Citation for the published paper:
Petter Öhrn, Niklas Björklund, Bo Långström. (2018) Occurrence, performance and shoot damage of Tomicus piniperda in pine stands in southern Sweden after storm-felling. *Journal of applied entomology*.
Volume: 142, Number: 9, pp 854-862.
https://doi.org/10.1111/jen.12533.

Occurrence, performance and shoot-damage of *Tomicus piniperda* in pine stands in southern Sweden after storm-felling

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Acknowledgements

This study was funded by the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning (FORMAS) and the Swedish Forest Agency (Skogsstyrelsen). We are also grateful to staff at Sveaskog, the County administration (Länsstyrelsen) of Kronoberg and SLU research stations at Asa and Tönnersjöheden for helping in supplying field sites. We also thank Teresa Nordling for collecting data at Asa in 2005, and Jan-Eric Englund for statistical guidance.

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Abstract

The pine shoot beetle, *Tomicus piniperda* (L.), is considered one of the most destructive pests of Scots pine, *Pinus sylvestris* (L.), in Europe. At high population densities, its feeding in the shoots of living pine trees may lead to substantial shoot and subsequent growth losses. After a storm-felling in southern Sweden in January 2005, there were high amounts of breeding material and a subsequent risk for bark beetle outbreaks. To study the beetle's reproductive success, population levels and risks for growth losses, we analyzed bark samples of colonized trees, and counted fallen pine-shoots. During the first season after the storm-felling the pine shoot beetle population level were low. However, due to high reproductive success beetle numbers markedly increased in the second season, and there were high rates of successful colonization of available host material in following years. Shoot damage levels concomitantly rose in 2005-2006, then declined in 2007 and 2008. However, the accumulated shoot losses do not indicate any subsequent growth losses, as the recorded shoot damage levels were below those earlier seen in connection with growth reductions in damaged pine stands.

Keywords Pine shoot beetle**;** bark beetle outbreak; shoot-feeding; growth losses; *Pinus sylvestris; Tomicus piniperda*

1 Introduction

Storm-fellings facilitate outbreaks of bark beetles by providing abundant suitable breeding material, which often triggers rapid increases in their populations (Grégoire and Evans 2004; Gilbert et al. 2005). Thus, there were clear risks of such outbreaks after the storm “Gudrun” swept over southern Sweden on 8-9 January 2005, and blew down 50-75 million m^3 wood (Skogsstyrelsen 2006; Kempe and Wulff 2007) (Fig. 1a). This was the largest storm-felling ever recorded in Sweden (Nilsson et al. 2004; Kempe and Wulff 2007), corresponding to ca. half of the total annual growth of Swedish forests. “ Gudrun” was followed by another storm (“Per”) which caused more scattered tree-felling in January 2007 (Fig. 1b), amounting to ca. 12 million m^3 of primary damage in south and central Sweden according to the Swedish Forestry Agency (Alexandersson and Edquist 2007).

The majority of the fallen trees was Norway spruce and the resulting outbreak of the spruce bark beetle *Ips typographus* has been described elsewhere (Långström et al. 2009). Scots pine, *Pinus sylvestris* (L.), accounted for approximately 18 % of the wind-damaged volume after the storm in 2005 (Valinger et al. 2006). With approximately 10 million m^3 Scots pine on the ground, there was at least local risks for growth losses caused by the feeding of pine shoot beetles *Tomicus piniperda* (L.) and *T. minor* (Hart.) (Col., Scolytinae). Due to the growth losses it can cause, *T. piniperda* is regarded as one of the most severely threatening bark beetles in Europe (Grégoire and Evans 2004).

Tomicus is a Palaearctic genus consisting of eight mainly Asian species, of which both *T. piniperda* and *T. minor* are widely spread over Europe and Asia, although the latter is less common with a patchy distribution (Lieutier et al., 2015). In 1992 *T. piniperda* was detected in North America, close to Cleveland, Ohio (Haack and Kucera 1993), from where it has spread to several other US states and Canadian provinces (Haack and Poland 2001, Haack 2006, Humble and Allen 2006).

T. piniperda and *T. minor* are univoltine, although they may develop sister-broods during the same season. However, in the northern range of their distribution (e.g. Sweden), sister-broods only seem to occur occasionally (Långström, 1983). During the dispersal flight, which takes place in early spring when air temperature exceeds 12^{o}C, these beetles respond to host odors, which guide them to suitable host material, preferably fresh timber or standing weakened trees (Byers 2004).

Both species are monogamous and lay their eggs in niches along a gallery underneath the bark. The larvae feed on the phloem and after pupation the callow adults emerge via individual exit holes. After parent beetles have finished oviposition they fly to feed mainly in last years shoots of living pine trees. After completing their development, the offspring beetles also feed in the pine crowns but now mainly in the fully grown current-year shoots (Lieutier et al. 2015). The shoot feeding of the parent beetle is more serious as it lasts from late spring to autumn (if no sister broods occur) and each attack affects several expanding current shoots whereas the damage of the young beetle normally occurs in one current shoot and lasts from mid-summer to autumn. On the other hand, there are many more offspring beetles so they normally account for most of the shoot damage (for further details, see Långström 1983). All age classes of pine may be attacked, but middle-aged and old trees are preferred (Långström 1980). At high population densities, this feeding may lead to substantial shoot and subsequent growth losses (Nilsson 1976; Långström and Hellqvist 1990; Långström and Hellqvist 1991; Borkowski 2006).

The common pine shoot beetle, *T. piniperda*, may also kill pine trees that have been severely weakened, for example by defoliation, whereas the lesser pine shoot beetle, *T. minor*, seems to be less aggressive (Annila et al. 1999; Långström et al. 2001; Cedervind et al. 2003). Adult *T. piniperda* beetles are good flyers and may disperse over several km (Lieutier et al. 2015). However, most beetles reportedly fly less than 100 m, and nearly all (95%) disperse within 400 m (Barak et al. 2000). Accordingly, numbers of infested pine shoots and subsequent pine growth losses decrease rapidly with distance from an infested source, for example Långström and Hellqvist (1991) observed a decline in growth losses from 70% at source to 10% at a distance of 500 m.

Numerous studies have addressed various aspects of pine shoot beetles' interactions with storm-felled pine timber (Trägårdh and Butovitsch 1935; Lekander 1955; Niemeyer and Thalenhorst 1974; Luitjes 1976; Annila and Petäistö 1978; Führer and Kerck 1978a; Führer and Kerck 1978b; Bychawska 1983; Långström 1984; Saarenmaa 1989; Eidmann 1992). However, only a few studies have related risks for growth losses to pine shoot beetle propagation in storm-felled pine trees (Führer and Kerck 1978a; Komonen et al. 2009).

Thus, the aims of this study were to investigate the occurrence, activity and performance of the pine shoot beetles in the windthrown pines after a storm felling, and assess risks for subsequent growth losses in the areas affected by storm-felling.

2 Material and methods

2.1 Study sites

The occurrence and performance of *T. piniperda* were studied in southern Sweden (Götaland) at, seven sites in boreal forest stands with predominance of pines at latitudes of 56° 20' 20' - 56° 40' 56' N, longitudes of 12° 30' 52'-15° 57' 58' E and altitudes of 97 (Tönnersjöheden) to 314 (Vitthult) m a.s.l. (Fig. 1).

All of the study sites are within the area affected by Storm Gudrun in 2005 (Fig. 1a), and all sites except Braås and Hunneberg were also affected by Storm Per in 2007 (Fig. 1b) (Alexandersson and Edquist 2007). At each site one storm-damaged pine stand was left unharvested and used as a study area (Table 1).

2.2 Colonization of wind-damaged trees and brood production

At all study sites, no windthrown tree or high stump (i.e. the standing part of a wind-broken tree) was harvested during the period 2005-2007, but all pines of both classes that were damaged by the storms in 2005 or 2007 were sampled (Table 2). All sampled trees had root contact maintaining some water supply and were inspected each autumn (late August to mid-October).

Each wind-damaged tree attacked by pine shoot beetles was recorded as successfully attacked if exit holes were observed, and unsuccessfully attacked otherwise. All trees that were not colonized or were unsuccessfully attacked in the first autumn after wind damage were inspected in the following autumn. Three bark samples (0.1 m wide and 0.3 m long) were taken from each tree on the part of trunk with thick bark, which is suitable for *T. piniperda* (Bakke 1968). This part extended approximately 8 m from the roots (ca. 2.5 m on high stumps) and was divided into three sections (basal, middle and upper) of roughly equal lengths, each of which was sampled.

The basal sample was selectively chosen from an area that beetles had colonized, but locations of the middle and upper samples were randomly selected in the respective sections. Bark samples were taken from each attacked tree, then colonization density (defined as number of maternal galleries per m^2), brood production (defined as number of exit holes per m^2) and reproductive success (defined as the number of daughters per maternal gallery, obtained by dividing half of the number of exit holes per m^2 by the number of maternal galleries per m^2) were recorded. The selective sampling was done to avoid false zero observations, but might have the disadvantage of overestimating the attack density. The significance of differences between years in attack density, production and reproductive success were tested by one-way analysis of variance (ANOVA) in MINITAB version 17 (Minitab Inc., State College, Pennsylvania). When differences were significant ($P < 0.05$), they were further examined using Tukey's test. The significance of differences in colonization density between successful and unsuccessful attacks was tested using a GLM ANOVA. Possible differences in attack parameters between high stumps and windthrown trees could not be rigorously evaluated because observations were not evenly distributed among sites.

2.4 Shoot damage

At five sites (Table 1), every autumn during the study period (2005-2008), the number of fallen shoots was counted on four 10 m^2 circular plots adjacent to storm gaps with wind-damaged pine trees to obtain a measure of maximum shoot damage levels in the landscape. Similarly, to obtain a measure of general shoot damage levels in the landscape, four plots were established in mature pine stands 150 to 1900 m away from each storm gap (Table 1).All shoots that had a tunneling hole in the shoot axis characteristic for *Tomicus* attack, were categorized as attacked by *Tomicus.*

All fallen shoots were removed at each inspection, so the same plots could be re-inspected for newly fallen shoots. The fallen shoots that were categorized as brown and dry had probably been attacked in the previous autumn, so they were included in the total number of pine shoots attacked in that year. The fallen green shoots were considered to have been attacked in the current season. Differences in the number of fallen shoots between years, wind-damaged and other areas, and sites were tested using a GLM ANOVA in MINITAB.

The volume of damaged pine trees at each site was estimated from the average diameter of damaged trees using data on volume (m^3wood) and diameter (cm at breast height) for pine provided by Johan Möller of Skogforsk, the Forestry Research Institute of Sweden (pers. comm.) to calculate a correlation function: Volume = number of trees x (0.1284 x exp(0.0055 x diameter)). Correlations between numbers of fallen pine shoots fed on by *T. piniperda*, volumes of wind-damaged trees per ha, and production of beetles were all tested using general regression analyses implemented in MINITAB. Presented data are means ± SE unless otherwise stated.

3 Results

3.1 Colonization of wind-damaged trees

The common pine shoot beetle *T. piniperda* was by far the most frequently observed bark beetle species, both on the colonized windthrown trees and high stumps. Populations of the lesser pine shoot beetle, *T. minor,* at the study sites seem to have been very low, as individuals were only occasionally seen on the logs. Regarding the selective sampling, our results did not indicate that the procedure influenced the estimated attack densities, which decreased close to linearly from the basal, through the middle to the upper samples (from 44 ± 77, through 37 ± 75 to 25 ± 54 galleries/m^2; n = 434 in each case), in accordance with results presented by Bakke (1968).

In the autumn of 2005, 236 wind-damaged trees were inspected. The volume of wind-damaged trees corresponded in average to 16 m^3/ ha and ranged from 6 to 25 m^3/ha among the sites (Table 1). A total of 202 windthrown trees were inspected. Of these, 27% had been colonized by *T. piniperda*, 25% had been unsuccessfully attacked, and 48% had escaped attack (Table 2). High stumps (height: 5 ± 2 m) seemed to be preferred over windthrown trees, as the corresponding proportions for 34 high stumps were 56, 9 and 35%, respectively.

In 2006, more than half of the remaining uncolonized (52%) and unsuccessfully attacked (59%) windthrown trees from the previous year were attacked and successfully colonized (Table 3). The corresponding figures for high stumps show that 21% of the remaining uncolonized high stumps from the previous year were attacked and successfully colonized, but none of those that had been unsuccessfully attacked were attacked. In total, during the two seasons following the storm in 2005 nearly 70% of all wind-damaged trees (windthrown trees and high stumps) were successfully colonized by *T. piniperda.*

In 2007, neither windthrown trees, nor high stumps from 2005 were any longer suitable for breeding due to desiccation or degradation. However, the storm in January 2007 had left 11 new windthrown trees and one high stump. All except one windthrown tree were successfully colonized by pine shoot beetles.

3.2 Attack density and brood production

As expected, the colonization density of *T. piniperda* was generally low (ca. 50 galleries per m^2 bark) during 2005, but it varied considerably among the study areas, from 11 to 74 egg galleries/m^2 (Table 2). The attack density (both successful and unsuccessful attacks) tended to be higher in windthrown trees (45 ± 26) than in high stumps (32 ± 18). During the first season (2005) following Storm Gudrun, the attack densities were generally lower in windthrown trees that had been unsuccessfully attacked than in those that that were successfully colonized (39 ± 25 and 51 ± 25, respectively: $F = 4.36$; $P = 0.039$) (Table 2).

As shown in Table 2, in 2005: beetle production reached 624 ± 337 and 270 ± 180 beetles per m^2 in windthrown trees and high stumps, respectively; reproductive success varied among the sites, from 4 to 11 daughters (mean, 7) per mother beetle (egg gallery); and reproductive success was similar in windthrown trees and high stumps (7.0 ± 3.3 and 5.8 ± 4.2 daughters per mother beetle, respectively).

In the following year (2006) all attacked trees were successfully colonized and the attack density increased to ca. 70 and 160 egg galleries per m^2 in windthrown trees and high stumps, respectively (Table 3). The reproductive success remained at the same level in the windthrown trees, whereas there was a tendency towards a decrease in the high stumps. In 2007, the trend continued in windthrown trees as colonization density increased significantly, to more than 180, but reproductive success and beetle production significantly fell (Table 3). Nothing can be said about trends in high stumps in 2007 as only one was attacked.

3.3 Shoot damage

After the storm-felling there was a general increase in shoot damage, but (as expected) the shoot losses were higher in stands adjacent to wind-damaged sites than in stands further away (comparison sites) (Fig. 2). From 2004 to 2005 there was a 9-fold increase in shoot losses in stands adjacent to wind-damaged sites compared to a 6-fold increase in the stands further away. In both types of stands, the levels of shoot losses remained elevated during 2006 and 2007, then in 2008 returned to levels recorded before the first storm-felling. The peak level of 3 fallen shoots per m^2 corresponds, at an assumed stand density of 1000 trees per ha, to 30 lost shoots per tree in a year, and the accumulated level over the study period approaches 100 shoots per tree.

There were significant differences in pine shoot feeding among years ($F = 4.61$; $P = 0.007$), indicating that levels of shoot damage were higher during 2005 and 2006 than during 2004, 2007 and 2008 (Fig. 3). There also tended to be more shoot feeding in areas with than in areas without wind-damaged trees ($F = 4.13$; $P = 0.054$). There was no significant difference in shoot feeding between sites ($F = 1.91$; $P = 0.44$). There were significant positive relationships between the volume of successfully colonized wind-damaged trees and the number of fallen pine shoots (Fig. 3a), and between average beetle production and the number of fallen pine shoots per square meter (Fig. 3b).

4 Discussion

4.1 Beetle occurrence

The storm-felling in 2005 resulted in increases of pine shoot beetle populations that followed a similar pattern observed for the spruce bark beetle during the same period (Långström et al. 2009).

T. piniperda was by far the most frequent *Tomicus*-species, in both the storm-felled trees and high stumps, while only a few specimens of *T. minor* were seen on the pine stems. This was also the case after storms in Sweden in 1954 and 1969 (Lekander 1971), as well as after storm-fellings elsewhere in Europe (Luitjes 1976; Annila and Petäistö 1978; Bychawska 1983; Winter and Evans 1990; Gilbert et al. 2005). These results indicate that *T. piniperda* is the only *Tomicus* species that reach outbreak populations after stormfellings.

In the first summer after the storm-felling in January 2005, high stumps were more frequently attacked by pine shoot beetles than windthrown trees, which seemed to have some resistance to beetle attacks since they still had some intact roots to supply the crown (see also Führer & Kerck 1978a). This may explain why attacks were unsuccessful in nearly half of the windthrown pines, but only ca. 15% of the high stumps. Due to the large quantity of breeding material available, about half of the trees were not attacked in the first year. The observed attack rate (ca. 50%) is much higher than the rate (9%) recorded for the entire storm-damaged area by the Swedish National Forest Survey (Wulff 2006), but lower than the percentage (60-70%) of surveyed pine trees reportedly attacked by *T. piniperda* in 1970 (after the 1969 storms) in central parts of the storm area (Lekander 1970).

Similar attack rates have been recorded following other damaging storms in Finland (Annila and Petäistö 1978) and Sweden (Långström 1984). Saarenmaa (1987) reported attack rates varying between 30 and 80% in the first summer after a storm in autumn 1982 in Finnish Lapland, but also noted that up to half of the trees were unsuccessfully attacked in the second summer. In contrast, we found that substantial proportions of both windthrown trees and high stumps also escaped pine shoot beetle attack in the second season (2006). However, in this year the attacks of trees mostly led to successful colonization, indicating that the remaining trees may have become more susceptible, or that trees were attacked more selectively, probably due to variations in attractiveness of their host odors, as reviewed by Byers (2004). Thus, some of the wind-damaged pine trees remained sufficiently vigorous to deter beetle attacks, in accordance with findings that high stumps with a few live branches can resist pine shoot beetle attacks (Schroeder and Eidmann 1993). Windthrown pine trees may even produce new shoots after a storm-felling (Annila and Petäistö 1978). However, all the trees we monitored that escaped attack in 2005 and 2006 had become unsuitable for attack in spring 2007, due to desiccation and/or degradation of phloem quality, processes that the warm and dry summer in 2006 might have increased the speed of. Führer & Kerck (1978a) report a similar reduction in suitability of windthrown pines in The Netherlands. In addition, the fresh windthrown trees (from the storm in January 2007), which were all successfully attacked, provided more attractive substrate for these beetles in spring 2007.

4.2 Beetle performance

The mean attack densities recorded in 2005, indicate that the phloem was not fully colonized, leading up to a 6- to 7-fold population increase: a performance (reproductive success) measure within the range observed in previous studies (Annila and Petäistö 1978; Långström

1984; Saarenmaa 1987). The same pattern was observed in the windthrown trees in the following year (2006), while attack density rose and reproductive success dropped in the high stumps. These findings imply that the windthrown pine trees still provided abundant breeding material in 2006, despite the population increase in 2005. They also highlight needs for continued forest protection operations during periods with increased population levels, i.e. removal of brood material to suppress the populations and minimize further damage.

In the years following the storm-felling in 2005, attack densities (in both windthrown trees and high stumps) were higher than in previous years. This was presumably due to increases in population density and reductions in amounts of fresh wind-damaged trees suitable for breeding, leading to intra-specific competition. This pattern of population dynamics, regarded as common for both bark beetles generally (Sauvard 2004) and *T. piniperda* specifically (Eidmann and Nuorteva 1968, Saarenmaa 1983), shows that beetle production (offspring number) per unit bark area increases rapidly at low attack densities, stabilizes at an optimum level at medium attack densities, and decreases due to larval mortality at higher attack densities. However, since the number of inspected windthrown trees in 2007 was low (11), the conclusions drawn from comparisons of observations in 2007 and previous years should be treated cautiously.

4.3 Shoot damage

The observed temporal patterns in shoot damage and beetle production were similar, and both the volume of colonized trees and average beetle production were correlated to the number of fallen shoots. Hence, the numbers of fallen pine shoots can be used as indicators of both beetle populations and damage risks.

After the storm-felling there was a general increase in shoot damage and the accumulated level of shoot losses over the study period was below levels where measurable growth losses occur (Ericsson et al. 1985; Långström and Hellqvist 1990; Långström and Hellqvist 1991). However, such shoot damage is not equally distributed, tending to be largest by infestation sources and decreasing quite rapidly with distance from stand edges close to the sources (Långström and Hellqvist 1991; Komonen et al. 2009). Occasionally we found shoot densities corresponding to losses of several hundred shoots per tree, which could result in 20-30% volume growth losses during a few years (Ericsson et al. 1985; Långström and Hellqvist 1990; Långström and Hellqvist 1991). Levels observed in the undamaged study stands of mature pine forests (< 1.2 shoot per m^2 and year) remained well below critical levels for growth losses. As up to 1000 pine shoot beetles could be produced per m^2 bark, and each beetle destroys close to one pine shoot on average (Långström 1979), growth losses may have occurred locally in the storm areas at sites where large amounts of windthrown pine trees were left to produce pine shoot beetles. However, data presented here indicate that such situations were rare. This conclusion is corroborated by information compiled by the Swedish National Forest Inventory (NFI) showing a clear increase in pine shoot beetle damage in the storm area in the years following Storm Gudrun (Wulff 2006; Wulff 2008).

However, the levels recorded by NFI (Wulff 2006; Wulff 2008) was less than a tenth of the levels recorded at our study sites. This discrepancy is probably due to the survey covering numerous plots in areas where almost all of the windthrown timber had been removed, while our data is from areas where the windthrown timber were left on the ground. However, both datasets clearly indicate that the increase in pine shoot beetle populations following Storm Gudrun in 2005 was too low to be expected to result in any major national- or regional-scale losses in pine growth. National forest statistics confirm that there was no significant difference in pine growth between the 5-year-periods before and after the storm (Nilsson et al. 2006; Fransson 2010). In contrast, dramatic growth losses (18-40 million m^3) were estimated to have occurred between 1970 and 1973 after storms in 1969 (Nilsson 1976), but the recorded growth data indicate that possible losses amounted to 2.0 - 2.5 million m^3 in the early 1970s (Svensson 1980).

4.4 Conclusions

The presented data show that the storm-felling in 2005 resulted in increased pine shoot beetle populations and subsequent shoot damage in exposed pine stands in affected areas. Initially, high stumps were preferred by the beetles over windthrown trees, which often resisted attacks even in the second season. Moderate shoot damage of pine trees indicating that growth losses may have occurred locally at sites with high beetle densities, but both survey and growth data indicate that the beetles had little or no effect on landscape-level pine growth. The damage level was low compared to levels during a previous outbreak in the 1970s, probably mainly due to low beetle populations resulting from improvements in forest protection practices during the intervening decades, including strict rules and routines for handling potential host material introduced to keep beetle populations low. The current Swedish forest management legislation allows to leave up to $5m^3$/ha of fresh conifer wood. The volume of wind-damaged pine wood at the sites in this study was up to 5-fold the legislation threshold, but the resulting shoot damage did not reach the levels required for substantial growth losses. Hence, in a future storm-felling situation, forest protection practice should focus on salvaging the worst areas with most fallen trees first in order to save timber quality and avoid local population build-ups. Keeping beetle populations low between outbreaks is still crucial, but the threshold levels for pine could be reconsidered with more focus on the landscape than the stand level.

Author contributions

BL conceived the research. PÖ and BL conducted experiments. PÖ, NB and BL analyzed data, conducted statistical analyses and wrote the manuscript. BL secured funding. All authors read and approved the manuscript.

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Figure and table legends

Table 1. Total area, diameter and total amount of wind-damaged trees (windthrown trees and high stumps) in 2005, distance to comparison sites for counting damaged pine shoots, and site characteristics.

Table 2. Occurrence and performance (mean ± SE) of *Tomicus piniperda* in windthrown trees and high stumps at all sites during the first summer after the storm-felling in January 2005. Overall average values are weighted by the number of trees at the respective sites.

Table 3. Performance of *Tomicus piniperda* (mean ± SE) in windthrown trees and high stumps, on average per year (2005-2007). Numbers in parentheses refer to old windthrown trees or high stumps (from the previous year).

Figure 1. Maps of southern Sweden (Götaland) showing volumes of wind-damaged forest after the storms in January 2005 (a) and 2007 (b). Study sites are marked with stars in map a. Map a is modified from the Swedish Forest Agency (Skogsstyrelsen 2006) and map b from www.skogsstyrelsen.se 2007-01-19.

Figure 2. Numbers (mean ± SE) of fallen pine shoots/m^2 in stands affected (wind-damaged sites) and not affected (comparison sites) by storm-felling at Asa, Braås, Hornsö, Tönnersjöheden and Vitthult during 2004-2008 ("n" refers to the number of locations). SE bars indicate standard errors for the sum of both green shoots (year x) and brown shoots (year x+1) attacked during the same year. No brown shoots were counted in 2009, so the total shoot number in 2008 has been underestimated (see Material and Methods for calculation procedure). (Missing data was due to damaged plots).

Figure 3. Relationships between the number of fallen pine shoots and both the total volume of wind-damaged trees per ha and volume of trees successfully attacked by *T. piniperda* per ha (a), and between the number of fallen pine shoots and beetle production in the same year (b) at each location (n = 9).

Table 1.

Site	Area (ha)	Diameter (Mean ± SE) (cm)	Total amount wind-damaged trees		Distance to comparison site (m)	Site description
			Number	Volume (m^3/ha)		
Asa	0.7	20.8 ± 3.0	48	19	700	1st thinning
Tönnersjöheden	0.9	25.6 ± 2.6	44	24	1900	1st thinning
Klockesjömyren	1.5	34.7 ± 4.0	23	15	N/A	Shelterwood cutting
Hornsö	3.7	33.9 ± 5.0	30	7	150	Shelterwood cutting
Hunneberg	4.4	36.1 ± 3.7	25	6	N/A	Seed-trees cutting
Braås	1.8	34.3 ± 3.0	36	19	250	2nd thinning
Vitthult	0.6	26.7 ± 2.8	30	25	300	1st thinning
Total sum/average	1.9	29.0 ± 6.0	236	16	660	N/A

Table 2.

Site	Not attacked	Number attacked trees: Unsuccessful	Number attacked trees: Successful	Attack density (galleries/m^2): Unsuccessful	Attack density (galleries/m^2): Successful	Production (exit holes/m^2)	Reproductive success (♀/♀)
Windthrown trees							
Asa	3	22	6	33 ± 13	44 ± 15	756 ± 222	9.6 ± 3.7
Tönnersjöheden	34	0	0	N/A	N/A	N/A	N/A
Klockesjömyren	15	0	2	N/A	11 ± 0	111 ± 22	5.0 ± 1.0
Hornsö	14	5	11	0	31 ± 10	514 ± 229	7.4 ± 2.5
Hunneberg	1	4	19	44 ± 28	60 ± 27	814 ± 366	7.9 ± 3.2
Braås	27	5	4	33 ± 13	28 ± 17	282 ± 130	10.6 ± 4.3
Vitthult	2	15	13	56 ± 42	74 ± 17	609 ± 326	4.2 ± 1.8
Total /Average	96	51	55	39 ± 25	51 ± 25	624 ± 337	7.0 ± 3.3
High stumps							
Asa	2	3	12	56 ± 52	32 ± 18	259 ± 135	5.6 ± 4.8
Tönnersjöheden	5	0	5	N/A	16 ± 5	120 ± 34	4.4 ± 1.9
Klockesjömyren	5	0	1	N/A	11	222	10.0
Hunneberg	0	0	1	N/A	56	1189	10.7
Total /Average	12	3	19	N/A	28 ± 19	270 ± 180	5.8 ± 4.2

Table 3.

Year	Not attacked	Number attacked trees: Unsuccessful	Number attacked trees: Successful	Attack density (galleries/m^2): Unsuccessful	Attack density (galleries/m^2): Successful	Production (exit holes/m^2)	Reproductive success (♀/♀)
Windthrown trees							
2005	96	51	55	39 ± 25	51 ± 25 ^{a}	624 ± 337 ^{ab}	7.0 ± 3.3 ^{a}
2006	63	0	84	N/A	72 ± 40 ^{a}	741 ± 394 ^{a}	7.0 ± 4.2 ^{a}
2007	1 (64)	0	10 (10)	N/A	182 ± 83 ^{b}	353 ± 308 ^{b}	1.0 ± 0.6 ^{b}
p-value	N/A	N/A	N/A	N/A	*< 0.001*	*0.031*	*< 0.001*
High stumps							
2005	12	3	19	44 ± 44	28 ± 19 ^{a}	270 ± 180 ^{a}	5.8 ± 4.2 ^{a}
2006	2 (14)	2 (2)	6 (9)	172 ± 94	161 ± 96 ^{b}	286 ± 146 ^{a}	2.5 ± 2.4 ^{a}
2007†	16	0	1 (1)	N/A	111	589	2.7
p-value	N/A	N/A	N/A	N/A	*< 0.001*	*0.859*	*0.093*

Means followed by a different letter within a column are significantly different (α = 0.05).

†Excluded from the statistical tests.

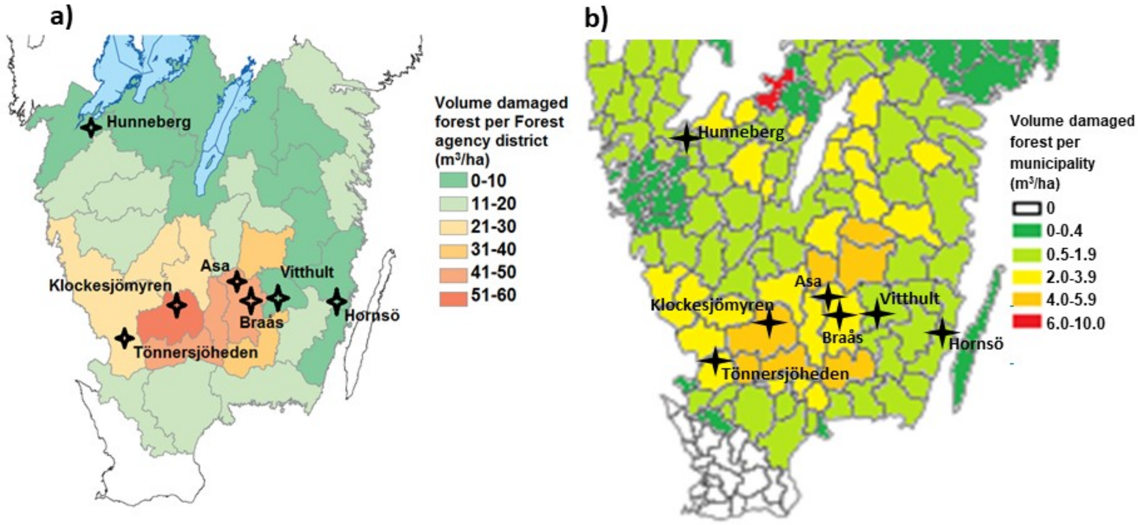
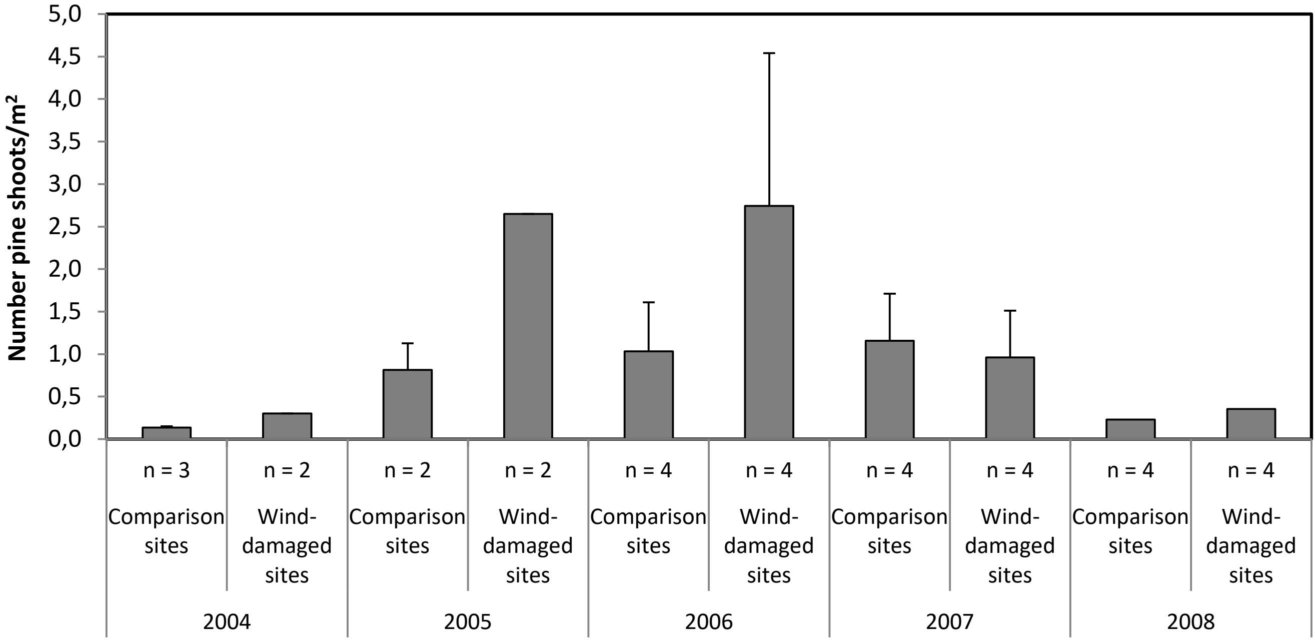

a)
Volume damaged forest per Forest agency district (m³/ha)
0-10
11-20
21-30
31-40
41-50
51-60
Hunneberg
Klockesjömyren
Asa
Vitthult
Braås
Hornsö
Tönnersjöheden
b)
Volume damaged forest per municipality (m³/ha)
0
0-0.4
0.5-1.9
2.0-3.9
4.0-5.9
6.0-10.0
Hunneberg
Klockesjömyren
Asa
Vitthult
Braås
Hornsö
Tönnersjöheden

Figure 1.



5,0
4,5
4,0
3,5
3,0
2,5
2,0
1,5
1,0
0,5
0,0
Number pine shoots/m²
n = 3
Comparison sites
n = 2
Wind-damaged sites
n = 2
Comparison sites
n = 2
Wind-damaged sites
n = 4
Comparison sites
n = 4
Wind-damaged sites
n = 4
Comparison sites
n = 4
Wind-damaged sites
n = 4
Comparison sites
n = 4
Wind-damaged sites
2004
2005
2006
2007
2008

Figure 2.

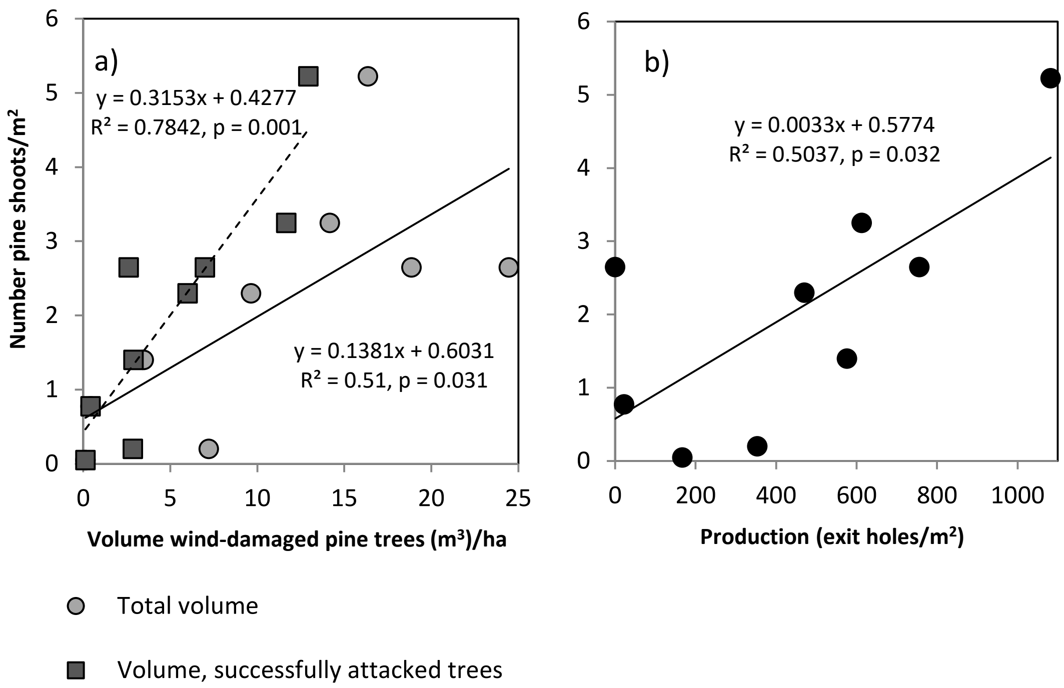

a)
y = 0.3153x + 0.4277
R² = 0.7842, p = 0.001
y = 0.1381x + 0.6031
R² = 0.51, p = 0.031
Number pine shoots/m²
Volume wind-damaged pine trees (m³)/ha
b)
y = 0.0033x + 0.5774
R² = 0.5037, p = 0.032
Production (exit holes/m²)
Total volume
Volume, successfully attacked trees

Figure 3.