to colonize damaged trees. Assuming that the basal area of recently dead standing spruce trees correlates with *I. typographus* population density, basal area could be used to adjust the estimates based on the characteristics of damaged trees. The attraction effect of damaged spruce trees is probably based on the volatiles, mainly ethanol and acetaldehyde, emitted from stressed plants (Kimmerer & Kozłowski, 1982) and damaged conifers (Sjödin et al., 1989) and known to attract *I. typographus* (Lindelöw & Risberg, 1992). A large number of small volume trees would, therefore, probably have the same effect, but as trees with only a thin layer of phloem are not suitable for colonization, the attack might be directed away from damaged to standing trees.

During the first summer (2002) after the storm-felling and restoration cuttings, 71% (N = 65) of the windthrow

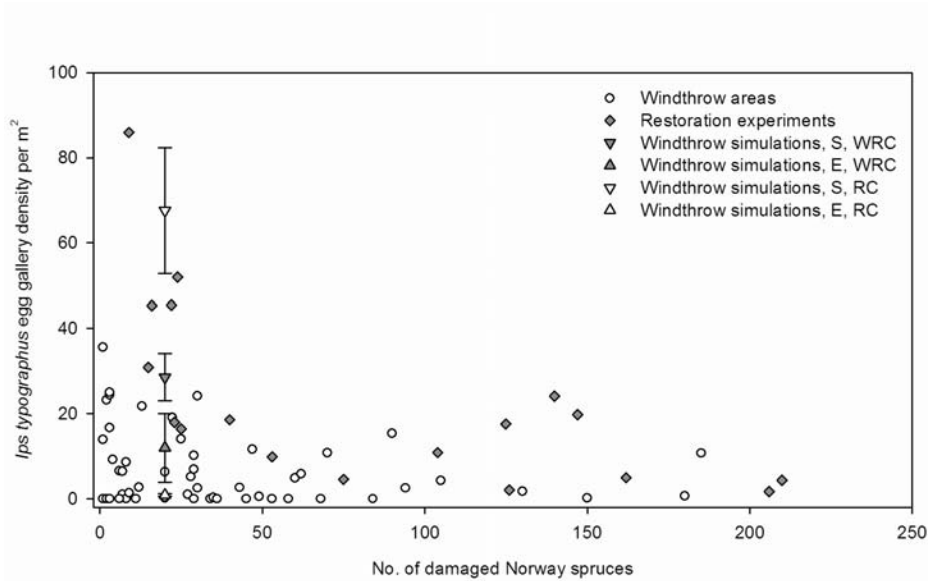


**Figure 1.** Relationship between the percentage of damaged trees colonized by *Ips typographus* and the number of damaged trees. At windthrow areas the damaged trees were wind-felled. In experimental settings (restoration experiments and windthrow simulations) trees were cut (II, IV) or pulled down (IV). The triangles represent mean values ( $\pm$ SE) of each felling treatment-study area combination in windthrow simulations. S = southern study area, E = eastern study area, WRC = without root connections, RC = root connections. The data is obtained from studies I, II and IV.

areas (I) and 100% ( $N = 18$ ) of restoration areas (II) with cut trees were colonized by *I. typographus*. Similarly, the percentage of colonized wind-felled and cut trees shows that cut trees were either more attractive or simply easier to colonize, as on average 19% ( $SE \pm 0.03$ ) and 54% ( $\pm 0.07$ ) of wind-felled and cut trees, respectively, were colonized in these areas (Fig. 1). The level of colonization seems also to be higher in cut trees if the mean density of egg galleries in damaged trees is considered (Fig. 2). In wind-felled trees (I) the recorded average density ( $\pm SE$ ) of egg galleries per  $m^2$  of bark was 5.78 ( $\pm 1.06$ ,  $n = 62$ ) (unpublished), while the same figures for cut trees (II) were 22.9 ( $\pm 5.18$ ,  $n = 18$ ) (unpublished). Of course these figures are not straightforwardly comparable, considering the differences in study methods used. Moreover, the experimental stands in the restoration

experiment were all more open, favoring *I. typographus* swarming and breeding, than the rather shady windthrows with just a few wind-felled trees.

It seems that the progress of the colonization process depends both on the susceptibility of the possible host and the size of the beetle population (IV). In windthrow simulation experiments egg gallery density was significantly affected by study area and the interaction between study area and felling treatment (with or without root connections). Similar results have been obtained in experimental studies of *Dendroctonus rufipennis* suggesting that host acceptance behavior changes with the population phase of eruptive bark beetles (Wallin & Raffa, 2004). In this study (IV) *I. typographus* could only occasionally colonize damaged trees with partial root connections in the eastern study area, with very low *I. typographus*



**Figure 2.** Relationship between the density of *Ips typographus* egg galleries in wind-felled and felled trees and the number of damaged trees. At windthrow areas the damaged trees were wind-felled. In experimental settings (restoration experiments and windthrow simulations) trees were cut (II, IV) or pulled down (IV). The triangles represent mean values ( $\pm$ SE) of each felling treatment-study area combination in windthrow simulations. S = southern study area, E = eastern study area, WRC = without root connections, RC = root connections. The data is obtained from studies I, II and IV.

populations, while the colonization of trees without root connections was much more common (Fig. 2). By contrast, in the southern study area that suffered from the autumn storms 2-3 years earlier, with higher population levels, the beetles colonized trees with partial root connections significantly more densely than trees without root connections.

Therefore, if the population before the disturbance is very low, even the colonization of felled trees with partial root connection might fail. Similarly 9% of attacks on wind-felled trees with root contact and 1.5% of attacks on trees with broken stems were defined as unsuccessful after extensive storms in Sweden (Martin Schroeder, personal communication). Several other factors may have an effect on the process of colonization. Firstly, at very low population densities colonization attempts might be unsuccessful as the low numbers of beetles cannot overcome the

resin exudation from the newly damaged trees with root connections. Secondly, there might be differences, between damaged trees with and without root connections, in the production of host volatiles (e.g. Kimmerer & Kozłowski, 1982; Sjödin et al., 1989; Kelsey, 1994) and in the production of both aggregation and anti-aggregation pheromones by invading beetles and associative yeasts (Birgersson, 1989).

#### 4.2 Breeding success

Overall, egg gallery densities in felled spruce trees were very low (Fig. 2). Thus, it was not surprising that no significant differences (at the  $p < 0.05$  level) in offspring production were found between areas (IV), felling treatments (with or without root connections) (IV) or down wood retention level (II). However, the results in study IV suggest that damaged trees without root

connections were more suitable for *I. typographus* reproduction, as the breeding success was on average 58% higher in cut trees than in trees with root connections ( $p < 0.10$ ). On the other hand, breeding success in non-burned stands was significantly higher than in areas that had undergone burning treatment (II). It also seems that burning treatment had a more devastating effect on offspring survival in areas with a high DWR (down wood retention) level ( $60 \text{ m}^3$ ) than at the two lower levels. Actually, studies by Lilja et al. (2005) in the same experimental areas show that living tree mortality within experimental areas was highest when the DWR level was high, because the flames climbed up to the canopy, using down retention trees as a "ladder". Thus, the low breeding success at the highest level of DWR with burning treatment was attributable to the intensity of the fire. It seems that the risks of dead wood creation, regarding consequential tree deaths induced by *I. typographus*, can be effectively lowered by timely conducted restoration burnings. Burnings applied immediately after the colonization of felled trees trap beetles inside the bark, killing the beetles or at least lowering their breeding success. The effectiveness of burning can be adjusted by the amount of down wood retention trees, which affects the intensity of fire (Lilja et al., 2005).

#### 4.3 Tree mortality

In contrast to the relatively extensive colonization by *I. typographus* and *P. chalcographus* in windthrow and restoration areas, the numbers of tree deaths at forest edges surrounding study areas were overall very low (Fig. 3). In both experimental setups (II, IV) the number of tree deaths was so low, probably as a consequence of rather small amount of damaged trees, that no significant effects of treatments were found. In windthrow

areas, however, our results suggest that the amount of tree deaths following storm-disturbance is related to the number and size ( $D_{1.3}$ ) of wind-felled spruce trees and the quantity of recently dead standing spruce trees. Earlier, Schroeder & Lindelöw (2002) found a strong correlation between the number of wind-felled spruce trees and the number of tree deaths. In this study the correlation was much weaker, but even so, the risk of tree deaths seems to increase along with the increasing number of wind-felled spruce trees. The preference of *I. typographus* for large trees has also been reported with wind-felled (Butovitsch, 1971; Göthlin et al., 2000; I), cut (II) and standing spruce trees (Butovitsch, 1938, 1971; Lekander, 1972; Lexer, 1997), and also mechanically created high stumps (Schroeder et al., 1999) of large tree diameter. In addition older standing trees seem to be more susceptible to *I. typographus* attack than younger ones (Lexer, 1997).

A new finding was that the quantity of recently dead standing spruce trees was linked to tree deaths (III). This may express partly the size of local bark beetle populations and partly the susceptibility of spruce trees to insect damage. The first interpretation is supported by the results of Martikainen et al. (1999), who reported that the amount of recently dead wood best explained the number of all bark beetle individuals caught per sample plot. There are no studies directly supporting the second interpretation, but Veteli et al. (2006) found that pine shoot beetles (*Tomicus* spp.) were significantly more common in unthinned Scots pine (*Pinus sylvestris*) stands, where the natural mortality of trees is high, than in thinned stands. Several stand level factors such as stand age (Becker & Schröter, 2001; Lexer, 1995, 1997), altitude, soil nutrients (Nef, 1994; Dutilleul et al., 2000), water supply, the proportion of stand borders exposed to



study further shows that local population levels of *I. typographus* varied greatly within the study area (approx. 200 x 200 km) (I) and that the recent forest disturbance history has a significant effect on the size of local beetle populations (IV). In addition, it seems that the progress of the colonization of damaged trees is affected by the size of the local *I. typographus* population and its interaction with tree resistance level (IV).

If the purpose of the Finnish Forest Insect and Fungal Damage Prevention Act (Anon., 1991) is to prevent all windthrow-induced bark beetle damage in managed forests, then the limit of twenty conifers has probably been set at an appropriate level. However, if the aim is to improve managed forests as a habitat for dead wood-dwelling insects and even to try to follow the objectives set out in the European Biodiversity Strategy (Anon., 1998), which aims to anticipate, prevent and attack the causes of significant reduction or loss of biodiversity at the source, the limit could be higher. For example Hanski (2000), studying extinction debt and species credit in boreal forests, concluded that in order to prevent the imminent wave of extinctions of specialist forest species, an extensive restoration program for managed forests is needed. It has been shown that the retention of wind-felled trees in managed forests would be a cost-effective measure for improving the habitats of saproxylic species if the avoidance of consecutive insect damage is possible (Ranius et al., 2005; Jonsson et al., 2006). Considering the benefits for biodiversity, the low economic benefits of collecting small groups of wind-felled trees, and the low risk of the creation of a few dead standing trees per windthrow by bark beetles, it should not be too difficult to take advantage of natural wind-throws.

Even if the risks of leaving damaged trees in managed forests in the

present situation seem to be minor, the situation might, however, change. Consecutive storms in following years, for example, could increase beetle populations to outbreak levels. The predicted climate warming (Anon., 2001) should also be considered. A raised mean temperature in combination with climate extremes, such as spring temperature backlashes and summer drought, will negatively precondition Norway spruce to secondary damage through pests and pathogens (Schlyter et al., 2006). During very warm summers *I. typographus* has been observed to swarm a second time in Scandinavian countries (e.g. Austarå, 1977; Anon., 2006). Although the probabilities of the second generation surviving through winter in standing trees are small, the broods in felled trees are more likely to develop adults mature enough to survive winter (Austarå, 1977). This would radically increase the possibility of outbreaks in Finland too, as with two generations a year the beetles could exploit a larger proportion of the low resistant wind-felled trees before they become unsuitable for breeding.

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