



Protecting forest edges using trap logs – Limited effects of associated push-pull strategies targeting *Ips typographus*

Matilda Lindmark^{a,*}, Erika A. Wallin^b, Bengt-Gunnar Jonsson^{a,c}

^a Department of Natural Sciences, Mid Sweden University, Sweden

^b Department of Chemical Engineering, Mid Sweden University, Sweden

^c Department of Fish, Wildlife and Environmental Studies, Swedish University of Agricultural Science, Sweden

ARTICLE INFO

Keywords:

Ips typographus

Push and pull

Semiochemical diversity hypothesis

Non-host volatiles

ABSTRACT

Bark beetles can cause epidemic outbreaks and kill millions of cubic meters of economical and ecologically important forests around the world. It is well known what attracts and what repels different species of bark beetle, and these chemical cues can be used to protect trees and catch the beetles without using pesticides. Applying this knowledge, we investigated the use of push–pull strategies with trap logs along susceptible edges of a Swedish boreal spruce forest. The repellents (push) used were non-host volatiles (NHV) attached to tree trunks at the forest edge, and the attractants (pull) was a commercial aggregation pheromone attached to trap logs. The aim was to test whether the *Ips typographus* catch could be significantly increased by combining a push–pull system with traditional trap logs, thereby providing additional protection. The experiment was performed over two years and included the main flight period of *I. typographus*. The study sites were clear-cuts that had been harvested the preceding winter, and sun-exposed forest edges of mature spruce were targeted for protection. A full factorial setup was used comprising two treatments (repellent and attractant) and a control. Seven replicates of the trap logs were used, three during the first year and four during the second. The number of established *I. typographus* maternal galleries per square meter of log surface was used as the response variable. The trap logs captured large numbers of *I. typographus*, at an average density of 353 and 169 maternal galleries per m² during year 1 and year 2, respectively, over all treatments. Based on the catch data, with a sufficient number of trap logs, the risk of tree mortality at forest edges may be reduced and we recommend its general use. However, we did not see any significant effect of either the repellent or the attractant on the density of maternal galleries. Hence, we cannot recommend the addition of chemical cues to improve the efficiency of trap logs. Although trap logs are efficient in capturing bark beetles and hence may protect forest edges, it does not imply that they can provide protection on a larger scale. In line with other studies, we hence recommend that forest management to target nature-based solutions that strengthen the resilience of forest stands, by using mixed forest stands and resistant plant species, and nurture habitats for natural predators of *I. typographus*.

1. Background

The Eurasian spruce bark beetle, *Ips typographus* (L.) is widespread throughout European forests that contain Norway spruce, *Picea abies* (L.) H. Karst. (Lieutier et al., 2004). In common with many other bark beetles, *I. typographus* is an integral part of natural forest ecosystems, and normally uses recently dead trees for its reproductive cycle (Biedermann et al., 2019; Netherer et al., 2016). However, during the last few decades, epidemic outbreaks have become common, and healthy as well as weak trees have been attacked. More than 50 million m³ of Norway spruce forest in Europe has been killed by *I. typographus*, equating to

50% of all the biotic damage caused to European forestland during the 19th and 20th centuries (Schelhaas et al., 2003). The increasing number of outbreaks has had devastating economical and ecological effects (Kolb et al., 2016; Christiansen and Bakke 1988).

Outbreaks of *I. typographus* are highly correlated with areas of dense spruce monocultures (Groot et al., 2019), and the overall area of Norway spruce stands has increased significantly (Davis and Norman, 1987). As a consequence of modern silviculture, monocultures include species planted outside their natural niche, which can reduce their resistance to bark beetle attacks (Spiecker 2003; Klimo et al., 2000). In the context of a changing climate, including rising temperatures and storm- and

* Corresponding author.

E-mail address: Matilda.lindmark@miun.se (M. Lindmark).

<https://doi.org/10.1016/j.foreco.2021.119886>

Received 8 September 2021; Received in revised form 17 November 2021; Accepted 19 November 2021

Available online 26 November 2021

0378-1127/© 2021 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

drought events, the increasing susceptibility of stressed trees to natural disturbances such as bark beetle outbreaks is a major concern (Hlásný et al., 2021; Honkaniemi et al., 2020; Netherer et al., 2019).

Different strategies have been applied to try and control epidemic outbreaks of *I. typographus*. Sanitation logging (removing trees attacked by bark beetles) is frequently used in European forestry. However, it is a time-consuming process that needs to be carried out immediately after infestation, and only has a marginal effect on beetle population size (Havašová et al., 2017; Stadelmann et al., 2013). Salvage logging (removing all trees in a defined area with increased risks of attacks by bark beetles) can be used to rescue timber and help recover an economic return after a disturbance (Lindenmayer 2006; Lindenmayer et al., 2004), and can also help prevent future insect outbreaks (Marini et al., 2017; Stadelmann et al., 2013; Wermelinger 2004; Schroeder, 2001). However, badly executed salvage logging can have negative ecological impacts, by removing the protective and other functions of deadwood, altering browsing pressure by modifying forage availability and cover for herbivores and predators, and increasing microclimatic stress because of greater radiation and temperature fluctuations (Leverkus et al., 2021).

A combination of sanitation and salvage logging after storm events and outbreaks of *I. typographus* has been shown to reduce the number of trees killed by *I. typographus* (Karha et al., 2018; Stadelmann et al., 2013). One way to mimic this is to use trap logs, particularly to protect exposed forest edges after clear-cutting. Standing trees left at the forest edge are subject to stress by sun and wind exposure and may have been damaged by forest machines. As a result, forest edge trees are more susceptible to bark beetle attack (Långström et al., 2009). Trap logs mimic weak and damaged trees, attracting the beetles preferentially over standing wounded trees. Large diameter trees in non-shaded sites are felled just before the beetles emerge, then the logs, containing the beetles, are removed from the area (Holusa et al., 2017). Trap logs have been used to capture *I. typographus* for more than 200 years, the first mention of them dating to the beginning of the 19th century (Pfeil 1827). They have been proven to be effective, and during the critical emergence period in the spring they can catch more insects than pheromone-baited traps (Lubojacky and Holusa 2014).

Another method used to control *I. typographus* attacks is to repel the insects from susceptible trees. When seeking suitable hosts, bark beetles encounter and reject old-host and non-host trees (Seybold et al., 2018; Schiebe et al., 2011; Raffa 2001; Borden 1997; Raffa et al., 1993). This rejection is a negative response to stimuli based on different volatile compounds (Schroeder 1992). When *I. typographus* encounters a non-host, or old-host, plant volatile, the degree of attraction is reduced, and the beetle continues its search for other point-sources of pheromones or kairomones indicating a more suitable host. The semiochemical diversity hypothesis (SDH) postulates a reduced searching efficiency by specialist herbivores in the presence of non-host volatiles (NHV, including old-host volatiles) (Zhang and Schlyter 2004). By using NHV, SDH can theoretically be used as an effective pest control for *I. typographus*. Higher tree species diversity with a mixture of broad-leaved and deciduous trees emits a higher diversity of volatiles, potentially masking the location of suitable hosts (Berthelot et al., 2021; Schiebe et al., 2011).

The first NHV used to divert *Ips* species was verbenone (Bakke 1981). Verbenone comes from *Picea* and other conifers by microbial oxygenation of α -pinene in damaged bark (Hunt and Borden 1990) and the term old-host volatile has been proposed (Schiebe et al., 2011). Since then, more efficient full-spectrum NHV have been developed, along with green leaf volatiles (GLV), in laboratory bioassays and pheromone traps with reduced trap catches (Unelius et al., 2014; Zhang and Schlyter 2003; Zhang et al., 2000; Schlyter et al., 1995). Isolated *trans*-conophthorin, verbenone and GLV-alcohols, including 3-octanol and 1-octen-3-ol from non-host bark, 1-hexanol and (Z)-3-hexen-1-ol from both leaves and bark and (E)-2-hexen-1-ol from leaves, have been used successfully (Zhang and Schlyter 2003). For practical applications a

reduced blend has been developed, consisting of verbenone, *trans*-conophthorin and 1-hexanol which showed similar efficacy (Unelius et al., 2014).

The potential of SDH to protect forest edges, by diverting and pushing *I. typographus* away from susceptible Norway spruce trees, has been tested previously. Schiebe et al. (2011), in their push-pull study, converted spruce monocultures into artificial semiochemically mixed forests by using NHV-dispensers placed on tree trunks along the forest edges. They saw a reduction in trees killed by *I. typographus* compared with untreated zones without NHV-dispensers. However, when applied in the field, the insects were just diverted to nearby trees or stands.

To provide an effective protection system, a combination of trap logs with a push-pull system based on semiochemicals has been considered earlier (Schiebe et al., 2011). The push-pull effect is established by exploiting semiochemicals to repel pest insects from valuable plants or crops (push) and attract them into a trap (pull). Push-pull systems have a long history. The technique was first developed for African agriculture: lepidopterous stem borers, which attack maize, sorghum and other cereal crops, were controlled by establishing a semiochemical-based push-pull system using companion crops (Pickett et al., 1997; Smart et al., 1997; Pyke et al., 1987).

In this study we investigated the use of a semiochemical push-pull strategy in combination with trap logs to protect susceptible forest edge trees from *I. typographus* attack. The aim was to not only push the insects away from the forest edge by using NHV, but also pull them into groups of trap logs treated with a commercial aggregation pheromone for *I. typographus*. Earlier push-pull studies (Unelius et al., 2014; Schiebe et al., 2011) have been using attractant pheromone baited traps close to stand edges. However, the pull effect was low. That supports our idea of testing other 'pull' sources in our study, as trap logs.

This is the first full-scale push-pull experiment using trap logs to protect forest edges from *I. typographus*, and it was based on a two-year field study.

2. Materials and method

2.1. Field experiments

Norway spruce dominated stands in areas with a minimum of 10 % (basal area) of spruce killed by *I. typographus* previous summer were identified in Västernorrland County, Sweden. Identification was made by help from the landowner, SCA Forest AB. The geographical area in Sweden have a recent history of epidemic outbreaks of *I. typographus* for several years in a row (Swedish forest agency, 2021). The study stands had been clear-cut the winter before the experiment began and all trees in the stand were removed (except for a few trees left for nature conservation purposes). All stands were between 70 and 90 years old with a former composition of minimum 75% spruce (basal area) and sun-exposed forest edges oriented to the south-east, south and south-west. The surrounding forest edges were between 50 and 75 years old and minimum 75% spruce (basal area). The experimental stands were located relatively close to each other and hence with similar climate and history (coordinate position N62°18'–33', E16°22'–39' and 310–421 m a. s.l.). For year 1, 3 clear-cuts with one replicate on each was used (15.1 ha, 23.6 ha and 15.9 ha each). For year 2, two clear-cuts with two replicates on each clear-cut was used (17.2 ha and 10.4 ha each).

The experiment was carried out along the sun-exposed forest edges of stands with healthy, uninfested, spruce trees. 10–20 m from the forest edges, four groups of trap logs were established with a minimum of 100 m between each trap log group; two groups of trap logs were baited with attractant and two stretches of forest edge were baited with repellent. The repellent was attached to tree trunks along the forest border close to the trap logs at a height of 1.5 m. The treatments were arranged in a randomized block design, given the four different treatments: repellent only (R + 0), attractant only (A + 0), both repellent and attractant (A + R), no repellent or attractant (0 + 0) (i.e. a control) arranged randomly

within the block (Fig. 1).

For the “push” repellents, dispensers were filled with a blend of NHV (the repellent), to repel *I. typographus*. The “pull” attractant was a commercial aggregation pheromone for *I. typographus* (“Ips-lure”; Chemtica International S.A., Costa Rica). More detailed information of the repellent and attractant is presented below.

Two monitoring traps (Lindgren Funnel traps baited with two dispensers of Ips-lure) were placed in the middle of each clear-cut, at least 100 m from the nearest trap log group, to monitor the presence of *I. typographus*. Because of the distance between the bait traps and the trap log groups, no influence or change in attack behavior by the beetles was expected (Wichmann and Ravn 2001; Byers 1999).

For both study years, the experiment was run for 4 weeks in the early summer (May–June), spanning the main flight period of *I. typographus*. This was also to ensure a minimum of 10 days with a maximum daily temperature above 18 degrees (i.e. days suitable for *I. typographus* flight activity) (Faccoli 2009). During the first year, the experiment ran from 19 May to 6 June, and the maximum daily temperature exceeded 18 degrees for 10 days (SMHI, 2021). During the second year, the experiment ran from 28 May to 24 June, and the maximum daily temperature exceeded 18 degrees for 18 days (SMHI, 2021).

2.1.1. Trap logs (attractant)

The arrangement of the trap logs was identical for both years of the field experiment. The trap log groups were created at the beginning of May (approximately 2 weeks before *I. typographus* starts to fly) from newly felled, undamaged and uninfected spruce trees with a top diameter of more than 12 cm. Each group was made from two spruces cut into 3–4 m logs. The root log of each tree was placed on the ground, parallel to the forest edge, and the remaining logs were placed on top of them, at a 90 degrees angle towards the forest edge (6–8 logs per trap) (Fig. 2a). The groups of trap logs were placed 10–20 m from the forest edge, with a minimum of 100 m between each group. All the groups were placed along sun-exposed edges, i.e. facing south, south-west or south-east (Fig. 1).

Half of the trap log groups were baited with a commercial

aggregation pheromone for *I. typographus* approximately 1 week before *I. typographus* started to fly in early summer. The aggregation pheromone was a blend of 2-methyl-3-buten-2-ol, *cis*-Verbenol, and 2-methyl-6-methylene-2,7-octadiene-4-ol (Ipsdienol) (Chemtica International S. A., Costa Rica). Four dispenser bags were attached underneath the outer corners of each trap log group.

2.1.2. NHV-dispensers (repellent)

2.1.2.1. Year 1. Wick dispensers (Varkonda 1996) containing *trans*-conophthorin (tC) (Syntastic, Sweden) and 1-hexanol (Sigma Aldrich) in nonane (VWR) were used. They were set up to last for 10 weeks, based on the release rate determined in a laboratory over 30 consecutive days. At room temperature, the release rate was about 2 mg/day for *trans*-conophthorin (tC) and 6 mg/day for 1-hexanol.

This is release rates of NHV comparable to those from a non-host tree, and comparable to earlier studies used NHV in field trials (Unelius et al., 2014; Zhang and Schlyter 2003).

The dispensers were protected from direct sunlight and rain by aluminum foil and a protection shield of transparent plastic attached 10 cm above the dispenser. The dispensers were attached to 5 tree trunks with metal wires at a height of 1.5 m (Fig. 3a), and were placed at 2 m intervals to create a 10 m long barrier of NHV. That is a slightly lower spatial concentration than earlier studies (Unelius et al., 2014; Zhang and Schlyter 2003).

After the experiment, the dispensers were collected to measure the actual release in the field. However, no conclusive field release rate was possible because of highly variable results: some dispensers were almost empty while others were still relatively full.

2.1.2.2. Year 2. Given the high variation in release rate by the wick dispensers in the field during year 1, other dispensers were evaluated in the laboratory to achieve a more consistent release rate. 1-octanol and verbenone were also added to the NHV blend to try and improve the effectiveness of the repellent (Zhang and Schlyter 2004; Zhang and

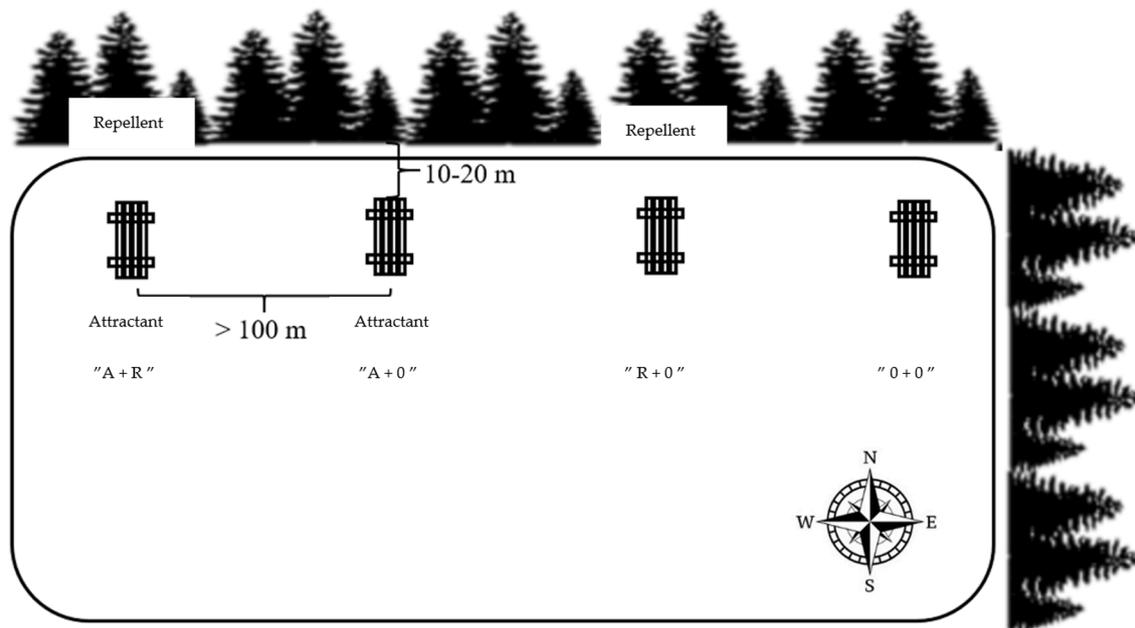


Fig. 1. The field experiment design, showing one replicate of the push–pull system used. Four groups of trap logs were placed 10–20 m from the forest edge, with a minimum of 100 m between them. For the attractant, two of the trap log groups were baited with a commercial aggregation pheromone for *I. typographus*, and two groups were left untreated. For the repellent, on tree trunks at stretches of forest edge near two of trap log groups, NHV dispensers were attached at a height of 1.5 m and two stretches of forest edge near the remaining two trap log groups was left untreated. All four treatments were performed within each replicate: attractant and repellent (A + R), only attractant (A + 0), only repellent (R + 0), untreated control (0 + 0). The different treatment combinations were randomly placed within the replicate.



Fig. 2. An overview of a trap log group and an example of *I. typographus* galleries on a sample of bark. 2a: One trap log group made from two uninfested spruces, newly felled and cut into 3–4 m logs. 2b: Insect galleries in a 0.063 m² bark sample. The maternal galleries (each representing one egg-laying female *I. typographus*) present on the inner bark were easily distinguishable and were counted to provide an estimate of the density of the beetles.



Fig. 3. An overview of the NHV-dispensers. 3a: Year 1: a wick dispenser loaded with NHV was attached to standing tree trunks with a metal wire. It was protected from direct sunlight and rain by aluminum foil and a plastic shield attached above it. 3b: Year 2: PE-vials and PE-bags filled with cotton pads (wettex) loaded with NHV were attached to standing tree trunks with metal clips. The vials and bags dispensed *trans*-conophthorin (tC), and verbenone, 1-hexanol and 1-octanol, respectively. Because these dispensers were closed, there was no need for extra weather protection.

Schlyter 2003; Zhang et al., 2000; Huber et al., 2021). The aim was to achieve a higher release rate of a more efficient cocktail of the different compounds (Schiebe et al., 2011; Jakus et al., 2003) (Fig. 3b). In addition, a longer forest edge was treated compared to the first year to match a spatial concentration used in earlier studies (Unelius et al., 2014; Zhang and Schlyter 2003). Different dispensers were evaluated in the laboratory for the different components in order to obtain an even and comparable (to other publications) release rate of the components. After evaluation of different dispensers, PE-vials were used to disperse *trans*-

conophthorin (tC), and PE-bags filled with cotton pads (wettex) were used to disperse verbenone, 1-hexanol and 1-octanol. At room temperature, the release rate for each substance was *trans*-conophthorin (tC) 2 mg/day, 1-hexanol 10 mg/day, 1-octanol 5 mg/day and verbenone 7 mg/day. The dispensers were filled to last for 10 weeks and were attached to the tree trunks in groups by metal clips (Fig. 3b). The release rate of 1-hexanol and 1-octanol is comparable to Zhang and Schlyter (2003) while the release rate of verbenone is significantly higher than earlier studies (Unelius et al., 2014; Schiebe et al., 2011; Zhang and

Schlyter 2003).

A group of dispensers was attached to 10 tree trunks at 2 m intervals to create a 20 m long barrier of NHV.

2.2. Evaluation of treatment effect

The density of *I. typographus* in the trap logs was estimated from samples of cut bark, the same method was used for both years. The bark samples were removed from the trap logs four weeks after the experiment had been setup (after the first flight period of *I. typographus*). Four pieces of bark (0.0624 m², the size of an A4 piece of paper), from the upper and lower surface of each end of the log, were gently peeled off the outer 2 logs of each trap log group using a sharp knife, providing an overall a sample of 0.5 m² per trap log group. Maternal galleries of *I. typographus* (each representing one egg-laying female) were clearly visible in the inner bark, and easily distinguishable from other insect galleries (see Fig. 2.b). The number of maternal galleries was counted, and the density of *I. typographus* is presented as the number of maternal galleries per square meter of bark (the number of female individuals of *I. typographus*) (Schroeder and Cocos 2017).

2.3. Statistical analysis

The average number of *I. typographus* maternal galleries per square meter (density) in each trap log group was used as the response variable in the statistical analyses. A Shapiro–Wilk normality test was performed for each treatment to confirm a normal distribution (R Core Team 2018). A one-way ANOVA and Welch F-test, which does not assume equal variances, was used to compare treatment effects.

3. Results

In total, 4231 (year 1) and 2708 (year 2) *I. typographus* maternal galleries were found in the bark samples, representing an average of 353 (year 1) and 169 (year 2) maternal galleries per square meter (Table 1). We could not confirm any significant treatment effect. All the trap logs caught approximately the same number of *I. typographus* regardless of treatment (Fig. 4a, Table 1). During year 1, a small decrease in the number of *I. typographus* maternal galleries was seen when repellent was used, contrary to our hypothesis (Fig. 4b), and the catch from trap log groups with repellent but without attractant (R + 0) was lower than the catch from the other trap log groups (Fig. 4a). In year 2, no treatment effect at all could be observed: all the trap logs caught approximately the same number of *I. typographus*, regardless of treatment (Fig. 4 a-c). A one-way ANOVA comparing the average number of *I. typographus* caught per square meter for each treatment also showed no significant difference between the four different treatments for either year (Table 2).

In line with previous unpublished observations, we found higher numbers of maternal galleries on the lower surface than the upper surface of the trap logs. In year one, we found approximately 50% more maternal galleries, and in year two approximately 225% more maternal

galleries, on the lower surface.

4. Discussion

This experiment has confirmed that trap logs represent an efficient method of catching large numbers of *I. typographus* and may therefore be a convenient and effective way of protecting forest edges. By felling a tree directly from the forest edge and cutting it into 3–4 m logs in the adjacent clear-cut area, the traps can be made with relatively little effort during the harvesting operation. In practice, one should consider a larger number of logs than used in our experiment, to maximize the catch of beetles. Our study does not evaluate the total volume of trap logs needed to effectively protect forest edges. To determine that, another experimental design would have been needed, including variation in trap log density.

We could not find any evidence that our treatments either increased the attractiveness of the trap logs to *I. typographus* or repelled the beetles from the forest edges. In neither year did we see any significant difference in catch between the different treatments. We choose to change the blend of NHV between the years, trying to enhance the anti-attractant smell of the forest edge. In Unelius et al. (2014) they concluded that a mix of verbenone, *trans*-conophthorin and 1-hexanol is efficient enough for decreasing the number of beetles caught in pheromone baited traps. However, we choose not to use verbenone in the blend the first year, since we were not using pheromone traps. Instead, as we targeted standing forest edges of old trees, we assumed that the forest edge in itself will release high levels of verbenone (an old-host volatile).

Based on the results from year 1, we changed the blend for the second year, by adding both 1-octanol and verbenone trying to enhance the effect and use a blend of earlier standard (Zhang and Schlyter 2004; Zhang and Schlyter 2003).

The lack of attractant effect was probably because the volatiles from freshly cut logs are highly attractive to *I. typographus*. As soon as the first male *I. typographus* attacks a log, it also starts to release a high concentration of aggregation pheromone to attract conspecifics. The artificial Ips-lure used in our experiment therefore had limited added value (Holušá et al., 2017; Blomquist et al., 2010).

The lack of repellent effect (NHV-dispensers) could be because the push–pull system is not efficient in a heterogeneous forest ecosystem. In theory, the combination of attractant and repellent could reduce the risk of beetles moving towards forest edges by pushing them towards the trap logs (Cook et al., 2007). Earlier studies have shown a local protection of trees in forest edge treated with NHV (Unelius et al., 2014; Schiebe et al. 2011). In our study we could not see such a protection, i.e. an increased number of catches in trap logs. In natural forest, several tree species occur together, therefore generating a mix of NHV. *I. typographus* has evolved to maneuver through the different NHV plumes and find their way to a suitable host tree species (Raffa et al. 2016). However, protecting specific trees, by pushing the beetles away with repellent, but not catching them, will not provide protection at a stand level, and hence is of limited value for forest management. The

Table 1

Summary table showing the total number of *I. typographus* maternal galleries from the samples for each treatment (8 × 0.063 m² per trap log group × N replicates) and the density of maternal galleries per square meter for both years of the field trial. Also shown is the average catch of *I. typographus* from the monitoring traps for each year.

Treatment	N replicates (push-pull-set)		Total no. <i>I. typographus</i> maternal galleries		Density (average no. female <i>I. typographus</i>		Average no. <i>I. typographus</i>	
			per trap log group		per square meter) ± SD		in monitoring traps	
Year	1	2	1	2	1	2	1	2
A + 0	3	4	1282	673	427 ± 106.7	168 ± 69.9		
R + 0	3	4	753	609	251 ± 93.9	152 ± 49.8		
A + R	3	4	1090	753	363 ± 138.2	188 ± 52.9		
0 + 0	3	4	1106	673	369 ± 42.4	168 ± 105.9		
TOTAL/AVERAGE			4231	2708	353	169	3250	7000

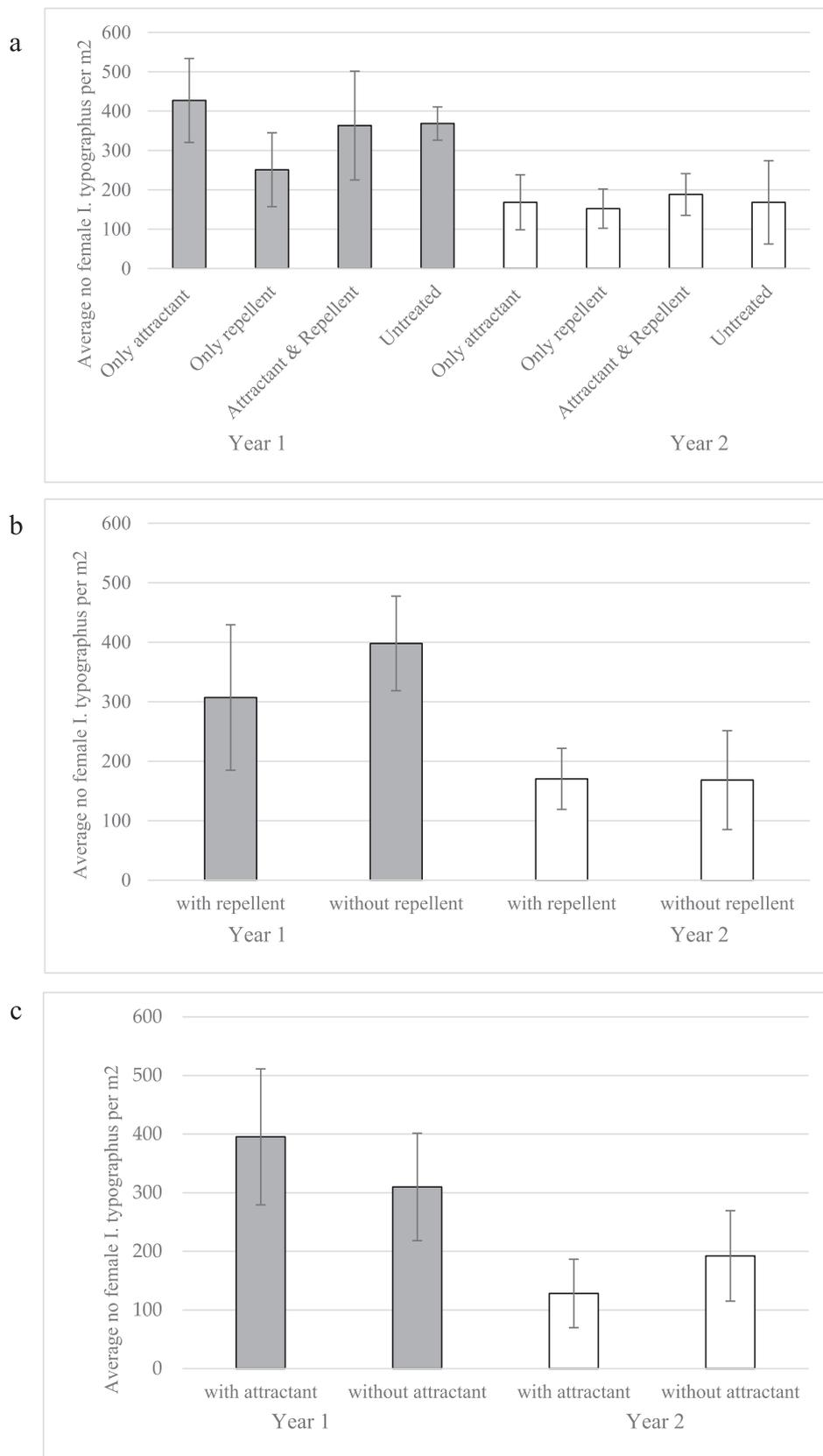


Fig. 4. The density of *I. typographus* each year, shown as the average number of maternal galleries per square meter. Error bars show the standard deviation. 4a: Average density of the *I. typographus* catch for each treatment. 4b: A comparison of the trap log groups with repellent (A + R & R + 0) and without repellent (A + 0 & 0 + 0). 4c: A comparison of the trap log groups with attractant (A + R & A + 0) and without attractant (R + 0 & 0 + 0).

Table 2

ANOVA-table for each year of the field experiment, comparing all four treatments individually. The Welch-test, which does not assume equal variances, was used.

ANOVA											
Source of variation	SS		df	MS		F		P-value		F crit	
Year		1	2		1	2		1	2	1	2
Between groups	48795.77		2616.35		3	3	16265.26		872.12	1.58	0.16
Within groups	82182.35		64140.76		8	12	10272.79		5345.06	0.27	0.92
Total	130978.13		66757.11		11	15				4.07	3.49

beetles will simply find alternative host trees.

The catches from the trap logs were lower overall in the second year, even though the monitoring trap catches were higher. This could be explained by the higher daily temperatures in year 2. In year 2, but not year 1, we saw a clear trend of higher numbers of maternal galleries on the lower surface of the logs (shaded surface) than the upper surface (sun-exposed surface). When counting entry holes on the upper surface, trap logs exposed to higher temperatures tend to show lower entry hole densities than trap logs exposed to lower temperatures (Holuša et al., 2017). Hence, we conclude that the lower catches in year 2 was likely due to the sun-exposed trap logs being too warm and thus partly avoided by the bark beetles.

Earlier studies have shown a treatment effect when using repellents in the field (Schiebe et al. 2011). However, based on our study, we cannot recommend to use repellents for increasing catches in trap logs. To be efficient, the insects that are pushed away need to find trap logs rather than neighboring trees, which our results do not support. Although the push-pull strategy is theoretically interesting, our results suggest it does not provide any additional benefit compared to using trap logs on their own to catch *I. typographus* in boreal forests. Hence, as we found no evidence of a positive effect of a push-pull system with trap logs, we recommend using trap logs on its own. No additional pheromone or NHV treatment is required to reach the full potential of trap logs of reducing the risk of tree mortality at forest edges.

However, while trap logs and other methods of catching *I. typographus* during an epidemic outbreak can provide some protection at susceptible forest edges, they can only reduce tree mortality locally (Holuša et al., 2017; Lubojacky and Holusa 2014). It is unlikely that any trapping method will be effective in limiting damage at larger scales, and forest management therefore needs to implement strategies that reduce the risk of outbreaks. This calls for alternative management practices based on nature-based solutions, such as including NHV-producing deciduous trees within a spruce stand (Hlásny et al., 2021). As an example, a recent study has shown a clear reduction in spruce damage caused by *I. typographus* by planting a mixed stand (Berthelot et al., 2021).

CRedit authorship contribution statement

Matilda Lindmark: Methodology, Investigation, Writing – original draft. **Erika A. Wallin:** Data curation, Methodology, Conceptualization, Writing – review & editing. **Bengt-Gunnar Jonsson:** Funding acquisition, Supervision, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

This research was funded by the Regional Development Fund for Västernorrland (grant ID: 17RS484) and Jämtland/Härjedalen county (grant ID: RUN/94/2017) and the Swedish Agency for Economic and

Regional Growth (grant ID: 20201370).

We thank SCA Forest AB for letting us conduct this study on their land, and Effektivt Skog AB for helping us with the manual felling of trees for the study. Thanks to all our colleagues at Mid Sweden University for their valuable support during field work.

This study is dedicated to the memory of Christian Schiebe and builds upon his work.

References

- Bakke, A., 1981. Inhibition of the response in *Ips typographus* to the aggregation pheromone – field-evaluation of verbenone and ipsenol. *Z. Angew. Entomol.* – *J. Appl. Entomol.* 92 (2), 172–177. <https://doi.org/10.1111/j.1439-0418.1981.tb01666.x>.
- Berthelot, S., Fruhbrot, T., Hajek, P., Nock, C.A., Dormann, C.F., Bauhus, J., Frund, J., 2021. Tree diversity reduces the risk of bark beetle infestation for preferred conifer species, but increases the risk for less preferred hosts. *J. Ecol.* 109 (7), 2649–2661. <https://doi.org/10.1111/1365-2745.13672>.
- Biedermann, P.H.W., Müller, J., Grégoire, J.-C., Gruppe, A., Hagge, J., Hammerbacher, A., Hofstetter, R.W., Kandasamy, D., Kolarik, M., Kostovcik, M., Krokene, P., Sallé, A., Six, D.L., Turrini, T., Vanderpool, D., Wingfield, M.J., Bässler, C., 2019. Bark beetle population dynamics in the anthropocene: challenges and solutions. *Trends Ecol. Evol.* 34 (10), 914–924. <https://doi.org/10.1016/j.tree.2019.06.002>.
- Blomquist, G.J., Figueroa-Teran, R., Aw, M., Song, M., Gorzalski, Abbott, N.L., Chang, E., Tittiger, C. 2010. Pheromone production in bark beetles. *Insect Biochem. Mol. Biol.* 40, 699–712. <https://doi.org/10.1016/j.ibmb.2010.07.13>.
- Borden, J.H., 1997. Disruption of Semiciochemical-mediated aggregation in bark beetles. In: Cardé, R.T., Minks, A.K. (Eds.), *Insect Pheromone Research: New Directions*. Springer, US, Boston, pp. 421–438.
- Byers, J.A., 1999. Effects of the attraction radius and flight paths on catch of Scolytid beetles dispersing outward through rings of pheromone traps. *J. Chem. Ecol.* 25, 985–1005. <https://doi.org/10.1023/A:1020869422943>.
- Christiansen, E., Bakke, A., 1988. The spruce bark beetle of Eurasia. In: Berryman, A.A. (Ed.), *Dynamics of Forest Insect Populations. Population Ecology: Theory and Application*. Plenum Press, New York, pp. 479–503.
- Cook, S.M., Khan, Z.R., Pickett, J.A., 2007. The use of push-pull strategies in integrated pest management. *Annu. Rev. Entomol.* 52 (1), 375–400. <https://doi.org/10.1146/ento.2007.52.issue-110.1146/annurev.ento.52.110405.091407>.
- Davis, L.S., Norman, J.K., 1987. *Forest management*. McGraw-Hill Book Company, University of Michigan, New York.
- Faccoli, M., 2009. Effect of Weather on *Ips typographus* (Coleoptera Curculionidae) Phenology, Voltinism, and Associated Spruce Mortality in the Southeastern Alps. *Environ. Entomol.* 38 (2), 307–316. <https://doi.org/10.1603/022.038.0202>.
- Groot, M., Diacib, J., Ogrisa, N., 2019. Forest management history is an important factor in bark beetle outbreaks: Lessons for the future. *For. Ecol. Manage.* 433, 467–474. <https://doi.org/10.1016/j.foreco.2018.11.025>.
- Havašová, M., Ferencík, J., Jakuš, R., 2017. Interactions between windthrow, bark beetles and forest management in the Tatra national parks. *For. Ecol. Manage.* 391, 349–361.
- Hlásny, T., König, L., Krokene, P., Lindner, M., Montagne-Huck, C., Müller, J., Qin, H., Raffa, K.F., Schelhaas, M.J., Svoboda, M., Viiri, H., Seidl, R. 2021. Bark Beetle Outbreaks in Europe: State of Knowledge and Ways Forward for Management. *Curr. Forestry Reports* 7, 138–165. DOI10.1007/s40725-021-00142-x.
- Honkaniemi, J., Rammer, W., Seidl, R., 2020. Norway spruce at the trailing edge: the effect of landscape configuration and composition on climate resilience. *Landscape Ecol.* 35 (3), 591–606. <https://doi.org/10.1007/s10980-019-00964-y>.
- Holuša, J., Hlásny, T., Modlinger, R., Lukášová, K., Kula, E., 2017. Felled trap trees as the traditional method for bark beetle control: Can the trapping performance be increased? *For. Ecol. Manage.* 404 (2017), 165–173. <https://doi.org/10.1016/j.foreco.2017.08.019>.
- Hunt, D.W.A., Borden, J.H., 1990. Conversion of verbenols to verbenone by yeasts isolated from *Dendroctonus ponderosae* (Coleoptera: Scolytidae). *J. Chem. Ecol.* 16 (4), 1385–1397.
- Huber, D.P.W., Fettig, C.J., Borden, J.H., 2021. Disruption of coniferophagous bark beetle (Coleoptera: Curculionidae: Scolytinae) mass attack using angiosperm nonhost volatiles: from concept to operational use. *Can. Entomol.* 153 (1), 19–35. <https://doi.org/10.4039/tce.2020.63>.

- Jakus, R., Schlyter, F., Zhang, Q.H., Blazenc, M., Vavercak, R., Grodzki, W., Brutovsky, D., Lajzova, E., Turcani, M., Bengtsson, M., Blum, Z. 2003. Overview of development of an anti-attractant based technology for spruce protection against *Ips typographus*: From past failures to future success. *Anzeiger Fur Schadlingskunde – J. Pest Sci.* 76 (4), 89–99. ISSN 1436-5693.
- Karha, K., Anttonen, T., Poikela, A., Palander, T., Laurén, A., Peltola, H., Nuutinen, Y., 2018. Evaluation of salvage logging productivity and costs in windthrown Norway spruce-dominated forests. *Scand. J. For. Res.* 9 (5), 280.
- Klimo, E., Hager, H., Kulhavy, J., 2000. Spruce monocultures in Central Europe Problems and prospects. *Eur. Forest Instit. Proc. No. 33(2000)*. ISSN1237-8801. ISBN952-9844-76-X.
- Kolb, Thomas E., Fettig, Christopher J., Ayres, Matthew P., Bentz, Barbara J., Hicke, Jeffrey A., Mathiasen, Robert, Stewart, Jane E., Weed, Aaron S., 2016. Observed and anticipated impacts of drought on forest insects and diseases in the United States. *For. Ecol. Manage.* 380, 321–334.
- Långström, B., Lindelöw, Å., Schroeder, L.M., Björklund, N., Öhrn, P., 2009. The spruce bark beetle outbreak in Sweden following the January-storms in 2005 and 2007. In: Kunca, A., Zubrik, M. (Eds.), *Insects and fungi in storm areas*. National Forest Centre, Proceedings of workshop of IUFRO Working Party 7.03.10, September 15–19. Strbske Pleso, Slovakia.
- Leverkus, Alexandro B., Buma, Brian, Wagenbrenner, Joseph, Burton, Philip J., Lingua, Emanuele, Marzano, Raffaella, Thorn, Simon, 2021. Tamm review: Does salvage logging mitigate subsequent forest disturbances? *For. Ecol. Manage.* 481, 118721. <https://doi.org/10.1016/j.foreco.2020.118721>.
- Lieutier, F., Day, K.R., Battisti, A., Gregoire, J.C., Evans, H.F., 2004. *Bark and woodboring insects in living trees in Europe, a synthesis*. Kluwer Academic Publishers, Dordrecht.
- Lindenmayer, David, 2006. Salvage harvesting—Past lessons and future issues. *Forestry Chronicle* 82 (1), 48–53. <https://doi.org/10.5558/tfc82048-1>.
- Lindenmayer, D.B., Foster, D.R., Franklin, J.F., Hunter, M.L., Noss, R.F., Schmiegelow, F. A., Perry, D. 2004. Salvage harvesting policies after natural disturbance. *Science* 303, 1303. DOI:10.1126/science.1093438.
- Lubojacky, J., Holusa, J., 2014. Attraction of *Ips typographus* (Coleoptera: Curculionidae) beetles by lure-baited insecticide-treated tripod trap logs and trap trees. *Int. J. Pest Manage.* 60 (3), 153–159. <https://doi.org/10.1080/09670874.2014.944610>.
- Marini, L., Økland, B., Jönsson, A.M., Bentz, B., Carroll, A., Forster, B., Grégoire, J.C., Hurling, R., Nageleisen, L.M., Netherer, S., Ravn, H.P., Weed, A., Schroeder, M., 2017. Climate drivers of bark beetle outbreak dynamics in Norway spruce forests. *Ecography* 40 (12), 1426–1435. <https://doi.org/10.1111/ecog.2017.v40.i1210.1111/ecog.02769>.
- Netherer, S., Panassiti, B., Pennerstorfer, J., Matthews, B., 2019. Acute Drought Is an Important Driver of Bark Beetle Infestation in Austrian Norway Spruce Stands. *Front. Forests Global Change* 2, 21. <https://doi.org/10.3389/ffgc.2019.00039>.
- Netherer, S., Ehn, M., Blackwell, E., Kirisits, T., 2016. Defence reactions of mature Norway spruce (*Picea abies*) before and after inoculation of the blue-stain fungus *Endoconidiophora polonica* in a drought stress experiment. *Forestry J.* 62 (4), 169–177. <https://doi.org/10.1515/forj-2016-0014>.
- Pfeil, W., 1827. *Über Insektenschaden in den Waldern, die Mittel ihm vorzubeugen und seine Nachteile zu vermindern*. Verlag Boicke, Berlin.
- Pickett, J.A., Wadhams, L.J., Woodcock, C.M., 1997. Developing sustainable pest control from chemical ecology. *Agric., Ecosyst. Environ.* 64(2), 149–156. [https://doi.org/10.1016/S0167-8809\(97\)00033-9](https://doi.org/10.1016/S0167-8809(97)00033-9).
- Pyke, B., Rice, M., Sabine, B., Zalucki, M., 1987. The push-pull strategy—behavioural control of *Heliothis*. *J. Agric. Chem. Environ.* 8 (1).
- R Core Team. 2018. R: A language and environment for statistical computing. R Foundation Statistical Computing, Vienna, Austria. <https://www.R-project.org/> (accessed 14 may 2020).
- Raffa, K.F., 2001. Mixed messages across multiple trophic levels: the ecology of bark beetle chemical communication systems. *Chemoecology* 11 (2), 49–65. <https://doi.org/10.1007/PL00001833>.
- Raffa, K.F., Phillips, T.W., Salom, S.M., 1993. Strategies and mechanisms of host colonization by bark beetles. In: Schowalter, T.D., Filip, G.M. (Eds.), *Beetle-pathogen interactions in conifer forests*. Academic, San Diego, pp. 102–128.
- Raffa, K.F., Andersson, M.N., Schlyter, F. 2016. Host Selection by Bark Beetles: Playing the Odds in a High-Stakes Game. In: Tittiger, C., Blomquist, G.J. (red), *Advances in Insect Physiology*. vol. 50, Academic Press, s. 1-74. <https://doi.org/10.1016/bs.aaip.2016.02.001>.
- Schelhaas, M.J., Nabuurs, G.J., Schuck, A., 2003. Natural disturbances in the European forests in the 19th and 20th centuries. *Glob. Change Biol.* 9, 1620–1633. <https://doi.org/10.1046/j.1529-8817.2003.00684.x>.
- Schiebe, C., Blazenc, M., Jakus, R., Unelius, C.R., Schlyter, F., 2011. Semiochemical diversity diverts bark beetle attacks from Norway spruce edges. *J. Appl. Entomol.* 135 (10), 726–737. <https://doi.org/10.1111/j.1439-0418.2011.01624.x>.
- Schlyter, F., Lofqvist, J., Jakus, R. 1995. Green Leaf Volatiles and Verbenone Modify Attraction of European Tomicus, Hylurgops, and Ips Bark Beetles-. In: Rain, F.P., Salom, S.S., Ravlin, W.F., Payne, T.L., & Raffa, K.F. (Eds.), *Behavior, Population Dynamics, and Control of Forest Insects*, Proceedings of a Joint IUFRO Working Party Conference- February 1994, Ohio State Univ. OARDC, Wooster, pp. 29 -44.
- Schroeder, L.M., Cocos, D., 2017. Performance of the tree-killing bark beetles *Ips typographus* and *Pityogenes chalcographus* in non-indigenous lodgepole pine and their historical host Norway spruce: Bark beetle performance in novel host. *Agric. For. Entomol.* 20 (3) <https://doi.org/10.1111/afe.12267>.
- Schroeder, L.M., 1992. Olfactory recognition of nonhosts aspen and birch by conifer bark beetles *Tomicus piniperda* and *Hylurgops palliatus*. *J. Chem. Ecol.* 18 (9), 1583–1593. <https://doi.org/10.1007/BF00993231>.
- Schroeder, L.M., 2001. Tree mortality by the bark beetle *Ips typographus* (L.) in storm-disturbed stands. *Integr. Pest Manag. Rev.* 6, 169–175. <https://doi.org/10.1023/A:1025771318285>.
- Seybold, S., Bentz, B., Fettig, C., Lundquist, J., Progar, R., Gillette, N., 2018. Management of western north American bark beetles with semiochemicals. *Annu. Rev. Entomol.* 63 (1), 407–432. <https://doi.org/10.1146/ento.2018.63.issue-110.1146/annurev-ento-020117-043339>.
- Smart, L.E., Pickett, J.A., Powell, W., 1997 Push-pull strategies for pest control. *Grain Legumes* 15, 14–15.
- SMHI (2021-08-24) <https://www.smhi.se/data/meteorologi/ladda-ner-meteorologiska-observationer#param=airtemperatureInstant,stations=all,stationid=126290>.
- Spiecker, H., 2003. Silvicultural management in maintaining biodiversity and resistance of forests in Europe—temperate zone. *J. Environ. Manage.* 67 (1), 55–65. [https://doi.org/10.1016/S0301-4797\(02\)00188-3](https://doi.org/10.1016/S0301-4797(02)00188-3).
- Stadelmann, G., Bugmann, H., Meier, F., Wermelinger, B., Bigler, C., 2013. Effects of salvage logging and sanitation felling on bark beetle (*Ips typographus* L.) infestations. *For. Ecol. Manage.* 305, 273–281. <https://doi.org/10.1016/j.foreco.2013.06.003>.
- Swedish Forest Agency, 2021. Thomas Mårtensson, oral communication.
- Unelius, Schiebe, Bohman, Andersson, Schlyter, Rodriguez-Saona, 2014. Non-host volatile blend optimization for forest protection against the European Spruce Bark Beetle, *Ips typographus*. *Plos One* 9 (1), e85381. <https://doi.org/10.1371/journal.pone.0085381>.
- Varkonda, S. 1996. Pheromone dispenser, office of industrial ownership of The Czech Republic.
- Wermelinger, B., 2004. Ecology and management of the spruce bark beetle *Ips typographus*—A review of recent research. *For. Ecol. Manage.* 202 (1–3), 67–82. <https://doi.org/10.1016/j.foreco.2004.07.018>.
- Wichmann, G., Ravn, H.P., 2001. The spread of *Ips typographus* (L.) (Coleoptera, Scolytidae) attacks following heavy windthrow in Denmark, analysed using GIS. *For. Ecol. Manage.* 148 (1–3), 31–39. [https://doi.org/10.1016/S0378-1127\(00\)00477-1](https://doi.org/10.1016/S0378-1127(00)00477-1).
- Zhang, Q.H., Schlyter, F., 2003. Redundancy, synergism and active inhibitory range of non-host volatiles in reducing pheromone attraction of European spruce bark beetle *Ips typographus*. *Oikos* 101, 299–310. <https://doi.org/10.1034/j.1600-0706.2003.111595.x>.
- Zhang, Qing-He, Schlyter, Fredrik, 2004. Olfactory recognition and behavioural avoidance of angiosperm nonhost volatiles by conifer-inhabiting bark beetles. *Agric. For. Entomol.* 6 (1), 1–20. <https://doi.org/10.1111/afe.2004.6.issue-110.1111/j.1461-9555.2004.00202.x>.
- Zhang, Q.H., Schlyter, F., Birgersson, G., 2000. Bark volatiles from nonhost angiosperm trees of spruce bark beetle, *Ips typographus* (L.) (Coleoptera : Scolytidae): Chemical and electrophysiological analysis. *Chemoecology* 10 (2), 69–80. <https://doi.org/10.1007/s000490050010>.