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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

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Abstract

1 To maintain biodiversity in forests more wind-felled trees must be left where they fall. However, there is concern among forest owners that this may result in higher tree mortality caused by the spruce bark beetle, *Ips typographus* (L.) (Col.: Scolytidae).

2 In the 5 years following a major storm disturbance the number of standing spruces killed by *I. typographus* was determined in a total of 53 stands. In five of the stands all wind-thrown trees were left (unmanaged stands) and in 48 of the stands, which were situated at distances of 1.4–10.0 km from each focal unmanaged stand, the wind-felled trees were removed directly after the storm (managed stands). In the winter preceding the fifth summer new storm-fellings occurred in the study area.

3 In the 4-year period between the first and second storm-fellings, 50–322 standing trees were killed by *I. typographus* per unmanaged stand. There was a direct linear relationship between the number of storm-felled spruces colonized by *I. typographus* and the number of trees subsequently killed in the unmanaged stands.

4 Tree mortality caused by *I. typographus* in the unmanaged stands was almost nil in the first year, peaked in the second or third year, and decreased markedly to a low level in the fourth and fifth years.

5 In the 4-year period between the first and second storm-fellings twice as many trees were killed per ha in the unmanaged stands than in the managed stands: the average difference being 6.2 killed trees per ha, equivalent to 19% of the number of spruce trees felled by the first storm in the unmanaged stands.

6 Much higher numbers of trees were killed per ha in the stand edges than in the interiors of both the unmanaged and the managed stands.

Keywords Bark beetle killed trees, *Ips typographus*, *Picea abies*, removal of wind-felled trees, spruce bark beetle, stand edges, storm-felling, wind-felled trees.

Introduction

The spruce bark beetle, *Ips typographus* (L.) (Coleoptera: Scolytidae), is one of the most important pests of mature spruce, *Picea abies* L. (Karst.), in Eurasia (Christiansen & Bakke, 1988). Generally, *I. typographus* prefers to reproduce in breeding material with non-existent or weak defences such as wind-felled or otherwise damaged trees, cutting slash and unbarked felled timber. In some situations the species is also able to kill apparently healthy trees in large numbers. One of the factors triggering such outbreaks is the occurrence of storm-fellings (Bombosch, 1954; Inouye, 1963; Lekander, 1972; Ravn, 1985; Christiansen & Bakke, 1988; Furuta, 1989). For successful colonization of living trees the number of attacking beetles must be high enough to overcome the defensive system of the trees (Christiansen, 1985; Mulock & Christiansen, 1986; Christiansen *et al*., 1987). Large-scale storm-fellings provide *I. typographus* with a surplus of breeding material with non-existent or weak defence. As a result the densities of *I. typographus* egg galleries in the colonized wind felled trees will be low, which means that the larvae are released from

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the strong intraspecific competition that they usually experience (Botterweg, 1983; Anderbrant *et al*., 1985; Anderbrant, 1990). This means that both the number of progeny per female and the quality (size, fat content) of the progeny increase. After storm-fellings the reproductive rate of *I. typographus* in wind-felled trees may exceed 10 daughters per mother (Lekander, 1955; Inouye, 1963; Butovitsch, 1971; Furuta, 1989). Consequently, the *I. typographus* populations may increase to densities high enough to enable the beetles to overcome the defence mechanisms of living trees in the years following storm-fellings. To prevent such population increases, removal of all wind-felled spruce trees directly after storm disturbances has for a long time been practised whenever possible.

In the newest version of the Swedish Forestry Act, the maintenance of biodiversity in forested areas has been given the same priority as wood production (Anon, 1993). Dead wood is a key factor in maintaining biodiversity in forests (Økland *et al*., 1996; Kaila *et al*., 1997; Martikainen *et al*., 2000). Unfortunately, forests in Europe today contain low amounts of dead wood (Andersson & Hytteborn, 1991; Albrecht, 1991; Fridman & Walheim, 2000). Thus, to maintain biodiversity more wind-felled trees must be left in managed forests after storm disturbances, and areas of forest reserves, where all wind-felled trees are left, must be increased. However, many forest owners are concerned that this will result in increased damage to living trees caused by bark beetles and consequently they are reluctant to leave any wind-felled trees at all. Furthermore, after large-scale storm-fellings the forest authorities generally require that the forest owners remove all wind-felled spruce trees in managed forests in order to reduce the risk of bark beetle outbreaks.

In the future more wind-felled trees must be left after storm-fellings to increase the amounts of dead wood in the forests. However, really large quantities, as in the present study, will probably at most be left in a few scattered stands that constitute only a minor part of the forest landscape. In this situation the beetles originating from the wind-felled trees in such stands will be too few to be able to influence the level of damage in the region as whole, but they might influence the level of damage in the same or adjacent stands. Only a few earlier studies have been conducted to study the risk for tree mortality in stands where wind-felled trees have been left. These document in some detail the number of wind-felled spruces (and/or areas affected) and the number of standing trees subsequently killed by *I. typographus* in the years following the wind-felling (Lekander, 1972; Ravn, 1985; Niemeyer *et al*., 1995; Weslien & Schröter, 1996; Peltonen, 1999; Schopf & Köhler, 1999; Schröter *et al*., 1999; Wichmann & Ravn, 1999). Only two of these studies included 'control areas' where wind-felled trees were removed or were present only in low numbers (Ravn, 1985; Peltonen, 1999). Trees may also be killed in such areas and a comparison between the two kinds of stand is necessary to evaluate the proportion of the tree mortality that is caused directly by the retention of wind-felled trees.

In November 1995, southern Sweden was hit by a severe storm so that spruce and pine trees amounting to 5 million m^3 in volume were wind-felled (Anonymous, 1996). Most of the wind-felled trees were removed from managed forests before the spring of 1996. However, in some unmanaged stands (forest reserves), all wind-felled trees were left. In the present study tree mortality caused by *I. typographus* was recorded in the 5 years following this storm in both unmanaged stands, where all wind-felled trees were left, and managed stands, where all wind-felled trees were removed. The managed stands selected for the study were situated some distance from the unmanaged stands. Thus, tree mortality in stands adjacent to the unmanaged stands was not investigated. The following four questions were addressed. (1) What is the magnitude of tree mortality caused by *I. typographus* in stands where wind-felled spruces are left? (2) What is the temporal pattern of the tree mortality caused by *I. typographus* in such stands? (3) How much greater is the risk that trees will be killed by *I. typographus* in stands where all wind-felled spruces are left than in stands where all wind-felled spruces are removed? (4) Is the tree mortality caused by *I. typographus* at stand edges, adjacent to storm gaps with and without retained wind-felled spruce trees, different to that in the interior of the stands?

Materials and methods

Stands investigated were situated within a 45×30 km area around the city of Jönköping in southern Sweden. Five stands were reserves that had been left unmanaged for several decades, whereas 48 stands were managed (referred to as unmanaged and managed stands in the following text, respectively). In the unmanaged stands all wind-felled trees were left, whereas in the managed stands all wind-felled trees were removed before the summer of 1996. The five unmanaged stands were the only ones known at the start of the study where large numbers of wind-felled trees had been left and attacked by *I. typographus*. One other similar stand was found in the region later, but was not included in the study. In 1997, four to six managed stands were chosen around each of the unmanaged stands. In 1998, three to six more managed stands were added per unmanaged stand. The managed stands were chosen at distances of 1.4–10.0 km (mean = 4.7 km) from the respective focal unmanaged stands. This minimum distance was chosen to ensure that the unmanaged stands did not influence the risk of bark beetle attacks in the managed stands. In accordance with this assertion, there was no significant correlation between the distance from unmanaged stands and the number of trees killed per ha in the managed stands in any of the years (1997: $r^2 = -0.02$, $P = 0.49$, $F_{[1,\ 23]} = 0.49$; 1998: $r^2 = -0.02$, $P = 0.38$, $F_{[1,42]} = 0.78$; 1999: $r^2 = -0.05$, $P = 0.18$, $F_{[1,39]} = 1.88$). The maximum distance ensured that the unmanaged and managed stands in each block were exposed to approximately the same regional population level of *I. typographus*. The unmanaged stands varied in size from 2.2 to 30.8 ha (mean = 15.0 ha) and the number of wind-felled spruces varied from 121 to 755 per stand (Table 1). It was not possible to find managed stands damaged by the storm that were as large as the unmanaged stands. The managed stands varied in size from 0.5 to 6.6 ha (mean = 2.0 ha). Average lengths of newly exposed stand edges adjacent to storm gaps (131 and 138 m/ha, respectively, in the managed and unmanaged stands; $P = 0.78$, $t = 0.31$, d.f. = 4, paired-sample t-test) and storm gap areas (0.17 and 0.10 ha/ha in the managed and unmanaged stands; $P = 0.23$, $t = 1.40$) were of the same magnitude in the two kinds of stands. A few managed stands were cut down during the study period and thus were excluded from subsequent inspections. In some of the managed stands the forest owners removed dead trees. When such stumps were found, information about the cause of death was obtained from the forest owners.

Both the unmanaged and managed stands were in most cases bordered by stands unsuitable for *I. typographus* reproduction, i.e. young stands or stands dominated by the non-host species, Scots pine (*Pinus sylvestris* L). Norway spruce was the dominant tree species (proportion = 60–100%) in all stands investigated. The mean diameter of the trees in the stands exceeded 20 cm at breast height (1.3 m above the base of the trees) and the mean age of the stands exceeded 60 years.

The study covered the 5 years (1996–2000) following the 1995 storm-felling. In November–December 1999, new storm-fellings occurred in the study area (Table 2). The magnitude of these storm-fellings was much lower than in the 1995 storm disturbance, but the presence of newly wind-felled trees in 2000 may have influenced the number of trees killed by *I. typographus* in this year. Thus, the data from 2000 (the fifth year) were not included when comparing the results of the present and earlier studies, as shown in Table 1. Because the new wind-felled trees may have influenced the population level of *I. typographus* in 2001 we decided to end the study after 2000.

The inspections conducted in the managed and unmanaged stands in each year are summarized in Table 3. The results of the 1997 inspections of wind-felled spruce trees from the November 1995 storm are presented in Göthlin *et al.* (2000). In 1998, no wind-felled trees suitable for *I. typographus* reproduction remained in the unmanaged stands. Only a few trees were wind-felled in the managed and unmanaged stands between the first and second storm-fellings. Means of the number of killed trees per ha were calculated for the managed stands belonging to each focal unmanaged stand. In the years 1996–1999, the diameter (at 1.3 m) of all killed standing trees was measured, together with group size, defined as the number of trees killed in the same year and closer than 10 m to the next killed tree. It was also noted whether the killed trees were situated on the edges of stands or in their interior (i.e. closer than or further than 10 m from a storm gap or clear cutting, respectively). In 2000, only the number of trees killed was recorded.

Results

At the time of the first storm-felling (1995) local populations of hibernating *I. typographus* in the unmanaged stands were small or non-existent. Only 17 standing trees, distributed among three of the five stands, were killed by

Table 1 Numbers of wind-felled trees, colonized wind-felled trees and standing trees killed by *I. typographus* in the years following storm-fellings in spruce stands. Data obtained from the unmanaged stands of the present study and from earlier studies. In Hochharz there were two generations of *I. typographus* per year and in all other locations one generation per year. The wind-felled trees were left in all the stands, except for Gruvskogen, where an unknown proportion had already been removed before the first summer following the storm

Locality[1]	Time of storm- felling	Area (ha)	No. of wind-felled spruce trees	No. of wind-felled spruce trees per ha	No. of colonised wind-felled trees	No. of killed trees[3]	No. of killed trees per ha	No. of killed trees per wind-felled tree
Sweden:								
This study								
Älgåsen	Nov. 1995	2.2	121	55.0	94	50	22.7	0.4
Bohult	Nov. 1995	12.8	268	20.9	99	81	6.3	0.3
Uvaberget	Nov. 1995	13.8	466	33.8	237	205	14.9	0.4
Jordanstorp	Nov. 1995	15.2	240	15.8	172	148	9.7	0.6
Ryfors	Nov. 1995	30.8	755	24.5	379	322	10.5	0.4
Sum.			1850		981	806		
Gruvskogen	Nov. 1945	346	< 9362	< 27.1	–	20 111	58.1	> 2.1
Germany:								
Bayerischer Wald	Aug. 1983, autumn 1984	85[2]						
Locality 1		–	–	–	–	110	–	–
Locality 2		–	–	–	–	58	–	–
Locality 3		–	–	–	–	142	–	–
Locality 4		–	–	–	–	118	–	–
Hochharz	Jan–Feb. 1990	53	679	12.8	–	2051	38.7	3.0
Bannwald Napf	Jan–Feb. 1990	105	702	6.7	316	3780	36.0	5.4

[1]Data from: the present study, Lekander (1972), Schopf & Köhler (1999), Niemeyer *et al.* (1995), Weslien & Schröter (1996).
[2]The total area in Bayerischer Wald where all wind-felled trees were left.
[3]Time period covered: the present study 1996–99, Gruvskogen 1946–52, Bayerisher Wald 1984–91, Hochharz 1990–95, Bannwald Napf 1990–96.

Table 2 Numbers of wind-felled trees, wind-felled trees colonized by *I. typographus* and standing trees killed by *I. typographus* in the year 2000 following the November–December 1999 storm-fellings in the unmanaged stands. Stand areas are given in Table 1

Stand	No. of wind-felled spruce trees	No. of wind-felled spruce trees per ha	No. of colonized wind-felled trees	No. of wind-felled trees not colonised by scolytids	No. of killed trees	No. of killed trees per ha
Älgåsen	5	2.3	2	1	8	3.6
Bohult	17	1.3	1	11	3	0.2
Uvaberget	27[1]	2.0	18	6	8	0.6
Jordanstorp	23[2]	1.5	13	9	1	0.1
Ryfors	27	0.9	12	10	13	0.4
Sum.	99		46	37	33	

[1]Seven of these were trees cut in spring 2000.
[2]Five of these were trees cut in spring 2000.

I. typographus in the unmanaged stands in 1995. No wind-felled trees that had been colonized in that year were found.

The number of trees killed by *I. typographus* in the unmanaged stands increased greatly in the years between the first and second storm-fellings. In this 4-year period 806 trees were killed (Table 1) compared with the 17 trees killed in the year preceding the storm disturbance. In the first summer after the storm-felling *I. typographus* only killed one standing tree in the unmanaged stands, whereas 531 wind-felled trees were colonized in the same year (Fig. 1) (Göthlin *et al*., 2000). In the second year both wind-felled and standing trees were attacked. Altogether, 450 wind-felled trees were attacked and 244 standing trees were killed. In the third year no wind-felled trees were attacked and 468 standing trees were killed. In the fourth year the number of killed trees decreased to 93. The decrease was not caused by a lack of host trees (living spruce trees were present in all unmanaged stands). Obviously the 4-year period of this study covered the major part of the progression of tree mortality caused by *I. typographus* as a result of the first storm-felling. Both the numbers of trees killed in the unmanaged stands and the differences in tree mortality between the unmanaged and managed stands (see below) decreased to low levels in the fourth and fifth years.

The number of wind-felled spruce trees colonized by *I. typographus*, the total number of wind-felled spruce trees and the area of storm-felling were significantly correlated with the number of trees killed by *I. typographus* in the unmanaged stands in the 4 years following the storm-felling (Fig. 2). Number of colonized wind-felled trees explained almost all of the variation between the stands in number of killed trees, whereas the other two variables explained somewhat less of this variation.

The temporal pattern of tree mortality after the first storm-felling differed between the five unmanaged stands (Fig. 1). In the two smallest stands (Älgåsen and Bohult) the number of killed trees peaked in 1997. In the three remaining unmanaged stands tree mortality peaked a year later, in 1998. Also the proportion of wind-felled trees attacked by *I. typographus* in the first summer after the 1995 storm-felling differed between the stands. A higher proportion was attacked in the smallest stand than in the larger stands (with more wind-felled trees) (Fig. 3).

In the four years between the first and second storm-fellings, the tree mortality caused by *I. typographus* was about twice as high in the unmanaged stands as it was in the managed stands. On average, 12.8 trees/ha (range = 6.3–22.7) were killed in the unmanaged stands and 6.6/ha (range = 4.0–12.6) in the managed stands. The average difference between the two kinds of stand was 6.2 killed trees/ha (range = −1.3–20.4, $P = 0.17$, $t = 1.66$, d.f. = 4, paired-sample *t*-test). This difference corresponds to 19% (range = 0–37%) of the number of wind-felled trees originally found in the unmanaged stands. In the first year (1996)

Table 3 Summary of the inspections conducted in the managed and unmanaged stands in each year. Colonized and killed trees refers to trees attacked by *I. typographus*

Year	Managed stands	Unmanaged stands
1996 Spring		Standing and wind-felled trees colonized in the previous year (prior to the November 1995 storm-felling) recorded.
1996 Autumn		Trees killed in the current year recorded.
1997 Autumn	Trees killed in the previous and the current year recorded	All wind-felled spruce trees from the November 1995 storm inspected. Trees killed in the current year recorded.
1998 Autumn	Trees killed in the current year recorded.	Trees killed in the current year recorded.
1999 Autumn	Trees killed in the current year recorded.	Trees killed in the current year recorded.
2000 Autumn	All wind-felled spruce trees from the November–December 1999 storms inspected. Trees killed in the current year recorded.	All wind-felled spruce trees from the November–December 1999 storms inspected. Trees killed in the current year recorded.

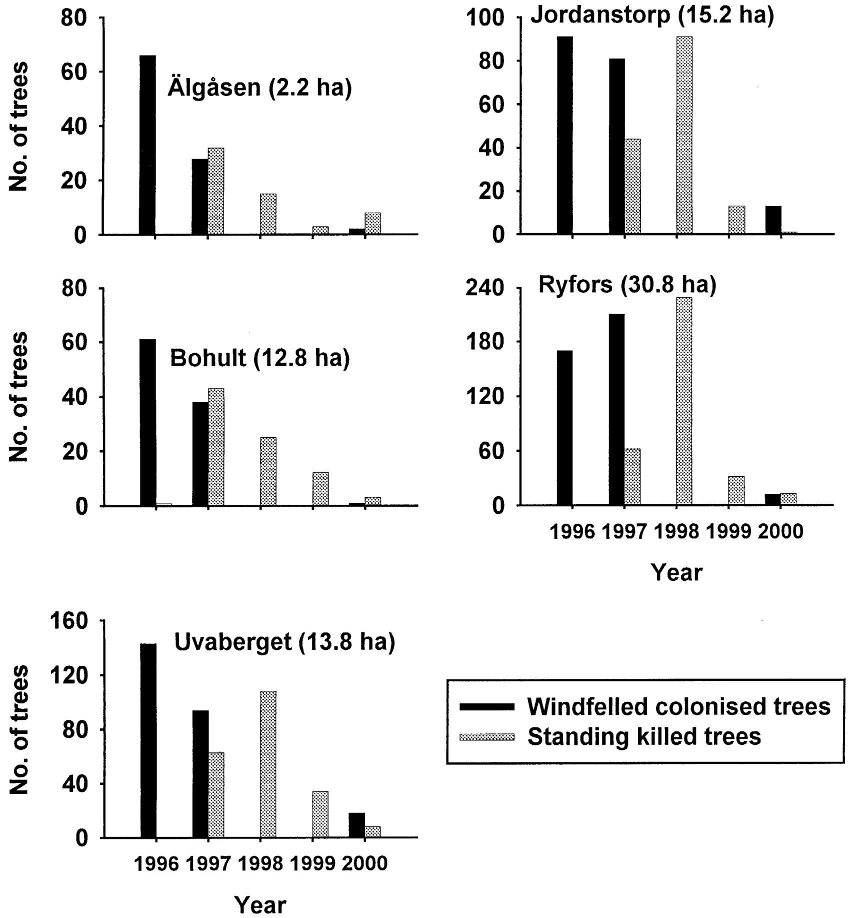

Figure 1 Number of wind-felled spruce trees colonized by *I. typographus* and number of standing spruces killed by *I. typographus* in the five unmanaged stands in the 5 years following the 1995 storm. Note the different scales of the ordinate. Number of spruce trees felled by the 1995 and 1999 storm disturbances are given in Tables 1 and 2.

the number of killed trees per ha was at least 30 times higher in the managed stands than in the unmanaged stands, a difference that was close to significant (Fig. 4a). The true difference might have been even larger because some trees killed by *I. typographus* in the managed stands in 1996 may have been removed in the same year. Stumps of such trees were not easily recognized during the first inspection conducted in the managed stands 2 years later (autumn 1997). In the three following years the number of trees killed per ha was higher in the unmanaged stands than in the managed stands. The difference peaked in 1998, the only year when the difference was significant.

The number of groups of trees killed by *I. typographus* per ha was much higher in the managed stands than in the unmanaged stands in 1996 (Fig. 4b), as only one tree was killed by *I. typographus* in the unmanaged stands in that year. In both 1997 and 1998 the number of groups per ha was somewhat higher in the unmanaged stands than in the managed stands but the difference was not significant. In 1999 the number of groups of killed trees per ha was about the same in the two kinds of stand.

Mean group size (number of killed trees per group) was significantly larger in the unmanaged stands than in the managed stands in 1998 and 1999 but not in 1996 and 1997 (Fig. 4c). Generally, the largest groups occurred in the unmanaged stands (eight of the nine largest groups in 1997, 11 of the 12 largest groups in 1998, and all of the 15 largest groups in 1999).

The number of trees killed per ha by *I. typographus* was much higher in the stand edges than in the interior of the stands in all years in both kinds of stand (Fig. 5). In the unmanaged stands the ratio between the trees killed per ha in edges and in the stand interiors decreased from 23 in 1997 to about seven in 1998 and 1999. This change over time was significant for all unmanaged stands except for Ryfors (Chi-square test, $P < 0.05$). The overall trend for the managed stands differed from the unmanaged stands. About 20 times more trees per ha were killed in the edges compared with the stand interiors both in 1997 and 1998 but the ratio decreased to 12 in 1999 (no statistical tests were conducted, as data for the individual stands differed too much to be pooled in the analyses).

The fact that the unmanaged stands were generally larger than the managed stands could have influenced the comparisons of the number of killed trees per ha. To evaluate this possibility the relationship between the stand size and the number of trees killed per ha was analysed both for the managed and unmanaged stands. For the managed stands there was a significant negative correlation between the stand area and the number of trees killed per ha by *I. typographus* in 1997 ($r^2 = -0.16$, $P = 0.04$, $F_{[1,23]} = 4.54$), but no such significant relationships were found in 1998

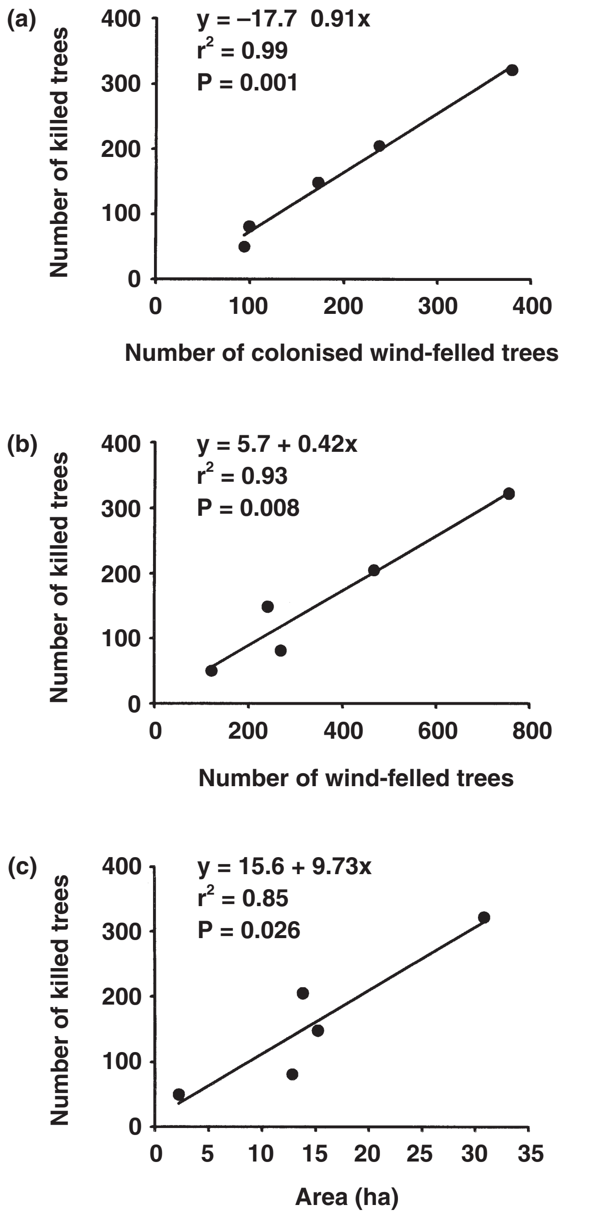

Figure 2 Relationship between the number of trees killed by *I. typographus* in the 4-year period following the November 1995 storm-felling and (a) the number of wind-felled spruces colonized by *I. typographus* ($F_{[1,3]} = 251.0$), (b) the total number of wind-felled spruces ($F_{[1,3]} = 41.3$) and (c) the area of the storm-felling ($F_{[1,3]} = 17.1$).

($r^2 = -0.03$, $P = 0.25$, $F_{[1,42]} = 1.33$) or 1999 ($r^2 = 0.05$, $P = 0.14$, $F_{[1,39]} = 2.25$) (results from 1996 were excluded due to uncertainties in the data, see above). For the five unmanaged stands there was no significant relationship between stand area and number of killed trees per ha in 1997 ($r^2 = -0.62$, $P = 0.12$, $F_{[1,3]} = 4.85$), 1998 ($r^2 = 0.04$, $P =$ 0.75, $F_{[1,3]} = 0.12$) or 1999 ($r^2 = -0.05$, $P = 0.70$, $F_{[1,3]} = 0.18$). Thus, the available data indicate that the difference in size between the two kinds of stand should not have influenced the results markedly.

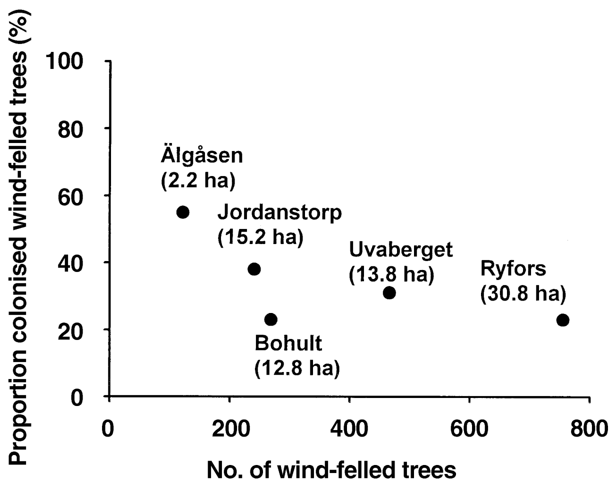

Figure 3 Relationship between number of wind-felled spruce trees and proportion of wind-felled spruce trees colonized by *I. typographus* in the five unmanaged stands in the first summer following the 1995 storm disturbance. Locations and stand areas are given.

The diameters of the standing trees killed by *I. typographus* were slightly greater in the unmanaged stands than in the managed stands (mean = 36.4 cm, SD = 11.8, n = 806 for unmanaged stands, and mean = 31.9 cm, SD = 9.0, n = 262; for managed stands $P < 0.001$, $t = 6.43$, data pooled for all stands of each kind and for the years 1997–1999 prior to analysis).

The second storm-felling in November–December 1999 was much less intensive than the first. The number of wind-felled spruce trees in the unmanaged stands was only 4–10% of the number felled by the 1995 storm. Of the 99 wind-felled spruce trees, 46 were colonized by *I. typographus* (Table 2). Thirty-seven of the remaining 53 had still not been attacked by scolytids in the autumn of 2000. A total of 33 standing trees, distributed amongst all of the five unmanaged stands, was killed by *I. typographus* in 2000. In the year after the second storm-felling (2000) the number of trees killed by *I. typographus* averaged 1.0 trees/ha (range = 0.1–3.6) in the unmanaged stands and 0.5 trees/ha (range = 0.1–0.9) in the managed stands. This difference was not significant ($P = 0.52$, $t = 0.69$, d.f. = 4, paired-sample t-test). As well as the killed trees, some wind-felled trees were also attacked by *I. typographus* in the managed stands in 2000. The number of wind-felled trees remaining in these stands in the autumn of 2000 averaged 1.0 trees/ha (range = 0.3–2.1). Of these, 0.5 trees/ha (range = 0.1–1.3) were colonized by *I. typographus*.

No standing trees attacked and killed solely by the bark beetle *Pityogenes chalcographus* (L.) (Col.: Scolytidae) were found in the unmanaged stands, whereas high proportions of the wind-felled trees were attacked by this species (Göthlin *et al.*, 2000).

Discussion

This study demonstrated an almost perfect linear relationship between the number of wind-felled spruces colonized

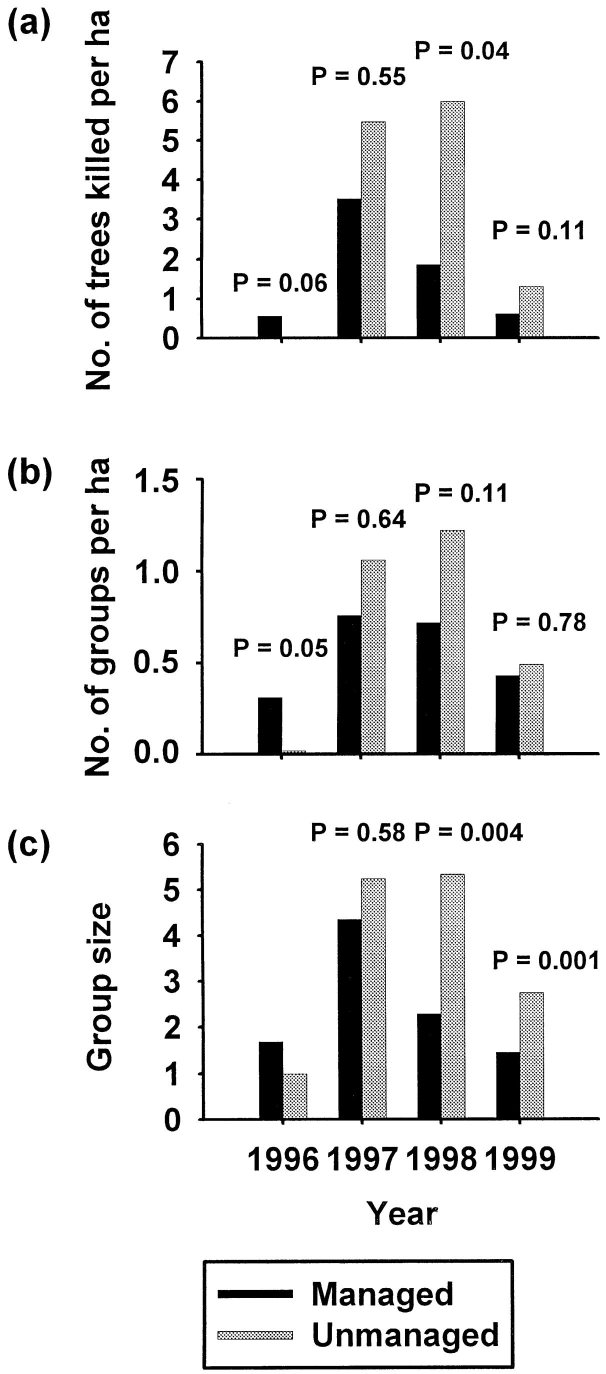

Figure 4 (a) Number of trees killed per ha by *I. typographus* (1996: $t = 2.61$, 1997: $t = 0.66$, 1998: $t = 3.06$, 1999: $t = 2.04$), (b) number of groups of killed trees per ha (1996: $t = 2.71$, 1997: $t = 0.51$, 1998: $t = 2.03$, 1999: $t = 0.30$) and (c) group size in managed and unmanaged stands in the years following the storm-felling (1997: $t = 0.55$, 1998: $t = 2.90$, 1999: $t = 3.49$). *P*-values refer to differences between stand types in each year. In (a) and (b) paired-sample *t*-tests were used, d.f. = 4. In (c) *t*-tests were used (data for all stands of each kind pooled prior to analyses). In (c) the number of replicates (groups) for managed and unmanaged stands were 14 and 1 (no statistical test was conducted) in 1996, 28 and 46 in 1997, 63 and 90 in 1998, 35 and 34 in 1999, respectively.

by *I. typographus* and the number of trees killed in the 4 years following the storm-felling. This result, as well as the temporal pattern of the tree mortality (see below), emphasizes the importance of the population propagation in wind-felled trees for the tree mortality caused by *I. typographus* after storm-fellings. However, the good fit is somewhat surprisingly because a considerable proportion of the beetles that attacked the standing trees in the unmanaged stands may have come from the surrounding managed forest landscape, as indicated by the tree mortality in the managed stands where all wind-felled trees were removed. One explanation for the good fit could be that this immigration from the surrounding managed forest has been of the same magnitude in all the unmanaged stands even though they were situated tens of kilometres from each other. Also, total number of wind-felled spruce trees and area of storm-felling explained a large part of the variation in number of subsequently killed trees in the unmanaged stands. However, if large areas with many wind-felled trees but with low colonization rates are included, the predictive power of both these variables will surely be much less.

Tree mortality caused by *I. typographus*, expressed as either the number of trees killed per ha or the number of trees killed in relation to the number of wind-felled trees (no data on colonized wind-felled trees in most studies), was found to be considerably lower in the unmanaged stands in the present study than in three earlier studies at Gruvskogen, Hocharz and Bannwald Napf (Table 1). This difference cannot be explained by the population increase of *I. typographus* in the wind-felled trees being lower in the present study because 30–70% of the wind-felled trees were found to be colonized by *I. typographus* here, whereas in Bannwald Napf the corresponding figure was 45% (Table 1) (no colonization data were provided in the other studies). Furthermore, the reproductive rate of *I. typographus* in the wind-felled trees was high in the present study, at about 10 daughters per mother in the year after the first storm-felling (unpublished data, no reproduction data in the earlier studies). In the three earlier studies the period with high tree mortality caused by *I. typographus* was much more prolonged than in either the present study or in an earlier study conducted in Bayerischer Wald. In Gruvskogen, tree mortality remained at a high level for 4 years. In Hochharz, with two *I. typographus* generations per year, high numbers of trees were killed over 4 years including the last year of the study. As a second storm-felling occurred during the study period, only the first 2 years with high tree mortality (corresponding to 4 years in areas with one beetle generation per year) are included in the comparison with the present study. In Bannwald Napf the tree mortality remained at a high level for 5 years, including the last year of the study. In contrast, high tree mortality only occurred during one to 2 years in the present study and in Bayerischer Wald. The latter part of the period of high tree mortality in the three earlier studies could not be attributed to new generation beetles emerging from the wind-felled trees because these trees should have been unsuitable as breeding material for *I. typographus* at that stage, which also was demonstrated in Bannwald Napf. Thus, some other factor must be

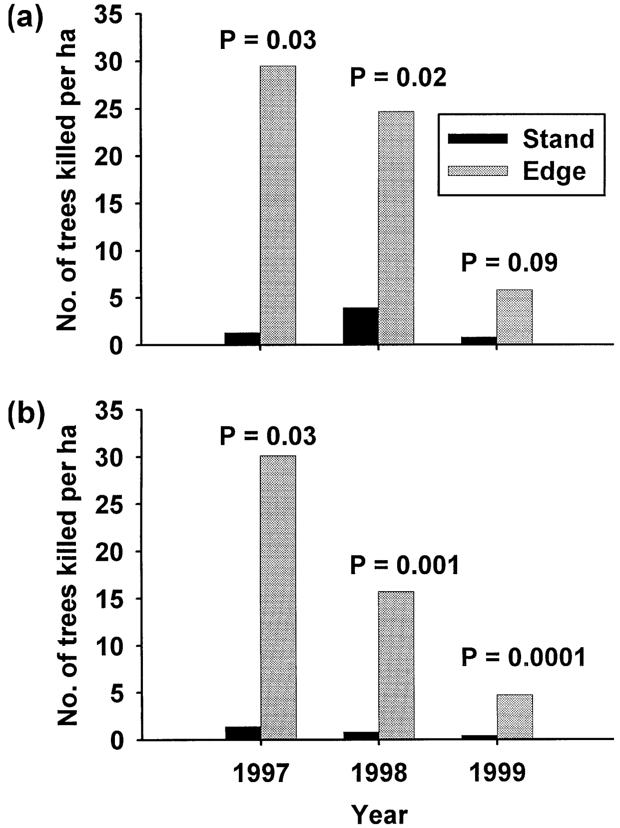

Figure 5 Number of trees killed per ha by *I. typographus* in the interiors of the stands and at their edges in the second to fourth year following the storm felling in (a) unmanaged stands and (b) managed stands. Stand interiors and edges are defined as areas of the forest further than and closer than 10 m from stand edges, respectively. Paired-sample *t*-test, $n = 5$ (data for all the individual managed stands grouped with each unmanaged stand were pooled prior to analyses).

responsible for the prolonged outbreaks. One such factor could be the larger size of the storm-damaged stands in these three earlier studies. In small stands, as in the present study and the Bayerischer Wald study, a large proportion of the new generation of beetles leave the stands. *Ips typographus* has a high dispersal capacity and after just a few minutes of flight the beetles may reach areas outside the stands (Forsse & Solbreck, 1985). With increasing stand size the proportion of beetles leaving the stands should decrease as the chances increase of beetles initiating attacks on new trees, or being attracted to trees already under attack, in the same stand.

In the unmanaged stands *I. typographus* almost exclusively reproduced in the wind-felled trees in the first year after the 1995 storm-felling. Only one standing tree was killed, whereas 531 (29%) of the wind-felled spruce trees were attacked. A low frequency of trees killed by *I. typographus* in the first year following storm disturbances, when beetles have a surplus of wind-thrown trees to breed in, seems to be a general pattern (Inouye, 1963; Lekander, 1972; Furuta, 1989; Weslien & Schröter, 1996; Forster, 1998; Schopf & Köhler, 1999). Because of the large differences in the number of wind-felled spruce trees per unmanaged stand, the peak years for the number of trees killed differed between the unmanaged stands. A higher proportion of the wind-felled trees were colonized by the first summer in the smallest stand (with fewer wind-felled trees) than in the larger stands. Hence, in this stand, fewer wind-felled trees suitable for *I. typographus* reproduction were left in the second summer, so the number of killed trees peaked earlier.

The present study demonstrated a clear difference in the number of killed trees between stands with and without retained wind-felled spruce trees. However, this difference was relatively small considering the large numbers of wind-felled spruce trees remaining in the unmanaged stands. Only twice as many trees were killed per ha in the unmanaged stands compared with the managed stands in the 4-year period between the first and second storm disturbance: a difference of 6.2 killed trees/ha. In the first year after the 1995 storm-felling, the number of killed trees per ha was actually higher in the managed stands (where no wind-felled trees were left) than in the unmanaged stands. Peltonen (1999) found no difference in the number of trees killed by *I. typographus* in stand edges (adjacent to clear-cuts) with and without wind-felled trees. In Peltonen's study the number of wind-felled trees per ha was much lower than in the present study. After a large-scale storm-felling, Ravn (1985) found that a slightly higher number of trees were killed by *I. typographus* in stand edges where a new generation of beetles was allowed to emerge from wind-felled trees compared to stand edges where the wind-felled trees were removed before being attacked. In Ravn's study the two kinds of stand edges were often in close proximity (Wichmann & Ravn, 1999) and this may have influenced the results. The main explanation for the small difference in tree mortality between stands with and without wind-felled trees is probably that a high proportion of the new generation beetles emerging from the wind-felled trees in the unmanaged stands left these stands (see above). Several mark–recapture experiments conducted with *I. typographus* have demonstrated that only a fraction of the released beetles are caught in adjacent pheromone-baited traps and that the majority of the captured beetles originate from other localities (Weslien & Lindelöw, 1989, 1990).

Both the number of groups of killed trees per ha and the group sizes were larger in the unmanaged stands than in the managed stands. However, the difference was only significant for the group size. In accordance with these findings, earlier studies have reported that increases in tree mortality caused by *I. typographus* are associated with increased group size (Lekander, 1972; Weslien *et al.*, 1989).

Earlier studies have documented that in the early years after storm-fellings *I. typographus* almost exclusively kills trees in edges adjacent to storm gaps where colonized wind-felled trees are already present (Butovitsch, 1941; Lekander, 1972). The present study demonstrates that the same pattern may appear even if the wind-felled trees are removed, as in the managed stands. Thus, this 'edge effect' cannot be fully explained by either the switching of attacks from newly colonized wind-felled trees in the gaps or by the high numbers of beetles subsequently emerging from the wind-felled trees in the storm gaps. Another explanation could be that *I. typographus* prefers breeding material that is exposed to the sun. Earlier studies have demonstrated that colonization rates of wind-felled trees are higher in gaps and stand edges than in stand interiors (Peltonen, 1999; Göthlin *et al.*, 2000). It could also be that newly exposed trees in edges are weakened and thus more susceptible to attacks by *I. typographus* than trees in stand interiors. In both the unmanaged and the managed stands the difference in the number of killed trees between edges and in stand interiors decreased over time. This is in accordance with earlier studies (Butovitsch, 1941; Lekander, 1972).

The results of the present study have important implications for the management of storm-disturbed spruce stands. The presence of large numbers of wind-felled spruce trees (15.8–55.0/ha) in scattered spruce stands, 2–30 ha in size, will at most result in one or two years of substantial tree mortality in these stands. In the present study the total number of trees killed by *I. typographus* averaged 44% (range = 30–62%) of the wind-felled spruce trees and the tree mortality peaked by the second or third summer following the storm disturbance. *Ips typographus* reproduced in a high proportion (58%) of the wind-felled spruce trees. If the *I. typographus* colonization rate of storm-felled trees is lower, the subsequent tree mortality could also be expected to be considerably lower than in the present study. One of the most important findings was that removal of all wind-felled spruce trees, which is the usual practice in a managed forest, will not necessarily prevent trees from being killed by *I. typographus* in the stands in the following years. However, total tree mortality will be reduced. In the present study this reduction (the difference in the number of trees killed between unmanaged and managed stands) for the 4 year period following the storm-felling averaged 6.2 trees/ha or about half of the total number of killed trees per ha in the unmanaged stands. This corresponds to 19% (range = 0–37%) of the original wind-felled spruce trees in the unmanaged stands. By contrast, removal of the wind-felled trees by winter or early spring (before the *I. typographus* flight period) will increase the risk of trees being killed in the affected stands in the first summer following the storm disturbance. This risk can be reduced by using all or some of the wind-felled trees as trap trees (i.e. trees removed after colonization by *I. typographus* but before the parent beetles and the new generation of beetles emerge). This measure, however, will only be effective if the number of retained wind-felled trees is sufficiently large in relation to the *I. typographus* population level in the region. This was the case after the first storm-felling in the unmanaged stands but evidently not after the second minor storm disturbance. Furthermore, suitable wind-felled trees must be available not only in the spring but also at later stages for parent beetles to establish sister broods (as well as for a second generation in southern Scandinavia and further south in Europe).

One important control measure against *I. typographus* is selective thinning of attacked trees before the new generation of beetles has emerged. However, it is a major problem to locate these trees in large areas of forest. The results of the present study indicate that a high priority should be given to stand edges. They also indicate that cutting operations that result in new stand edges of mature spruce forest should be avoided in years when there is a high risk of *I. typographus* damage.

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References

Albrecht, L. (1991) Die Bedeutung des toten Holzes im Wald. *Forstwissenschaftlich Centralblatt*, **110**, 106–113 (in German with English summary).

Anderbrant, O. (1990) Gallery construction and oviposition of the bark beetle *Ips typographus* (Coleoptera: Scolytidae) at different breeding densities. *Ecological Entomology*, **15**, 1–8.

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

Andersson, L.I. & Hytteborn, H. (1991) Bryophytes and decaying wood – a comparison between managed and natural forest. *Holarctic Ecology*, **14**, 121–130.

Anon (1993) *Skogsvårdslagen*, **1993**, 553.

Anon (1996) *Statistical Yearbook of Forestry 1996*. National Board of Forestry, Jönköping (in Swedish).

Bombosch, S. (1954) Zur Epidemiologie des Buchdruckers (*Ips typographus* L.). *Die Grosse Borkenkäferkalamität in Südwestdeutschland 1944–51* (ed. by G. Wellenstein), pp. 239–283. Forstschutzstelle Südwest, Ringingen, Ebner, Ulm.

Botterweg, P.F. (1983) The effect of attack density on size, fat content and emergence of the spruce bark beetle *Ips typographus* L. *Zeitschrift für Angewandte Entomologie*, **96**, 47–55.

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 1967–1969. *Department of Forest Zoologi Research Notes 8*. Royal College of Forestry, Stockholm (in Swedish with German summary).

Christiansen, E. (1985) *Ips/Ceratocystis*-infection of Norway spruce: what is a deadly dosage? *Zeitschrift für Angewandte Entomologie*, **99**, 6–11.

Christiansen, E. & Bakke, A. (1988) The spruce bark beetle of Eurasia. *Dynamics of Forest Insect Populations* (ed. by A. A. Berrymann), pp. 479–503. Plenum, New York.

Christiansen, E., Waring, R.H. & Berrymann, A.A. (1987) Resistance of conifers to bark beetle attack: searching for general relationships. *Forest Ecology and Management*, **22**, 89–106.

Forsse, E. & Solbreck, Ch (1985) Migration in the bark beetle *Ips typographus* L. duration, timing and height of flight. *Zeitschrift für Angewandte Entomologie*, **100**, 47–57.

Forster, B. (1998) Storm damages and bark beetle management: how to set priorities. *Methodology of Forest Insect and Disease Survey in Central Europe. Proceedings from the IUFRO WP 7.03.10 Workshop*, pp. 161–165. Ustron′-Jaszowiec, Poland.

Fridman, J. & Walheim, M. (2000) Amount, structure and dynamics of dead wood on managed forestland in Sweden. *Forest Ecology and Management*, **131**, 23–36.

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

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.

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.

Kaila, L., Martikainen, P. & Punttila, P. (1997) Dead trees left in clear-cuts benefit saproxylic Coleoptera adapted to natural disturbances in boreal forest. *Biodiversity and Conservation*, **6**, 1–18.

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

Lekander, B. (1972) A mass outbreak of *Ips typographus* in Gästrikland, Central Sweden, in 1945–52. *Department of Forest Zoology, Research Notes, 10*. Royal College of Forestry, Stockholm (in Swedish with English summary).

Martikainen, P., Siitonen, J., Punttila, P., Kaila, L. & Rauh, J. (2000) Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. *Biological Conservation*, **94**, 199–209.

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.

Niemeyer, H., Ackermann J. & Watzek, G. (1995) Eine ungestörte Massenvermehrung des Buchdruckers (*Ips typographus*) im Hochharz. *Forst und Holz*, **50**, 239–243.

Økland, B., Bakke, A., Hågvar, S. & Kvamme, T. (1996) What factors influence the diversity of saproxylic beetles? A multi-scaled study from a spruce forest in southern Norway. *Biodiversity and Conservation*, **5**, 75–100.

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

Ravn, H.P. (1985) Expansion of the populations of *Ips typographus* (L.) (Coleoptera, Scolytidae) and their local dispersal following gale disaster in Denmark. *Zeitschrift für Angewandte Entomologie*, **99**, 26–33.

Schopf, R. & Köhler, U. (1999) Untersuchungen zur Populationdynamik der Fichtenborkenkäfer im Nationalpark Bayerischer Wald. *Nationalpark Bayerischer Wald – 25 Jahre auf dem Weg zum Naturwald*, pp. 89–110. Nationalparkverwaltung Bayerischer Wald, Neuschönau, Germany.

Schröter, H., Becker, T. & Schelshorn, H. (1999) Die Bedeutung der Sturmwurfflächen als 'Borkenkäferquellen' für umliegende Wirtschaftswälder. *Die Entwicklung von Wald-Biozönosen nach Sturmwurf* (ed. by A. Fischer), pp. 292–314. Ecomed, Landsberg, Germany.

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

Weslien, J. & Lindelöw, Å. (1989) Trapping a local population of spruce bark beetles *Ips typographus* (L.): population size and origin of trapped beetles. *Holarctic Ecology*, **12**, 511–514.

Weslien, J. & Lindelöw, Å. (1990) Recapture of marked spruce bark beetles (*Ips typographus*) in pheromone traps using area-wide mass trapping. *Canadian Journal of Forest Research*, **20**, 1786–1790.

Weslien, J. & Schröter, H. (1996) Naturliche Dynamik des Borkenkäferbefalls nach Windwurf. *Allgemeine Forst-Zeitschrift*, **51**, 1052–1056.

Wichmann, L. & Ravn, H.P. (1999) GIS og forstzoologi. *Skoven*, 298–301 (in Danish).

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