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Sequential patterns of colonization of coarse woody debris by *Ips pini* (Say) (Coleoptera: Scolytidae) following a major ice storm in Ontario

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Abstract

1 It is widely known that many bark and wood-boring beetle species use nonresistant coarse woody debris (CWD) created by disturbances; however, the ability of these secondary species to cause mortality in healthy trees following a build-up of their populations remains unclear. We characterized the pattern of colonization by *Ips pini* (Say) following a major ice storm that created large amounts of CWD varying in resistance to colonization (i.e. ranging from snapped tops with no resistance to heavily damaged trees with intact root systems). A major question was how the beetles responded to the different types of storm-damaged material and whether healthy undamaged trees were colonized and killed following increases in beetle populations.

2 Six red pine, *Pinus resinosa* Ait., plantations in eastern Ontario were monitored from 1998 to 2001 inclusive: three with high storm damage (approximately 120 m^3/ha CWD) and three with minimal damage (approximately 20 m^3/ha CWD). Transects (200 × 2 m) were sampled yearly in each plantation to assess the type and amount of damaged pine brood material colonized by the pine engraver beetle, *I. pini*.

3 Beetles preferentially infested the most nonresistant material available each year (i.e. all snapped tops in year 1, all standing snags, up-rooted trees and many bent trees by year 2, but still less than 50% of trees blown over but with intact root systems by year 3). By years 3 and 4, the majority (approximately 75%) of severely damaged trees (with > 50% crown loss) died prior to beetle colonization.

4 The size of the beetle population tracked the abundance of available woody material from year-to-year within a plantation; populations were very large in the first 2 years, and declined significantly in the last 2 years.

5 Healthy standing red pines were apparently resistant to colonization by the beetles, despite the significant build-up in their populations. Hence, the results of the present study suggest that native bark beetle populations will not cause further tree mortality following such a disturbance in this region.

Keywords Bark beetle, brood material, disturbances, ice storm, *Ips pini*, outbreaks, *Pinus resinosa*, population dynamics, scolytid, tree mortality.

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Introduction

Bark beetles (Coleoptera: Scolytidae) colonize living, stressed, or recently dead trees, aiding in wood decomposition and nutrient recycling; thus, they play an important role in forest health. However, some species are highly damaging forest pests (Rudinsky, 1962) with extensive losses occurring when populations increase significantly from endemic levels. The factors involved in those shifts in population dynamics have been the focus of considerable research. Bark beetle population dynamics have been demonstrated to be influenced by weather, temperature, or climate (Kalkstein, 1976; Bentz *et al*., 1991; Hansen *et al*., 2001), intra- and interspecific competition (Beaver, 1974; Thomson & Sahota, 1981; Reeve *et al*., 1998; Wallin & Raffa, 2002), and predator-caused mortality (Riley & Goyer, 1986; Weslien, 1992; Reeve, 1997; Turchin *et al*., 1999; Aukema & Raffa, 2002). Host availability and susceptibility also plays a major role in the population dynamics of bark beetles (Berryman, 1976; Raffa & Berryman, 1983; Paine *et al*., 1984; Økland & Berryman, 2004), particularly for those less-aggressive species adapted to utilize stressed or weakened host trees. Increases in susceptible host material, such as following a disturbance, may lead to sudden, significant increases in associated scolytid populations.

Across eastern North America, ice or glaze storms are relatively common disturbance events that cause considerable damage and tree mortality to forests across the region (Lemon, 1961). Trees damaged by such storms are highly susceptible to secondary attacks by bark beetles (Gardiner, 1975; Futura *et al*., 1984; Barry *et al*., 1993; Schroeder & Eidmann, 1993; Reynolds & Holsten, 1994; Schroeder *et al*., 1999). In January 1998, a unusually severe ice storm throughout eastern United States and Canada caused extensive damage to numerous red pine, *Pinus resinosa* Ait., plantations across the region (Irland, 1998). The storm caused damage to red pine trees through up-rooting, blowing over, bending or completely breaking the stems (Ryall & Smith, 2005), creating a range of host material with varying levels of resistance to colonization by secondary bark and wood-boring beetles.

A major question that remains is whether healthy trees are also vulnerable to attack following a build-up of bark beetle populations in response to such large inputs of coarse woody debris. This vulnerability probably depends on the biology and behavioural characteristics of the bark beetle species in question. For example, additional tree mortality in healthy green trees after increases in beetle populations (Geiszler *et al*., 1984; Ravn, 1985; Christiansen *et al*., 1987; Klepzig *et al*., 1991; Schroeder & Lindelöw, 2002) may be associated with those species considered to be primary or more aggressive [e.g. *Ips typographus* (L.) Ravn, 1985; Schroeder & Lindelöw, 2002]. By contrast, studies that report that bark and wood-boring beetles are unable to cause additional tree mortality in healthy trees (Mason, 1969; Gardiner, 1975; Schroeder & Eidmann, 1993; Hanula *et al*., 2002) are often focused on scolytid species that are nonaggressive or more secondary in nature. However, the distinction between primary and secondary species is less than clear. In addition, many of these previous studies have failed to follow tree mortality and beetle populations beyond the first year or two after an event. Therefore, the likelihood of beetle outbreaks causing mortality in healthy pine trees following such a major storm event is unclear.

The pine engraver beetle, *I. pini* (Say), is a native, widespread species (Bright, 1976) that is common across the region affected by the 1998 ice storm and is the species most likely to pose a threat to damaged pine trees. Although this species usually infests dying or stressed trees for reproduction (Mason, 1969; Howse, 1995), it can cause considerable mortality of apparently healthy trees when populations are high (Kennedy, 1969; Schenk & Benjamin, 1969; Schmid, 1987; Miller & Borden, 1990; Klepzig *et al*., 1991; Gara *et al*., 1999). It is unclear what factors determine whether this species will cause tree mortality or not; thus, it is unknown whether *I. pini* will cause mortality in healthy trees in eastern Ontario.

The present study aimed to characterize the timing, pattern and volume of wood colonized by the scolytid *I. pini* in red pine plantations with and without ice storm damage for 4 years after the event. Based on the literature, it is predicted that damaged pine brood material will be rapidly and extensively colonized by this scolytid in the seasons following the ice storm. It is also predicted that mortality in healthy standing trees would occur in subsequent years as a result of the substantial build-up of beetle populations in the damaged plantations in response to the extremely large volume of coarse woody debris created by this unusually severe storm event.

Methods

The study area was located across eastern Ontario, Canada (45 °15′N, 75 °35′W). Sampling was conducted from 1998 to 2001 in six plantations similar in age (35–50 years), diameter at breast height (17–23 cm), and density (1000–1500 stems/ha). Plantations were pure red pine, *P. resinosa*, originally planted for erosion control on abandoned agricultural land, and all were of relatively flat terrain. Three plantations had considerable storm damage (approximately 200 ± 34 m^3 coarse woody debris, CWD/400 m^2) and three showed little or no damage (approximately 10 ± 4 m^3 CWD/400 m^2). Sites were selected in pairs across the study region (damaged and undamaged) with a minimum of 2 km between sites. In the damaged plantations, possible habitat for *I. pini* included snapped tops, standing snags, uprooted trees, blown-down trees and trees with varying degrees of crown loss (Table 1; Ryall & Smith, 2005).

Within each plantation, the volume of CWD of each type infested by beetles, along with the total volume available, was determined using a forest fire fuel-intersect method along a 200×2 m transect (Van Wagner, 1968). Transects were placed randomly through each site, providing an adequate representation of the level of damage in each stand. Transects were visited twice in 1998 (July and August) and then insect populations were monitored in August of 1999, 2000 and 2001 by recording the presence of new or fresh insect galleries, entrance holes, and emergence holes in different types of brood material (snapped-tops, snags, uprooted trees, etc.) along the transect in each plantation.

During each inspection, damaged material was carefully examined for signs of attack by bark and wood-boring

Table 1 Classification system used to measure the level of damage to pine trees following the January 1998 ice storm across eastern Ontario

Damage rating	Description of damage
0	No visible damage to crown
1	< 25% crown loss, typically only leader lost
2	25–50% crown loss
3	50–75% crown loss but with some green branches
4	Complete stem breakage below the crown
Snag	Standing portion of bole with no live crown remaining
Snap-top	Crown portion broken completely from bole, fallen to ground
Bent	Considerable arc in bole, often with crown touching ground
Up-root	Root system pulled out of soil and visible, tree lying on ground
Blow-down	Tree laying on ground but root system not visible above soil

beetles, such as entrance holes, exit holes, or boring sawdust. A preliminary subsample of approximately 60 *Ips* bark beetles was confirmed to be *I. pini* and it was expected that this species would be the most common *Ips* species encountered (D. Bright, pers. comm.). However, there is the possibility that small numbers of other *Ips* species occurring in the region (Bright, 1976) may have been included in subsequent samples. Other scolytids were encountered in very low numbers; therefore, sampling and analyses focused on only *I. pini*.

Beetle densities were measured in 1998 by excising two 20 × 30 cm pieces of bark from up to ten damaged trees or pieces of coarse woody debris encountered along the transect in each plantation; this included snapped tops, snags, blown-down and uprooted trees. Sampling of up to ten trees or CWD allowed for approximately 30% of the available habitat to be examined in the damaged stands. This sample was also used to measure the production of new beetle offspring during the first summer (July 1998). Although there is no specific sampling plan for this species, a similar number and size of samples was recommended for *Dendroctonus pseudotsugae* Hopkins, particularly when populations are expected to be low or high (Negrón *et al.*, 2000). Beetles were then monitored in 1999, 2000, and 2001 in each of the same six plantations using five red pine trap-logs (approximately 0.8 m in length). The trap-logs were cut and placed within each of the plantations during early May to allow for natural colonization. Logs were placed on the ground, a minimum of 20 m from the plantation edge and from any large gaps in the canopy. All logs were collected and returned to the laboratory before the new progeny emerged (usually collected in mid-July). Following emergence, a 20-cm wide strip of bark was dissected along the length of the top of each log to count the number of *I. pini* exit holes, *I. pini* galleries, which was then converted into no. per m^2 of bark surface area.

Within the damaged plantations, the percentage of various types of brood material (Table 1) colonized cumulatively by bark and wood-boring beetles was calculated for each year. Next, differences in *I. pini* gallery density and the number of offspring produced (from 1999 to 2001 when the same methodology was used) were each compared among years and between damaged and undamaged plantations, using repeated measures analysis of variance (ANOVA). Plantation type was the grouping factor (damaged or undamaged) using a mean value from the five trap-log subsamples for each plantation value. Finally, the number of colonized pieces per transect by the beetle was compared between years and plantation types using a repeated measures ANOVA. There were no significant damage – year interactions in the analysis; hence, these are not reported. Where assumptions of the ANOVA were not met, as indicated by the Huynh – Feldt correction, statistical results from the single degree of freedom polynomial contrasts were reported. Differences among years were contrasted with a *post hoc* Tukey's test. All analyses were conducted using SYSTAT Version 5.0 (SSI, California).

Results

In the first 4 years after the ice storm, *I. pini* colonized dead and dying trees in a specific pattern (Fig. 1a,b). Primarily snapped tops (snap top) were used as brood material in the first year, along with some standing trees without crowns (snags), trees with exposed root systems (uproot) and those

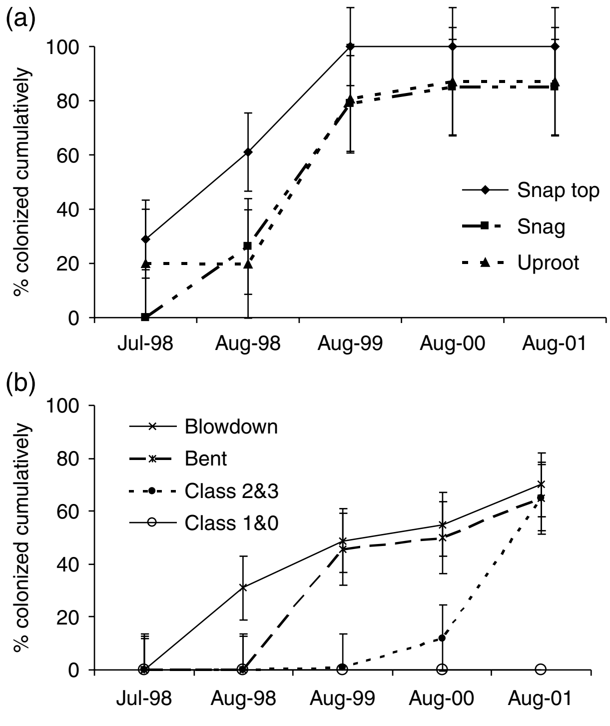

Figure 1 Cumulative pattern of colonization by *Ips pini* in (a) coarse woody debris (CWD) and (b) damaged trees in three damaged red pine (*Pinus resinosa*) plantations 4 years after the 1998 ice storm across eastern Ontario (damage classification is detailed in Table 1). Bars indicate standard error.

blown-down but with buried roots (blowdown) (Fig. 1a,b). In the second year (1999), beetles colonized the remainder of the snapped tops, most snags and uproots and almost half of the blown-down and bent trees. By the third year (2000), a small additional percentage of trees that were bent over (bent) or that had significant crown loss (classes 2 and 3 tree), were also used as brood material by the bark beetle. Colonization by beetles in the final year (2001) occurred primarily within the heavily damaged trees (classes 2–3 tree: > 50% crown loss) and a few additional blown-down or bent trees (Fig. 1b). No beetle activity was observed in standing trees with undamaged green crowns in any year (class 0–1 tree).

Based on the number of infested pieces of CWD in each 400 m^2 transect, there was no temporal change in colonization by *I. pini* after the storm in those plantations with low damage (undamaged) (Fig. 2). The number of pieces colonized was significantly higher in damaged than undamaged plantations ($F = 12.9$, d.f. = 1,4, $P = 0.02$). In the damaged plantations, *I. pini* rapidly colonized the abundant dead and dying wood in the first 2 years after the storm, but then populations dropped by > 65% in the third and fourth years, once the majority of nonresistant brood material had been used. Numbers of infested pieces differed significantly between years ($F = 8.3$, d.f. = 1,4, $P = 0.04$), with significantly higher numbers in the years 1 and 2 vs. 4 after the storm (1998–99 and 2001).

The density of *I. pini* galleries (n/m^2) in the trap-logs was similar between undamaged and damaged plantations ($F = 0.6$, d.f. = 1,4, $P = 0.48$), but differed significantly from year-to-year ($F = 16.9$, d.f. = 1,4, $P = 0.02$) (Fig. 3a). Gallery density in the third season (2000) was significantly lower than either 1999 or 2001, with no significant difference between 1999 and 2001. Offspring production (n exit holes/m^2) was also similar between undamaged and damaged plantations ($F = 2.9$, d.f. = 1,4, $P = 0.16$), but also varied considerably between each year ($F = 33.7$, d.f. = 1,4, $P < 0.0004$). Values were highest shortly after the storm (1999), dropped significantly (2000), and then began to recover (2001) (Fig. 3b).

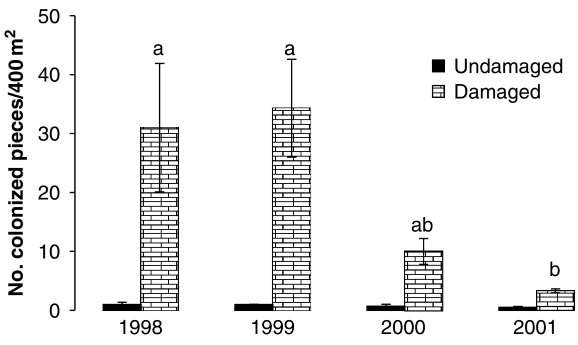

Figure 2 Amount of coarse woody debris (no. pieces is equivalent to the number of trees, snags or snapped tops) colonized by *Ips pini* 4 years after the 1998 ice storm along a 200 × 2 m transect in damaged and undamaged red pine plantations throughout eastern Ontario. (n = three undamaged and three damaged stands). Vertical bars indicate standard errors of means. Different letters above means indicate significant differences between years. Means are significantly higher in damaged compared with undamaged stands. Analyses based on two-way ANOVA with repeated measures.

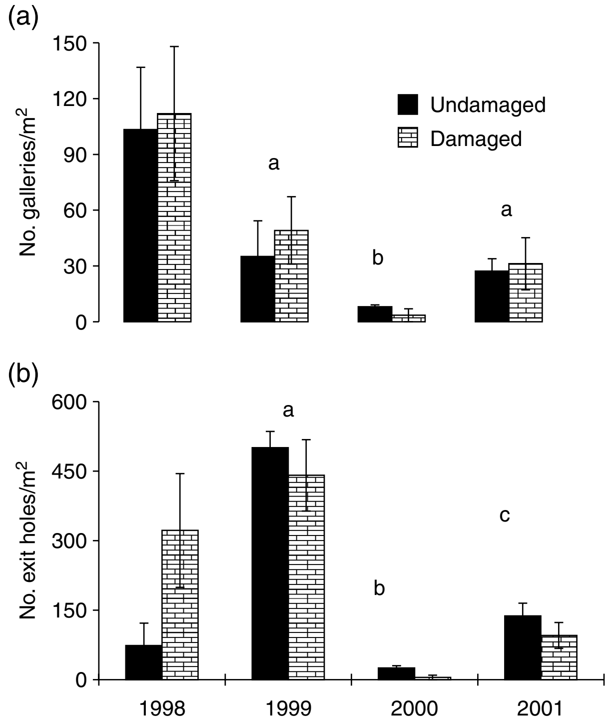

Figure 3 *Ips pini* (a) gallery density and (b) offspring production in coarse woody debris from undamaged and damaged red pine (*Pinus resinosa*) plantations 4 years after the 1998 ice storm in eastern Ontario (n = 5 trap-logs per site with six sites in total; three undamaged and three damaged stands). Vertical bars indicate standard errors. Bark samples were used in 1998 and trap-logs in 1999–2001. There was no significant difference between the two stand types. Different letters above means indicate significant differences between years using repeated measures ANOVA (1998 was not included in the analysis).

Discussion

The results of the present study demonstrate a pattern of sequential colonization of brood material apparently varying in resistance. *Ips pini* appeared to colonize damaged pine material after the ice storm according to the degree of damage to the tree's vascular system. Initially, beetles bred primarily in wood with little or no connected vascular system. Subsequently, they colonized damaged trees with disrupted systems (e.g. standing snags, blown-down trees, or uprooted trees with completely exposed broken roots), and only eventually utilized severely damaged trees with intact vascular systems. The results demonstrate that *I. pini* appears to be a relatively nonaggressive bark beetle in this region, attacking only recently dead or dying trees with little or no resistance (i.e. very disrupted vascular systems).

The overall temporal pattern of scolytid colonization following the 1998 ice storm is similar to that found in other studies, with colonization of snapped tops and snags initially (Gardiner, 1975; Schroeder & Eidmann, 1993; Schroeder *et al*., 1999). However, there was some inconsistency with respect to the timing and extent of colonization of certain types of CWD. In our study, *I. pini* was found in only 30% of standing snags by the end of the first year, increasing to 80% by the second year. Lower levels of colonization of high stumps over 2 years compared with other substrate types (snapped tops, uprooted trees) were reported by Göthlin *et al*. (2000). By contrast, Schroeder *et al*. (1999) found that 95% of mechanically created snags of Norway spruce were colonized during the first summer. Schroeder & Lindelöw (2002) found that the majority of wind-felled trees were colonized in the first season following the disturbance, whereas the results of the present study demonstrated that these trees were not largely colonized until several years following the storm. This discrepancy may be because other types of coarse woody debris were unavailable as brood material in these two previous studies. For example, in Schroeder *et al*. (1999), the 'tops' had been removed during the silvicultural operation, and thus, were unavailable for colonization. Timing of damage may also affect patterns of colonization. For example, less than 30% of snags cut in January were colonized in the spring by *Tomicus piniperda* compared with 70–100% colonization when snags were created the previous autumn (Sjödin *et al*., 1989). This could explain why larger numbers of snags were not colonized in the first year following the 1998 ice storm in the present study. Finally, there could be an interaction between the susceptibility of damaged material and its suitability for reproduction (Redmer *et al*., 2001). For example, although uprooted or blown-down trees were apparently not susceptible to attack by *I. pini* in the first year, it is possible they were no longer suitable for reproduction in subsequent years, which could explain why a lower percentage of them were colonized. Thus, the results of the present suggest that the vulnerability of damaged trees appears to be relative to the amount and type of alternative host material, as well as to the timing of damage.

The present study also clearly demonstrates the inability of *I. pini* to colonize healthy trees in this region, in agreement with previous studies. For example, Mason (1969) found that *I. pini* populations moved readily into thinned slash but did not attack living trees. Factors that may be of importance in determining whether mortality occurs in healthy trees may include typical weather patterns, prevailing weather conditions prior to or following a disturbance event, forestry practices, site quality, tree species, and other regulatory factors, such as natural enemies. For example, outbreaks in other regions appear to be related to ongoing improper slash management following thinning operations (Schenk & Benjamin, 1969; Gara *et al*., 1999) and also tend to be exacerbated by climatic conditions, such as drought (Kennedy, 1969; Berryman, 1982).

The availability of susceptible resources clearly plays a major role in the population dynamics of this bark beetle species. The results of the present study demonstrate that the bark beetle responded rapidly to the volume of available CWD, as shown by the lack of change in population density in the undamaged plantations. This supports previous research demonstrating that the abundance of scolytids is strongly related to the volume of coarse woody debris within a given stand (Berryman, 1973; DeMars *et al*., 1986; Garraway & Freeman, 1990; Vaisanen *et al*., 1993; Økland *et al*., 1996; Peltonen *et al*., 1998; Hindmarch & Reid, 2001). Populations dropped significantly in subsequent years as the availability of nonresistant host material declined.

The relationship between the density of *I. pini* at the tree- and stand-level remains unclear. Unexpectedly, we found that the density of *I. pini* galleries/log was the same irrespective of stand-level damage and, thus, availability of woody resources. By contrast, higher gallery densities were reported in epidemic than endemic populations (Amman, 1984) and in areas that had previous high levels of resources (Garraway & Freeman, 1990). In addition, Berryman (1973) found that beetles became highly aggregated as the available resources collapsed; however, in the present study, gallery densities appeared to decline along with declining resource availability. DeMars *et al*. (1986) also found that gallery density declined from one generation to the next in collapsing populations of the western pine beetle, *Dendroctonus brevicomis*, supporting the findings of the present study, particularly in the final 2 years. Other factors also likely influence temporal fluctuations in scolytid densities, including numerical responses by predators to changing prey populations. Increased predator populations in response to the high density of *I. pini* in damaged plantations may have contributed to the decline of *I. pini* populations in subsequent years (Erbilgin *et al*., 2002; Ryall, 2003) at the tree- and stand-level.

Overall, the results obatined in the present study demonstrate a rapid response by the scolytid, *I. pini*, to increasing resource levels. Based on the absence of mortality or colonization in healthy, undamaged red pine trees, the results also clearly demonstrate the lack of aggressiveness or tree-killing behaviour in these beetles in this region under such conditions. Salvage operations aiming to reduce losses due to beetle colonization need to be conducted as soon as possible following a disturbance event to minimize losses caused by the introduction of stain and decay fungi by the beetles. However, the results of the present study demonstrate that managers need not be concerned about the future health of undamaged trees.

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