



Factors influencing northern spruce engraver colonization of white spruce slash in interior Alaska[☆]

Christopher J. Fettig^{a,*}, Roger E. Burnside^b, Christopher J. Hayes^c, James J. Kruse^d, Nicholas J. Lisuzzo^d, Stephen R. McKelvey^a, Sylvia R. Mori^e, Stephen K. Nickel^f, Mark E. Schultz^g

^a Pacific Southwest Research Station, USDA Forest Service, 1731 Research Park Drive, Davis, CA 95618, USA

^b Forest Health Protection Program, State of Alaska, Department of Natural Resources, Division of Forestry, 550 West 7th Ave., Suite 1450, Anchorage, AK 99501, USA

^c Forest Health Protection, USDA Forest Service, 200 E. Broadway, Missoula, MT 59802, USA

^d Forest Health Protection, USDA Forest Service, 3700 Airport Way, Fairbanks, AK 99709, USA

^e Pacific Southwest Research Station, USDA Forest Service, P.O. Box 245, Berkeley, CA 94710, USA

^f Community Forestry Program, State of Alaska, Department of Natural Resources, Division of Forestry, 550 West 7th Ave., Suite 1450, Anchorage, AK 99501, USA

^g 9170 Parkwood Dr., Juneau, AK 99801, USA

ARTICLE INFO

Article history:

Received 16 August 2012

Received in revised form 24 September 2012

Accepted 27 September 2012

Keywords:

Fuels reduction
Forest restoration
Ips perturbatus
Picea glauca
Semiachemical
Slash management

ABSTRACT

In interior Alaska, increased use of mechanical fuel reduction treatments, increased interests in the use of wood energy systems as alternatives to fossil fuels, and elevated populations of northern spruce engraver, *Ips perturbatus* (Eichhoff), have raised concerns regarding the impact of this bark beetle to forest resources. We conducted a large-scale field study in 2009–2011 (Study 1) to determine the effects of slash scoring (mechanical by chainsaw versus none), slash distribution (scattered versus decked), and cutting date (spring versus fall) on *I. perturbatus* colonization of and reproductive performance in white spruce, *Picea glauca* (Moench) Voss, slash, and to determine the effects of resulting treatments on adjacent levels of tree mortality caused by *I. perturbatus*. Unfortunately, attack densities were lower than expected, and did not provide for a very robust examination of the effects of these treatments. As a result, we reproduced several aspects of Study 1 in a second study (2011) using a baited design. Higher levels of *I. perturbatus* attack and emergence occurred on dispersed logs. Attack densities were highest in the dispersed, unscored treatment, and ~70% higher than observed in the decked, scored treatment. The scoring of dispersed logs significantly reduced attack densities by ~28%, but had no effect in decked treatments or on levels of emergence in either treatment. Higher levels of attack and emergence were observed on the tops of logs as compared to the bottoms of logs. Brood production (i.e., defined here as emergence/attacks) was also greater on the tops of logs compared to the bottoms of logs, suggesting the tops of logs are not only more attractive to *I. perturbatus*, but confer some advantage to brood development. Lower levels of attack and emergence occurred on small diameter logs. Higher levels of attack and emergence were observed on logs in a shaded fuelbreak (i.e., a more open condition of lower tree density) compared to the adjacent forest. Overall, our research suggests that unlike other works on *Ips* spp. in the western USA that promote the desiccation of slash to minimize colonization and brood production, *I. perturbatus* appears regulated by the apparency and accessibility of host material. This finding highlights the importance of developing management guidelines based on local science. A third study found two semiochemicals, *trans*-conophthorin and verbenone, reduced colonization of slash by *I. perturbatus*, and therefore holds promise as a tool for managing *I. perturbatus* populations. The implications of these and other results to the management of *I. perturbatus* in interior Alaska are discussed.

Published by Elsevier B.V.

1. Introduction

The northern spruce engraver, *Ips perturbatus* (Eichhoff), is a notable bark beetle whose distribution generally coincides with

[☆] This article was written and prepared by U.S. Government employees on official time and it is, therefore, in the public domain and not subject to copyright.

* Corresponding author. Tel.: +1 530 758 5151; fax: +1 530 747 0241.

E-mail address: cfettig@fs.fed.us (C.J. Fettig).

that of its primary host, white spruce, *Picea glauca* (Moench) Voss. Other hosts include Engelmann spruce, *Picea engelmannii* Carr., Lutz spruce, *Picea x lutzii* Little, and in rare cases, black spruce, *Picea mariana* (Mill.) B.S.P., or Sitka spruce, *Picea sitchensis* (Bong.) Carr. *I. perturbatus* has been recorded from Alaska, Idaho, Maine, Michigan, Minnesota, Montana, and Washington, USA, and from nearly all of the Canadian provinces (Burnside et al., 2011). The lifecycle is presumably univoltine throughout its range (Watson, 1927; Holsten, 1998; Robertson, 2000), although early accounts

suggested that the adult stage may last up to 2 years in eastern Canada (Gobeil, 1936).

Adults primarily overwinter in forest litter beneath brood trees, and disperse short distances (Werner and Holsten, 1997) in search of fresh host materials soon after emergence in spring. Males produce an aggregation pheromone (ipsenol, ipsdienol and *cis*-verbenol) that attracts both males and females (Holsten et al., 2000). Galleries are initiated in the phloem by males, which are later joined by and mate with up to four females in a central nuptial chamber (Robertson, 2000). Larvae hatch from eggs in ~7–10 d and feed on phloem tissue developing into pupae in ~4–5 weeks. The pupal stage lasts ~10 d. The feeding activity of *I. perturbatus* damages and kills the phloem and outer xylem of live hosts, which may result in tree mortality depending on its distribution and intensity, among other factors. Adults carry a variety of ophiostomoid fungi (Alamouti et al., 2006), which may also have deleterious effects on tree health.

In most years, endemic populations of *I. perturbatus* infest forest debris, widely scattered individual trees or small groups of trees. However, natural (e.g., flooding, wildfire, and wind storms) and anthropogenic (e.g., road building, construction of utility rights-of-way, and logging) disturbances may produce large quantities of damaged, dead, or dying spruce that serve as ideal hosts for *I. perturbatus* (Burnside et al., 2011). If favorable climatic conditions coincide with large quantities of suitable host material, *I. perturbatus* populations may erupt and result in mortality of apparently-healthy trees over extensive areas (Holsten and Werner, 1987; Holsten, 1998). For example, in the 1950s an outbreak impacted >375,000 ha near Fort Yukon, Alaska. Spring drought conditions, as well as warming attributed to climate change, led to recent outbreaks of *I. perturbatus* on the Kenai Peninsula in south-central Alaska (Holsten, 1998; Graves et al., 2008). Outbreaks are typically associated with small diameter trees (<15 cm diameter at 1.37 m, dbh), and may impact timber and fiber production, water quality and quantity, fish and wildlife populations, recreation, real estate values, biodiversity, carbon storage, cultural resources and other resources. Stand structure and composition may be altered in dramatic ways (Burnside et al., 2011).

In interior Alaska, increased use of mechanical fuel reduction treatments to reduce the risk of wildfire to rural communities (Chapin et al., 2008); increased interest in the use of low-cost wood energy systems as alternatives to fossil fuels (Nicholls and Miles, 2009); and elevated levels of tree mortality attributed to *I. perturbatus* (Snyder et al., 2008) have resulted in an increased desire to develop suitable management techniques for *I. perturbatus*. Furthermore, mean temperature in interior Alaska is projected to increase by an additional 3–7 °C by the end of this century (Walsh et al., 2008) with only modest increases in precipitation (Hinzman et al., 2006) likely insufficient to offset increases in evapotranspiration. As a result, drought-stress in *P. glauca* is expected to become more common (Wolken et al., 2011) enhancing conditions favorable to *I. perturbatus* outbreaks, particularly along the northern limit of its distribution in interior Alaska (Chapin et al., 2006; McGuire et al., 2010). Burnside et al. (2011) reviewed strategies for reducing resource losses attributed to *I. perturbatus*. They identified the primary preventive method as thinning followed by proper slash management aimed at maintaining healthy stands with moderate growth rates. During outbreaks, insecticides may be used to protect individual trees (Werner, 1988), and a behavioral interruptant (*trans*-conophthorin and verbenone) has recently been discovered that was demonstrated effective for protecting individual *P. x lutzii* from mortality attributed to *I. perturbatus* in south-central Alaska (Graves et al., 2008).

In 2007, a preliminary survey of management options for minimizing *I. perturbatus* colonization of *P. glauca* slash was conducted in interior Alaska (Burnside and Kruse, 2009). Our research ex-

pands on knowledge gained during that work. The overall objective of our research was to develop guidelines for managing *P. glauca* slash to minimize *I. perturbatus* colonization, brood production, and associated levels of tree mortality in newly disturbed sites. The specific objectives were: (1) to determine the effects of slash scoring (mechanical by chainsaw versus none), slash distribution (scattered versus decked), and cutting date (spring versus fall) on *I. perturbatus* colonization of and reproductive performance in *P. glauca* slash; (2) to determine the effects of slash management treatments on adjacent levels of *I. perturbatus*-caused tree mortality; and (3) to determine if *trans*-conophthorin and verbenone inhibit *I. perturbatus* colonization of slash, and therefore hold promise as a tool for managing *I. perturbatus* populations.

2. Materials and methods

2.1. Study 1

2.1.1. Study sites

This study was conducted near Delta Junction (63.93°N, 145.62°W; 428 m mean elevation), Fairbanks (64.74°N, 148.63°W; 244 m mean elevation) and Tok (63.35°N, 142.99°W; 494 m mean elevation), Alaska, 2009–2011. The experimental design was a randomized complete block with three blocks (locations), nine treatments, and two replicates per treatment per block. Eighteen 0.1-ha square plots were established in each block in May (Tok and Fairbanks) and July (Delta Junction) 2009 in stands dominated by *P. glauca* (Table 1). Adjacent plots were separated by >100 m. Ground cover was dominated by moss, *Sphagnum* spp. (primarily *S. squarrosum* Crome), with mean ($\pm$ SEM) litter and duff depths (i.e., overwintering habitat of *I. perturbatus*) of 12.2 ± 0.9 to 18.0 ± 1.0 cm at Delta Junction and Fairbanks, respectively (Table 2).

2.1.2. Treatments

Treatments were randomly assigned to each plot in each block and included: (1) spring, decked, scored, (2) spring, decked, unscored, (3) spring, dispersed, scored, (4) spring, dispersed, unscored, (5) fall, decked, scored, (6) fall, decked, unscored, (7) fall, dispersed, scored, (8) fall, dispersed, unscored, and (9) an untreated control. Sixty 1.4-m logs with end diameters of 8.9–21.6 cm were cut from live *P. glauca* harvested on or immediately adjacent to each plot. This generally required 10–14 trees depending on tree size and height. Scoring was achieved by partial removal of the bark and phloem on two sides of the log with a chainsaw, and is a common management technique used to promote drying of slash presumably reducing host suitability (Burnside et al., 2011). Fifteen logs were stacked in four piles (decked) or randomly distributed in four groups (dispersed) (Fig. 1). Decks and dispersed groups were located 7.9 m from plot center in each

Table 1

Stand conditions within 0.1-ha experimental plots at three sites (blocks) in interior Alaska, USA, 2009–2011.

	Delta Junction	Fairbanks	Tok
Basal area (BA, m ² /ha)	35.7 $\pm$ 1.48	31.9 $\pm$ 1.56	21.9 $\pm$ 1.09
<i>Picea glauca</i> BA	28.9 $\pm$ 1.7	30.8 $\pm$ 1.6	20.9 $\pm$ 1.1
Trees/ha	1060 $\pm$ 88	619 $\pm$ 52	1194 $\pm$ 83
% <i>Picea glauca</i>	81.2 $\pm$ 3.7	96.5 $\pm$ 1.6	95.1 $\pm$ 1.2
% <i>Populus tremuloides</i>	3.3 $\pm$ 1.9	0	4.9 $\pm$ 1.6
% <i>Populus balsamifera</i>	9.8 $\pm$ 3.3	0	0
% <i>Betula papyrifera</i>	0.7 $\pm$ 0.5	3.5 $\pm$ 1.6	0
% <i>Picea mariana</i>	0.2 $\pm$ 0.1	0.03 $\pm$ 0.03	0
% <i>Alnus incana</i>	1.9 $\pm$ 0.3	0	0
% <i>Salix</i> sp.	2.9 $\pm$ 1.0	0	0

Values are mean $\pm$ SEM, n = 18 plots per block, all trees $\geq$ 8.9 cm dbh.

Table 2

Percent ground cover within 0.1-ha experimental plots at three sites (blocks) in interior Alaska, USA, 2009–2011.

	Delta Junction	Fairbanks	Tok
Moss	33.8 ± 3.3	44.5 ± 3.4	62.1 ± 4.0
Shrubs	12.5 ± 1.4	19.1 ± 2.5	18.1 ± 2.6
Litter	31.2 ± 4.0	14.2 ± 2.7	9.4 ± 1.5
Forbs	21.5 ± 2.6	18.5 ± 2.1	0.9 ± 0.3
Graminoids	1.0 ± 0.2	3.5 ± 1.4	3.0 ± 1.0
Lichen	0	0.2 ± 0.1	6.5 ± 1.4
Bare ground	0	0	0
Litter/duff depth (cm)	12.2 ± 0.9	18.0 ± 1.0	15.9 ± 0.9

Values are mean ± SEM, $n = 18$ plots per block.

cardinal direction. Each log was numbered, and the diameter at center was recorded. Top and bottom aspects were marked. Decks were photographed so that each log could be returned to its original position following sampling. Untreated controls were included to determine effects on overstory trees, and therefore no logs were placed on these plots. Treatments were implemented in September 2009 (fall) and May 2010 (spring), and therefore were subjected to the same population of *I. perturbatus*.



Fig. 1. Experimental logs in *Picea glauca* stands presented in one of four piles (decks) in a decked, unscored plot (top), and randomly distributed in four groups in a dispersed, scored plot (bottom), Delta Junction, Alaska, USA, 2010. Photos: R.E. Burnside, Alaska Department of Natural Resources.

2.1.3. Data collection and analyses

I. perturbatus attack and emergence holes were recorded on the bark surface of each log (960 logs × 3 blocks) in a 25.4-cm wide sampling (entire circumference) window at the center of each log. The center point of each log served as the center of the sampling window. Due to the large number of logs (2880) to be sampled, a preliminary analysis was conducted in 2009 (i.e., from data obtained during Study 3) that determined there was no difference in attack densities between samples obtained from the center and ends of logs, and therefore sampling was confined to the center of each log. The border of each window was marked with plastic zip ties, which were removed after the study was completed. In brief, attacks (i.e., piles of frass and entrance holes created by *I. perturbatus* burrowing into bark) and emergence holes (i.e., the holes created by offspring vacating logs) (Hayes et al., 2008) were recorded in July and September 2010, respectively. Attack and emergence holes were marked with different colors using paint pens to facilitate tally and quality control. Data were recorded for top and bottom aspects separately. Following sampling, logs were returned to their original positions with minimal disturbance. Logs were categorized into one of three diameter classes (<12.7 cm, 12.7–16.5 cm, >16.5 cm) based on measurements at log center to assess importance of log size. The amount of scoring (i.e., percentage of bark and phloem removed from each log) was estimated by placement of a 100-cm² grid, and later by ocular estimate alone. Colonization by other scolytids (e.g., spruce beetle, *Dendroctonus rufipennis* Hopkins) was recorded (data not presented).

A 100% cruise (census) was conducted on each experimental plot to locate trees attacked and killed by *I. perturbatus* or other agents. Cruises were initially conducted in May 2010 to capture any tree mortality that occurred before the study was implemented. Subsequent cruises were conducted in September 2010 and 2011. All recently-killed trees ≥8.9 cm dbh were tallied and the causal agent of mortality identified. Tree species, dbh, crown color, and colonizing bark beetle species were recorded.

An over-dispersed Poisson regression from the family of Generalized Linear Models (McCulloch and Searle, 2001) was used to model *I. perturbatus* attack and emergence densities. These responses were regressed on fixed effects: treatments (1) slash scoring (mechanical by chainsaw versus none) and (2) slash distribution (scattered versus decked), and aspect (top versus bottom) for each cutting date (spring versus fall). The counts were adjusted by the log surface area using logarithm of the surface area as an offset in the regression model. A block-treatment-aspect interaction and plot nested in block were added to the model as random effects to account for over-dispersion due to blocking effects. Since the three blocks (Delta Junction, Fairbanks and Tok) had very different attack and emergence densities (Figs. 2–4) their variance is not the same. Therefore, we assume that the variances are heteroscedastic. Contrasts of the treatments/aspects/cutting dates were used to test the hypotheses (using Likelihood Ratio test). When applicable, the Bonferroni's approach was used to achieve an experiment-wise error rate = 0.05. The SAS GLIMMIX procedure (SAS 9.3, Cary, North Carolina, USA) was used for the estimation of parameters and testing of contrasts.

2.2. Study 2

2.2.1. Study site

Unfortunately, attack densities during Study 1 were lower than we anticipated, and did not provide for a robust examination of the effects of treatments on *I. perturbatus* colonization and brood production. As a result, we reproduced several aspects of Study 1 on a smaller spatial scale using a baited design to help ensure substantial numbers of *I. perturbatus* attacks on experimental logs. Study 2 was conducted near Tok (63.35°N, 143.00°W; 496 m mean

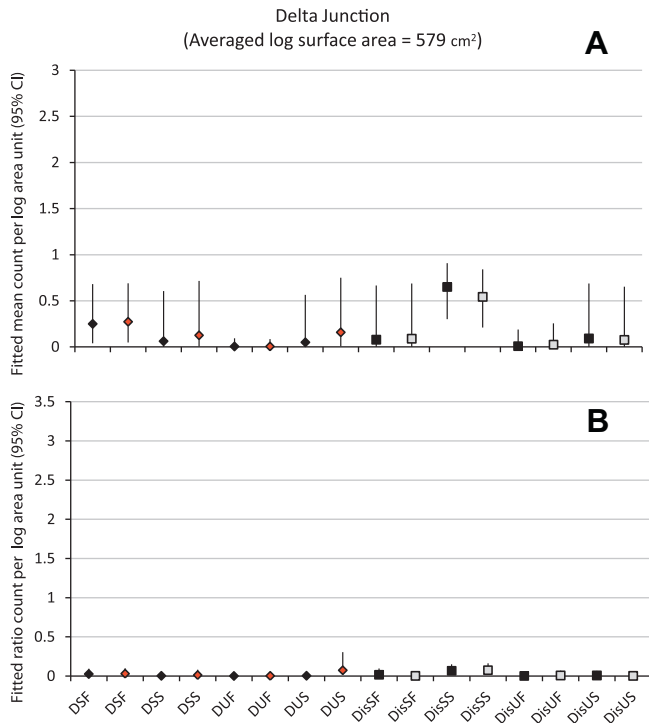


Fig. 2. Estimated count (95% CI) for a log mean with surface area equal to the block average of log surface areas at Delta Junction for *Ips perturbatus* (A) attacks and (B) emergence holes, 2010. DSS = decked, scored, spring; DUS = decked, unscored, spring; DSF = decked, scored, fall; DUF = decked, unscored, fall; DisSS = dispersed, scored, spring; DisUS = dispersed, unscored, spring; DisSF = dispersed, scored, fall; DisUF = dispersed, unscored, fall. Solid black points represent counts from the bottoms of logs.

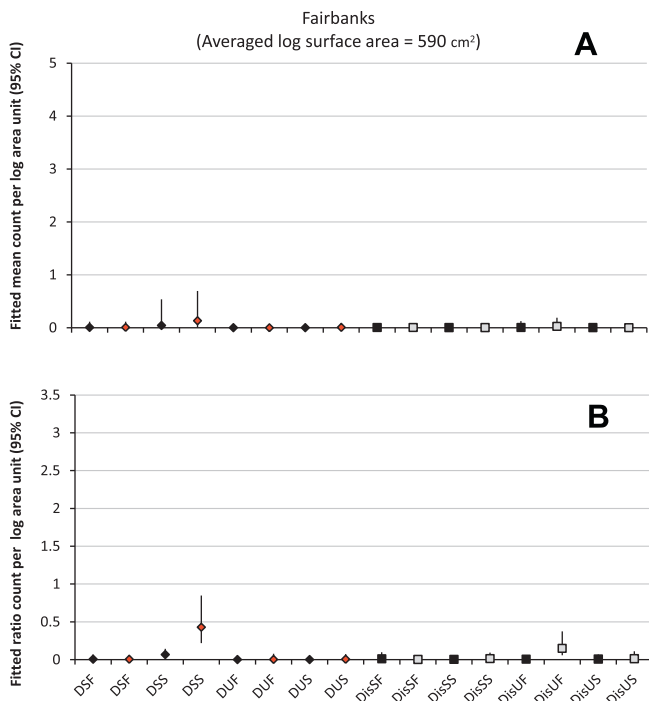


Fig. 3. Estimated count (95% CI) for a log mean with surface area equal to the block average of log surface areas at Fairbanks for *Ips perturbatus* (A) attacks and (B) emergence holes, 2010. DSS = decked, scored, spring; DUS = decked, unscored, spring; DSF = decked, scored, fall; DUF = decked, unscored, fall; DisSS = dispersed, scored, spring; DisUS = dispersed, unscored, spring; DisSF = dispersed, scored, fall; DisUF = dispersed, unscored, fall. Solid black points represent counts from the bottoms of logs.

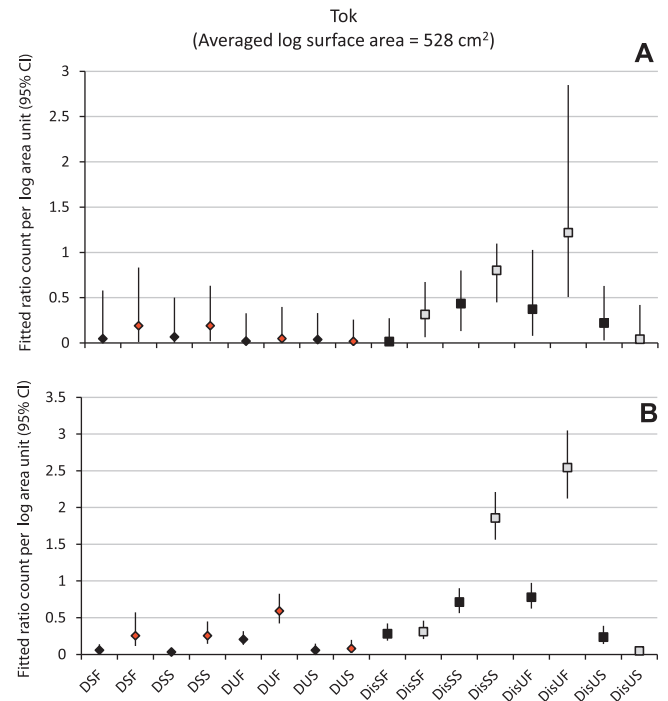


Fig. 4. Estimated count (95% CI) for a log mean with surface area equal to the block average of log surface areas at Tok for *Ips perturbatus* (A) attacks and (B) emergence holes, 2010. DSS = decked, scored, spring; DUS = decked, unscored, spring; DSF = decked, scored, fall; DUF = decked, unscored, fall; DisSS = dispersed, scored, spring; DisUS = dispersed, unscored, spring; DisSF = dispersed, scored, fall; DisUF = dispersed, unscored, fall. Solid black points represent counts from the bottoms of logs.

elevation), Alaska, in 2011 in close proximity (<1 km) to Study 1. Site selection was based on observations during Study 1 indicating higher populations of *I. perturbatus* occurred in this area. The experimental design was a randomized complete block with two blocks (forest and shaded fuelbreak), four treatments, and eight replicates per treatment per block. Thirty-two plots were established in both the shaded fuelbreak and adjacent forest in early May 2011 in stands dominated by *P. glauca* (Table 3). Adjacent plots were separated by >100 m. Plots were located in the shaded fuelbreak and forest >50 m from the interface (edge) between the shaded fuelbreak and forest. Ground cover was dominated by shrubs (species undetermined) in the shaded fuelbreak and by moss, *Sphagnum* spp. (primarily *S. squarrosum*), in the forest (Table 4). Mean ($\pm$ SEM) litter and duff depths were 6.6 ± 0.2 to 8.4 ± 0.1 cm in the shaded fuelbreak and forest, respectively (Table 4).

2.2.2. Treatments

Treatments were randomly assigned to each plot in each block and included: (1) decked, scored, (2) decked, unscored, (3) dispersed, scored, and (4) dispersed, unscored. Fifteen 1.4-m logs with

Table 3
Stand conditions at two sites (blocks) in Tok, Alaska, USA, 2011.

	Forest	Shaded fuel break
Basal area (BA, m ² /ha)	67.5 $\pm$ 1.0	16.0 $\pm$ 0.7
<i>Picea glauca</i> BA	63.5 $\pm$ 1.0	12.5 $\pm$ 0.6
Trees/ha	1256.3 $\pm$ 57.1	170.7 $\pm$ 27.6
% <i>Picea glauca</i>	94.1 $\pm$ 1.1	78.3 $\pm$ 5.4
% <i>Populus tremuloides</i>	5.9 $\pm$ 1.1	21.7 $\pm$ 5.4

Values are mean $\pm$ SEM, n = 32 plots per block, all trees ≥ 8.9 cm dbh.

end diameters of 8.9–21.6 cm were cut from live *P. glauca* harvested on or immediately adjacent to each plot (requiring ~2–4 trees), and decked or dispersed in early May 2011 as described in Study 1 (Fig. 1). Each log was numbered and the top and bottom aspects marked. Scoring was achieved by partial removal of the bark and phloem on two sides of the log with a chainsaw. One *I. perturbatus* lure (Alpha Scents Inc., Portland, Oregon, USA; Table 5) was attached to 0.9-m tall stakes and placed in the center of dispersed treatments or 1.5 m west (i.e., the direction of prevailing winds) of decked treatments.

2.2.3. Data collection and analyses

I. perturbatus flight was monitored by placement of one 16-unit multiple-funnel trap placed in the forest and shaded fuelbreak. Traps were hung with collection cups ~80–100 cm above the ground and baited with one *I. perturbatus* lure (Alpha Scents Inc.; Table 5) on 22 May 2011. One No-Pest Insect Strip (dichlorvos; Chemsico, Division of United Industries Corp., St. Louis, Missouri, USA) was placed in the collection cup to kill arriving insects, and to reduce damage or loss to predaceous insects. Samples were first collected 24 May 2011 and then about weekly thereafter. Catches were transported to the laboratory for storage and analysis. Specimens were tallied and identified using available keys (Wood, 1982) and voucher specimens. Temperature was collected every 10 min within each multiple-funnel trap (Optic StowAway®, Onset Computer Corp., Bourne, Massachusetts, USA).

I. perturbatus attack and emergence holes were recorded on the bark surface of each log (960) as described in Study 1. A two-way analysis of variance (treatment and block) was performed on attack and emergence densities using $\alpha = 0.05$ (SigmaStat Version 12.0, Systat Software, Inc., San Jose, California, USA). If a significant treatment effect was detected, Tukey's multiple comparison test (Tukey's HSD) was used for separation of treatment means.

2.3. Study 3

2.3.1. Study site

This study was conducted adjacent to Tok School (63.33°N, 142.99°W; 501 m mean elevation), Tok, Alaska, 2009. Site selection was based on the presence of ongoing fuel reduction and bioenergy projects in nearby areas that provided abundant *P. glauca* for use in the study. Furthermore, large piles of logs stored at Tok School for use in their wood-fired boiler system were colonized by *I. perturbatus* in 2008 (Hermanns, 2008), suggesting sufficient populations of *I. perturbatus* existed for successful execution of this study.

2.3.2. Treatments

Twenty decks consisting of fifteen 1.4-m logs with end diameters of 8.9–21.6 cm were cut from recently-felled *P. glauca* in mid-May 2009. The experimental design was completely randomized with two treatments and 10 replicates per treatment. Treatments included: (1) untreated control and (2) *trans-conophthorin*

and (–)-verbenone (Table 5). *trans-Conophthorin* was attached to an end of the top log of each deck, and (–)-verbenone was stapled to the center of the top log. In some cases, red squirrels, *Tamiasciurus hudsonicus* (Erxleben), had dislodged the verbenone pouch and buried it within the deck likely affecting release rates and treatment efficacy.

2.3.3. Data collection and analyses

I. perturbatus attack and emergence holes were recorded in July and August 2009, respectively, on the bark surface of each log (300) in three 15.2-cm wide sampling (entire circumference) windows located at the center of each log (as in Study 1 and 2), and 20.3 cm from the ends of each log. A *t*-test was performed on attack and emergence densities using $\alpha = 0.05$ (SigmaStat Version 12.0).

3. Results and discussion

3.1. Study 1

Robertson (2000) collected data from three mature *P. glauca* (30–35 cm dbh) felled near Edmonton, Alberta in mid-April, and reported trees were completely colonized by *I. perturbatus* by 1 June with no new gallery initiations occurring thereafter. In our study, several logs exhibited new attacks after 13 July (i.e., based on prior sampling date), although this was rare. Overall, few logs were attacked by *I. perturbatus* during this study. Fairbanks had the fewest with ~97% of logs exhibiting no attacks (mean number of attacks/m² ± SEM = 4.5 ± 1.1; range = 0–595.9). At Delta Junction, ~78% of logs had no attacks (mean number of attacks/m² ± SEM = 30.5 ± 2.7; range = 0–1087.3). Similarly, ~78% of logs exhibited no attacks at Tok (mean number of attacks/m² ± SEM = 38.7 ± 3.5; range = 0–969.9). Robertson (2000) reported a mean density (±SEM) of 217 ± 23 attacks/m². On standing, live *P. x lutzii*, Graves et al. (2008) reported that 400.5 attacks/m² resulted in ~60% of trees dying, whereas 1100.3 attacks/m² caused 100% tree mortality.

Overall, treatment (decked versus dispersed) and seasonality (spring versus fall) had no effect on levels of *I. perturbatus* attack and emergence (Tables 6 and 7). It is interesting to note that at Tok, dispersed treatments tended to have the largest fitted means (Fig. 4; see Study 2). The time of year slash is created has been demonstrated to effect colonization and brood production in related species (Sartwell, 1970; DeGomez et al., 2008). For example, early work by Buckhorn (1957) demonstrated that ponderosa pine, *Pinus ponderosa* Dougl. ex Laws., mortality caused by *Ips* spp. in Oregon was greatest when slash was generated between February and July. Conversely, the “safe period” for producing slash was August through December. During this time, host material is generally thought to decline in suitability over time as phloem moisture is reduced (Redmer et al., 2001). Burnside et al. (2011) reported slash produced after *I. perturbatus* flight, but not within 3 months of the next flight period, reduced the suitability of slash for *I. perturbatus* colonization and brood production. While such an effect was not demonstrated in our study, it warrants further investigation. Previous studies on the effects of timing of slash production on colonization and brood production by *Ips* spp. in the western USA have been conducted in warmer and drier climates (DeGomez et al., 2008). The cooler and wetter conditions indicative of forest floor conditions in interior Alaska may preserve the quality of slash, making it more suitable for colonization and brood production for longer periods, thereby making comparisons with research conducted in other regions tenuous. To that end, DeGomez et al. (2008) suggested that abiotic conditions at higher elevations in the southwestern USA (i.e., generally cooler and more

Table 4
Percent ground cover at two sites (blocks) in Tok, Alaska, USA, 2011.

	Forest	Shaded fuel break
Moss	66.7 ± 4.4	14.5 ± 3.2
Shrubs	11.0 ± 2.4	36.7 ± 5.1
Litter	12.0 ± 2.8	13.8 ± 3.2
Forbs	4.5 ± 0.9	2.2 ± 0.7
Graminoids	2.7 ± 1.0	31.2 ± 4.5
Lichen	3.1 ± 0.9	1.4 ± 0.6
Bare ground	0	0.2 ± 0.2
Litter/duff depth (cm)	8.4 ± 0.1	6.6 ± 0.2

Values are mean ± SEM, *n* = 32 plots per block.

Table 5

Semiachemicals used in studies 2 and 3, Tok, Alaska, USA.

Semiachemical	Source ^a	Purity (%)	Release device	Release rate (mg/d)
Attractant				
Ipsdienol	Alpha Scents	95	0.4-ml polyethylene vial	0.1 ^b
cis-Verbenol	Alpha Scents	97	Cellulose pad, 3 mil LDPE pouch	0.1 ^b
trans-Conophthorin [racemic]	Contech	87	2 × 250 µl Eppendorf vial	2.8 ^c
Verbenone [77%-(–)]	Contech	97	7-g Contech pouch	50.0 ^b

^a Alpha Scents = Alpha Scents Inc., Portland, Oregon, USA; Contech = Contech Enterprises Inc., Delta, British Columbia, Canada.^b Reported by manufacturer of release device and measured in the laboratory at 20 °C.^c Measured in our laboratory at 20 °C.**Table 6**Comparisons of *Ips perturbatus* attack densities on *Picea glauca* logs, Delta Junction, Fairbanks and Tok, Alaska, USA, 2010.

Ratio	Estimated ratio	95% Lower CI	95% Upper CI	P-value
Top/bottom, all treatments	1.38	0.95	2.01	0.088
Top/bottom, DSS ^a	2.01	1.19	3.41	0.011
Top/bottom, DUS	3.17	1.7	5.91	0.001
Top/bottom, DSF	1.09	0.67	1.78	0.720
Top/bottom, DUF	1.25	0.12	12.81	0.845
Top/bottom, DisSS	1.2	0.86	1.67	0.28
Top/bottom, DisUS	1.21	0.76	1.94	0.416
Top/bottom, DisSF	1.12	0.7	1.78	0.630
Top/bottom, DisUF	3.08	0.73	12.95	0.121
Dispersed/decked, top	1.83	0.49	6.91	0.358
Scored/unscored, top	3.33	0.88	12.53	0.074
Spring/fall, top	2.35	0.62	8.84	0.199
Dispersed/decked, bottom	2.27	0.6	8.64	0.221
Scored/unscored, bottom	4.43	1.16	16.86	0.030
Spring/fall, bottom	2.13	0.56	8.12	0.258
Dispersed/decked, whole log	2.04	0.57	7.32	0.264
Scored/unscored, whole log	3.84	1.07	13.78	0.040
Spring/fall, whole log	2.24	0.62	8.03	0.209

^a DSS = decked, scored, spring; DUS = decked, unscored, spring; DSF = decked, scored, fall; DUF = decked, unscored, fall; DisSS = dispersed, scored, spring; DisUS = dispersed, unscored, spring; DisSF = dispersed, scored, fall; DisUF = dispersed, unscored, fall.**Table 7**Comparisons of *Ips perturbatus* emergence hole densities on *Picea glauca* logs, Delta Junction, Fairbanks and Tok, Alaska, USA, 2010.

Ratio	Estimated ratio	95% Lower CI	95% Upper CI	P-value
Top/bottom, all treatments	2.01	1.01	3.99	0.048
Top/bottom, DSS ^a	5.95	0.98	36.02	0.052
Top/bottom, DUS	6.22	0.95	40.65	0.056
Top/bottom, DSF	1.41	0.25	8.04	0.693
Top/bottom, DUF	2.23	0.18	26.95	0.518
Top/bottom, DisSS	1.85	0.36	9.41	0.448
Top/bottom, DisUS	1.82	0.26	12.73	0.537
Top/bottom, DisSF	3.21	0.43	23.97	0.246
Top/bottom, DisUF	7.14	1.01	50.57	0.049
Dispersed/decked, top	1.15	0.23	5.76	0.857
Scored/unscored, top	2.25	0.45	11.22	0.312
Spring/fall, top	2.52	0.51	12.56	0.250
Dispersed/decked, bottom	2.32	0.44	12.23	0.311
Scored/unscored, bottom	4.13	0.78	21.77	0.092
Spring/fall, bottom	1.65	0.31	8.71	0.543
Dispersed/decked, whole log	1.42	0.32	6.24	0.635
Scored/unscored, whole log	3.05	0.69	13.43	0.136
Spring/fall, whole log	2.04	0.46	8.99	0.335

^a DSS = decked, scored, spring; DUS = decked, unscored, spring; DSF = decked, scored, fall; DUF = decked, unscored, fall; DisSS = dispersed, scored, spring; DisUS = dispersed, unscored, spring; DisSF = dispersed, scored, fall; DisUF = dispersed, unscored, fall.

mesic environments) may prolong the suitability of slash to colonization by the pine engraver, *Ips pini* (Say).

Higher attack densities occurred on scored logs (i.e., after adjusting for the amount of bark and phloem removed by scoring) compared to unscored logs, but scoring had no effect on emergence (Tables 6 and 7). Given the relatively low attack densities and presumably low levels of intraspecific competition, this suggests

scoring increased attraction of *I. perturbatus*, but had a negative impact on brood production. Similarly, a preliminary study conducted in interior Alaska in 2007 found scoring had a negative impact on *I. perturbatus* brood production beyond the physical reduction in habitat achieved through scoring (Burnside and Kruse, 2009). Werner (1993) showed that α -pinene was attractive to *I. perturbatus* in trapping assays. The oleoresin of *P. glauca*

contains 2–21% α -pinene (Wilkinson et al., 1971), and presumably large quantities are released immediately following scoring perhaps explaining the effect. Fettig et al. (2006) showed that elevated levels of bark beetle (several species) attack following chipping of logging residues in *P. ponderosa* forests were partially explained by increased quantities of β -pinene, 3-carene, α -pinene, and myrcene eluting from chips. Several bark beetle species are attracted to such volatiles, specifically in the presence of their aggregation pheromone components. *I. perturbatus* brood production was greater on the tops of logs compared to the bottoms of logs (Table 7), but attack densities did not differ between these locations (Table 6). Generally, *I. perturbatus* attacks are most heavily distributed on the upper and side surfaces of logs (Robertson, 2000).

Only one tree (29.2 cm dbh *P. glauca*) was found to be attacked and killed by *I. perturbatus* during this study, which is not surprising given the low attack densities observed overall. This tree occurred on a dispersed, fall, scored plot at Tok that had one of the highest levels of attack on experimental logs observed in Study 1 (mean number of attacks/m² $\pm$ SEM = 23.2 $\pm$ 9.9; ranked 14 of 48 plots overall).

3.2. Study 2

In south-central Alaska, Graves et al. (2008) defined the seasonal flight activity of *I. perturbatus* based on captures in pheromone-baited traps in *P. x lutzii* forests. Flight began in mid- to late-May and ended in early to mid-August, with peak flight occurring in early June. The flight periodicity of *I. perturbatus* in our study within the forest (Fig. 5) was surprisingly similar to that reported by Graves et al. (2008) despite substantial differences in the locations of these two studies. However, flight peaked in early July in the shaded fuelbreak (Fig. 5). Our traps were installed on 22 May 2011 and immediately caught substantial numbers of *I. perturbatus* suggesting that we had missed detection of initial flight. In 2009, flight activity began on 19 May at a nearby location (2.9 km SSE, +5 m elevation) based on captures in pheromone-baited traps (data not presented).

Higher levels of attack and emergence were observed on the tops of logs compared to the bottoms of logs (attacks, $df=62$, $t=4.8$, $P<0.001$; emergence, $df=62$, $t=5.8$, $P<0.001$) (Fig. 6), which agrees with previous reports (Robertson, 2000), but differs from results obtained in Study 1 where no difference was observed in attack density. Brood production (i.e., defined here as emergence/attacks on individual logs) was also greater on the tops of logs compared to the bottoms of logs (4.5 $\pm$ 0.3 versus 3.4 $\pm$ 0.3;

$df=1115$, $t=2.636$, $P=0.008$), suggesting the tops of logs are not only more attractive to *I. perturbatus* for colonization, but confer some advantage to their developing brood. We suspect this is primarily due to differences in microclimate, and levels of interspecific competition with *D. rufipennis*. The bottom of logs, specifically those located in areas with substantial *Sphagnum* capable of storing large quantities of water (Shetler et al., 2008), exist in a cooler and moister environment (e.g., Table 4, forest). On numerous occasions, we observed the bottoms of logs to be wet and colonized by decay fungi (species undetermined), and assume these conditions are disadvantageous to brood production. Furthermore, *D. rufipennis* most frequently colonized the bottoms of logs in our study (88% of observations, 294 logs) thereby increasing levels of interspecific competition on the bottom of logs, and likely impacting survivorship of both species. In other work, broods of *I. perturbatus* and *Dryocoetes affaber* (Mann.) were reported to be the most important factor affecting the mortality of *D. rufipennis* larvae in *P. glauca* (Whitmore, 1983). Robertson (2000) reported the mortality of *I. perturbatus* in logs was as high as 98% from egg to adult stages.

Lower levels of attack ($F_{2,954}=22.8$; $P<0.001$) and emergence ($F_{2,954}=34.4$; $P<0.001$) occurred on smaller diameter logs (Fig. 7). Slash size has been demonstrated to be important in regulating the reproductive performance of *Ips* spp. in other systems (DeGomez et al., 2008), and some authors have recommended removal or treatment of all slash >10 cm diameter (Parker, 1991). Steed and Wagner (2004) reported *I. pini* exhibited a preference for large diameter logs, but that diameter had no effect on reproductive performance, which agrees with data from a preliminary study conducted in interior Alaska for *I. perturbatus* (Burnside and Kruse, 2009). Hayes et al. (2008) reported similar attack densities for *I. pini* on small and large diameter logs in Arizona, but reproductive performance decreased in large diameter logs.

Higher levels of attack and emergence were observed on logs in the shaded fuelbreak compared to the forest (attacks, $df=62$, $t=-3.578$, $P<0.001$; emergence, $df=62$, $t=-8.410$, $P<0.001$) (Fig. 8). Villa-Castillo and Wagner (1996) evaluated the effects of light intensity on the behavior and performance of *I. pini* adults and brood in *P. ponderosa* stands in Arizona. The authors reported that logs exposed to high natural light intensity (i.e., low density stands) were attacked less frequently and had lower brood production than logs exposed to low or moderate light intensity. They explained these effects as potentially due to reduced phloem quality

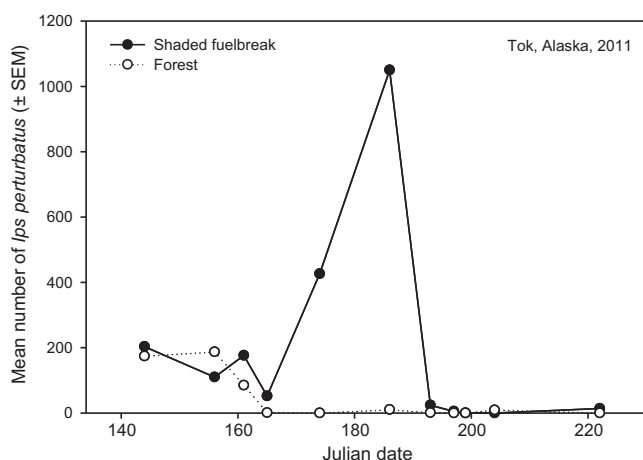


Fig. 5. Flight periodicity of *Ips perturbatus* based on captures in pheromone-baited traps, Tok, Alaska, USA, 2011.

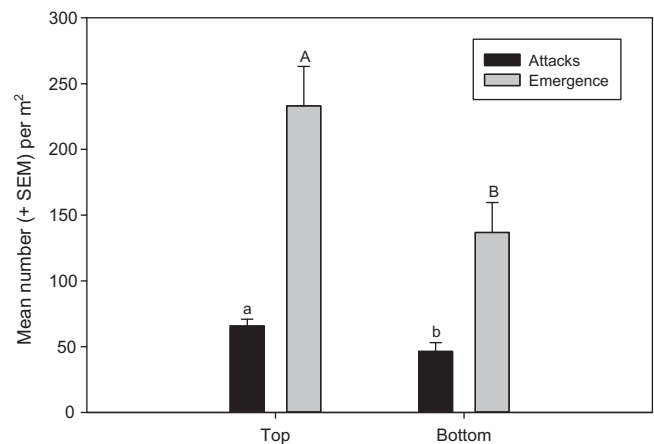


Fig. 6. Comparisons of *Ips perturbatus* attack and emergence hole densities on *Picea glauca* logs between the tops and bottoms of logs, Tok, Alaska, USA, 2011. Means ($\pm$ SEM) followed by the same letter within columns of the same color are not significantly different (t -test, $P>0.05$). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

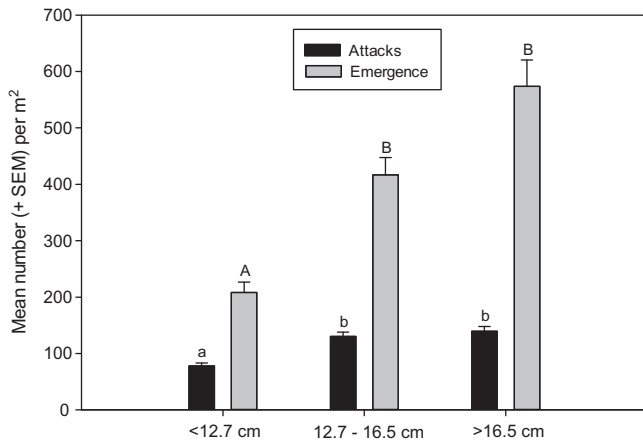


Fig. 7. Comparisons of *Ips perturbatus* attack and emergence hole densities on *Picea glauca* logs among diameter classes (measured at log center), Tok, Alaska, USA, 2011. Means (+SEM) followed by the same letter within columns of the same color are not significantly different (Tukey's HSD, $P > 0.05$). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

and host finding ability due to changes in microclimate (i.e., increased wind speed). Hayes et al. (2009) in a similar study of the effects of light intensity on the performance of *I. pini* brood in *P. ponderosa* logs in Arizona found high natural light exposure caused phloem heating high enough to cause brood mortality on the tops of logs. In a study conducted in Alberta, Hindmarch and Reid (2001a) reported male *I. pini* within felled trees attracted more females in thinned than unthinned lodgepole pine, *Pinus contorta* Dougl. ex Loud., stands, and that females in thinned stands extended their egg galleries farther, laid more eggs, and had higher egg densities than in unthinned stands. Differences in the results of these studies may be attributed to abiotic conditions. More specifically, the Alberta study was conducted in a northern location where higher temperatures resulting from increased solarization following thinning may have been advantageous to beetle mating and brood production. This condition is likely more analogous to that of interior Alaska. Furthermore, in our study, temperatures were warmer in the shaded fuelbreak than the adjacent forest (mean temperature $\pm$ SEM = 13.2 ± 0.1 and 12.6 ± 0.1 °C, 17 May–12 September 2011; range = -3.4 to 38.2 °C and -3.0 to

36.8 °C for the shaded fuelbreak and forest, respectively), likely affecting several aspects of the ecology of *I. perturbatus* (e.g., activity levels, flight periodicity, pheromone plumes, and survivorship) important to host colonization and brood production. In addition, several studies have found differences in the numbers of bark beetles, including *Ips* spp., collected under closed canopy forests compared to more open habitats (Beckwith, 1972; Hindmarch and Reid, 2001b; Werner, 2002; Dodds, 2011). For example, Beckwith (1972) examined the response of *Ips* spp. to window traps baited with fresh *P. glauca* in south-central Alaska, and reported higher numbers were collected in open as compared to forested conditions. We observed a similar trend as more *I. perturbatus* were collected in the pheromone-baited trap used to monitor flight periodicity in the shaded fuelbreak than in the adjacent forest (2060 versus 467). Discrepancy in trap catches could represent true differences in the abundance of beetles or simply differences in trap efficiency (or apparency) due to environmental conditions. Werner and Holsten (1997) collected *I. perturbatus* in late May in pheromone-baited traps and then marked the beetles with fluorescent powder releasing them from a small stadium 1.2 m above ground level. Most *I. perturbatus* were recaptured within 30 m of the release point, suggesting that trap catches may be indicative of localized population levels.

Treatment had a significant effect on levels of *I. perturbatus* attack ($F_{3,56} = 34.7$; $P < 0.001$) and emergence ($F_{3,56} = 21.2$; $P < 0.001$), which differs from Study 1 presumably due to elevated attack densities. Significantly higher levels of attacks and emergence occurred on dispersed logs (Fig. 9). Attack densities were highest in the dispersed, unscored treatment, and $\sim 70\%$ higher than observed in the decked, scored treatment. The scoring of dispersed logs significantly reduced attack densities by $\sim 28\%$, but had no effect in decked treatments (Fig. 9) or on levels of emergence in either treatment (Fig. 9). Further analyses found the effect of scoring on attack densities was limited to the top of dispersed logs (108.7 ± 8.5 and 76.0 ± 9.0 for top and bottom, respectively; $P < 0.001$). While scoring likely results in release of additional monoterpenes that may be attractive to *I. perturbatus* (see above, Study 1), the effect of scoring on attack densities in this study differs from that in Study 1. This may be an artifact of differences in population density between these studies (i.e., densities in dispersed treatments were >10 -fold higher in Study 2). For example, high attack densities likely resulted in elevated production of *I. perturbatus* aggregation pheromone components, presumably masking any subtle effects of

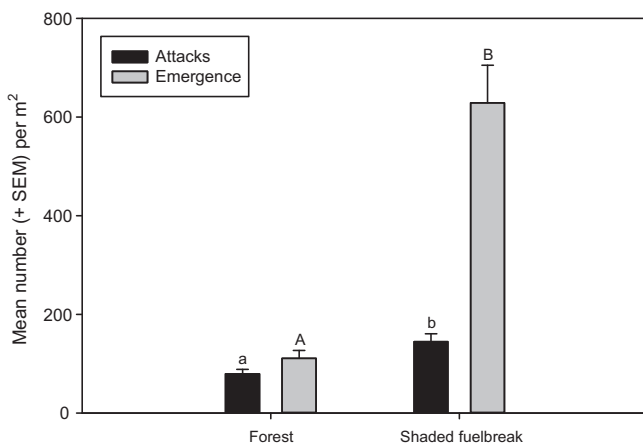


Fig. 8. Comparisons of *Ips perturbatus* attack and emergence hole densities on *Picea glauca* logs between forest and shaded fuelbreak conditions, Tok, Alaska, USA, 2011. Means (+SEM) followed by the same letter within columns of the same color are not significantly different (t -test, $P > 0.05$). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

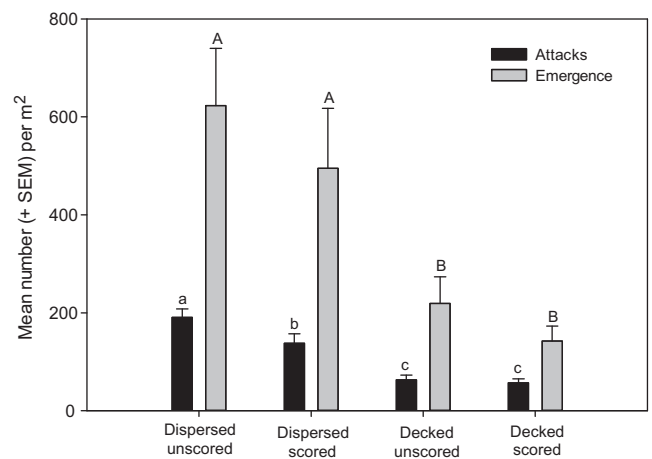


Fig. 9. Comparisons of *Ips perturbatus* attack and emergence hole densities on *Picea glauca* logs among treatments, Tok, Alaska, USA, 2011. Means (+SEM) followed by the same letter within columns of the same color are not significantly different (Tukey's HSD, $P > 0.05$). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

elevated levels of α -pinene (see Study 1) on *I. perturbatus* attraction due to scoring. Given the limited attack densities observed during Study 1, we feel the results obtained during Study 2 are more indicative of what might be expected under epidemic conditions. There was no significant treatment $\times$ block interaction for either variable (attacks, $F_{3,56} = 1.2$; $P = 0.32$; emergence, $F_{3,56} = 1.7$; $P = 0.17$), indicating treatments had similar effects regardless of forest condition.

3.3. Study 3

Higher levels of attack ($df = 18$, $t = 3.85$, $P = 0.001$) and emergence ($df = 18$, $t = -3.92$, $P < 0.001$) occurred on the untreated control compared to decks treated with *trans*-conophthorin and (–)-verbenone (Fig. 10). Verbenone is produced by both sexes of *I. perturbatus* (Holsten et al., 2000), and interrupts the response of *I. perturbatus* to attractant-baited traps (Holsten et al., 2001). Graves et al. (2008) found *trans*-conophthorin and (–)-verbenone were effective for reducing the number of *I. perturbatus* attacks and level of tree mortality attributed to *I. perturbatus* on individual *P. x lutzii* in south-central Alaska. Verbenone is an antiaggregation pheromone of several notable bark beetles (Gillette and Munson, 2009), and is produced by auto-oxidation of the host monoterpene α -pinene via the intermediary compounds *cis*- and *trans*-verbenol (Hunt et al., 1989), by the beetles themselves (Byers et al., 1984), and/or through degradation of host material by microorganisms associated with bark beetles (Leufvén et al., 1984). It is assumed that verbenone reduces competition by altering adult behavior to minimize overcrowding of developing brood within the host (Byers et al., 1984). Lindgren et al. (1996) proposed that verbenone is an indicator of host tissue quality and that its quantity is a function of microbial degradation.

Conophthorin is an anti-aggregation pheromone of the cone beetles *Conophthorus coniperda* (Schwarz) and *Conophthorus resinosae* Hopkins, and several other bark beetles (Pierce et al., 1995; Birgersson et al., 1995; Dallara et al., 2000), but is found in a number of angiosperms (Byers et al., 1998; Huber et al., 1999; Zhang et al., 2000, 2001; Shepherd et al., 2007) including *Populus tremuloides*, a species represented in our studies (Tables 1 and 3). Conophthorin is known to be antennally-active to some bark beetles (Zhang and Schlyter, 2004), and has been demonstrated to disrupt positive chemotactic responses in several bark beetles species (Huber et al., 1999, 2001; Zhang et al., 2001; Zhang and Schlyter, 2004). Conoph-

thorin is also an attractant produced by *Pityophthorus* spp. (Dallara et al., 2000).

Recent efforts to more fully explore the olfactory environment of forests have led to the use of systems-level concepts in the development of semiochemical-based tools and tactics for tree protection (Shepherd et al., 2007). The diverse mixture of tree species encountered by most bark beetles during foraging, combined with the high biological costs associated with landing on unsuitable hosts and nonhosts, suggests that bark beetles should be able to discriminate among olfactory cues in order to locate suitable hosts and associated habitats (Shepherd et al., 2007). Based on the semiochemical-diversity hypothesis (Zhang and Schlyter, 2004), this seems critical for species like *I. perturbatus* that have narrow host ranges (i.e., a few species in *Picea*) and often forage in mixed forests and/or on downed material (e.g., slash) that might be shrouded in other vegetation. We assume the effectiveness of this inhibitory blend (Fig. 10) is mediated through several pathways, including perceived increases by *I. perturbatus* in intraspecific (verbenone) and interspecific competition (verbenone and conophthorin); and perceived reductions by *I. perturbatus* in host availability (conophthorin) and host suitability (verbenone).

Unlike verbenone, conophthorin is not yet registered by the U.S. Environmental Protection Agency for control of bark beetles in forests. Furthermore, the synthesis of conophthorin is expensive and sufficient quantities for large-scale projects are difficult to procure (Fettig et al., 2005). Study 3 expands on earlier work by Graves et al. (2008) and provides evidence that *trans*-conophthorin and (–)-verbenone is effective for reducing colonization of *P. glauca* slash, and may have utility as a semiochemical-based tool when other options (e.g., use of insecticides) are not feasible.

4. Conclusions

Resource managers are challenged to manage forests in a sustainable manner and for a variety of uses that require knowledge about the resiliency of these systems to natural and anthropogenic disturbances. While *I. perturbatus* is recognized as an important tree-killing bark beetle in boreal and sub-boreal forests of North America (Burnside et al., 2011), its pest status will likely increase due to climate change, particularly along the northern limit of its distribution, highlighting the need for effective management. Most previous efforts that focused on providing guidelines for managing slash and other forest residues to minimize *Ips* colonization and brood production have been conducted with other *Ips* spp. In these cases, recommendations consistently advise generating slash during periods of adult bark beetle inactivity; limiting the size of harvested blocks; separating slash production in time and space; limiting the size and length of slash; avoiding piling of logs or slash against residual host trees; and treating infested slash through solarization, burning, direct removal or other treatments (DeGomez et al., 2008). While many of these recommendations are of relevance to the management of *I. perturbatus* in interior Alaska (Burnside et al., 2011), others are not. For example, other studies have shown that fewer *Ips* attacks occur on logs in more open areas or when exposed to high levels of sunlight (e.g., Hayes et al., 2008, 2009 for *I. pini*), but we found *I. perturbatus* colonization and brood production to be higher in the more open conditions (Table 3) of the shaded fuelbreak (Fig. 8). In addition, others (e.g., Hayes et al., 2009) have reported *Ips* attacks to be concentrated on the bottoms of logs particularly when exposed to high levels of sunlight, which disagrees with our results as higher levels of attack and emergence were observed on the tops of logs (Fig. 6). While the impacts of drying on the suitability of slash have been well demonstrated for other *Ips* spp. (Livingston, 1979; Villa-Castillo and Wagner, 1996; DeGomez et al., 2008; Hayes et al., 2008), *I. perturbatus* colonization and brood

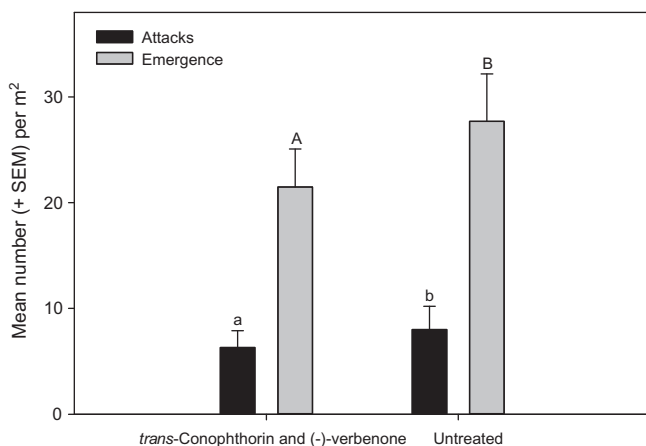


Fig. 10. Comparisons of *Ips perturbatus* attack and emergence hole densities on *Picea glauca* logs between treated and untreated decks, Tok, Alaska, USA, 2009. Means (+SEM) followed by the same letter within columns of the same color are not significantly different (t -test, $P > 0.05$). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

production seem regulated more by the apparency and accessibility of hosts in interior Alaska, at least during the initial 9–10 months following production of host material. This is supported by our results documenting increases in attack and emergence densities on the tops of logs (Table 7, Fig. 6) and in the shaded fuelbreak (Fig. 8); and the limited impact of scoring (Tables 6 and 7, Fig. 9). Under high population levels (Study 2) scoring of dispersed logs significantly reduced attack densities, but had no effect in decked treatments or on levels of emergence in either treatment (Fig. 8). During low population levels (Study 1), higher attack densities occurred on scored logs, but again scoring, which is assumed to promote the desiccation of slash, had no effect on brood production. Finally, the most effective and efficient method of storing slash to minimize *I. perturbatus* colonization and brood production was the decked, unscored treatment (i.e., this treatment did not differ significantly from decked, scored; Fig. 9). In decked treatments, the apparency and accessibility of logs in the middle of decks are reduced.

Wood is an important energy source in Alaska, particularly in rural communities of the Interior where fossil fuel costs are very high (Nicholls and Miles, 2009). Furthermore, management of fuel loads in the wildland urban interface is critical for human safety and protection of infrastructure in interior Alaska, but concerns abound about the proper storage of harvested material prior to use as fuelwood or incorporation into wood energy systems (J. Hermanns, pers. comm.). Our research reaffirms concerns about applying results obtained from studies conducted elsewhere (e.g., the western USA) to understudied areas like the boreal forests of interior Alaska, and highlights the need for local science to guide management activities. Based on our studies we offer the following suggestions concerning the management of slash to minimize *I. perturbatus* colonization and brood production in *P. glauca*: (1) logs <12.7 cm in diameter are less attractive and produce less brood, and therefore represent less of a concern to the residual stand than larger diameter material, (2) scoring of logs is ineffective for reducing brood production, and is likely not justified despite previous reports, (3) logs should be stored in areas of forest condition with limited sunlight, but not against residual host trees, and (4) logs should be stored in a manner similar to the decked, unscored treatment. While decking of logs is laborious, the technique is commonly used in rural communities throughout interior Alaska. Finally, *trans*-conophthorin and (–)-verbenone are effective for inhibiting *I. perturbatus* attacks on decked, unscored logs, and may be useful for reducing host colonization during localized outbreaks. However, the efficacy of these compounds has not been examined for larger-scale applications.

Acknowledgements

We thank J. Hermanns and J. Douse (Alaska Department of Natural Resources), and D. Rees (Colorado State University) for providing access to study locations. We thank D. Cluck, C. Dabney and C. Frank (USDA Forest Service), M. Sprau and E. Osborne (U.S. Army), W. Upton (Texas Forest Service) and D. Rees for technical assistance. We thank A. Graves, S. Patterson and S. Seybold (USDA Forest Service), and R. Ott (RAO Ecological Consulting) for helpful insights. A special thanks to C. Dabney (USDA Forest Service) for his critique, which improved an earlier version of this manuscript. This work was supported, in part, by a USDA Forest Service Special Technology Development Program grant (R10-2009-01) to R.E.B., C.J.F., M.E.S., C.J.H., J.J.K., and J. Lundquist (USDA Forest Service), a U.S. President's Early Career Award for Scientists and Engineers to C.J.F., Alaska Department of Natural Resources, Forest Health Protection (USDA Forest Service), and the Pacific Southwest Research Station (USDA Forest Service).

References

- Alamouti, S.M., Kim, J.J., Breuil, C., 2006. A new *Leptographium* species associated with the northern spruce engraver, *Ips perturbatus*, in western Canada. *Mycologia* 98, 149–160.
- Beckwith, R.C., 1972. Scolytid flight in white spruce stands in Alaska. *Can. Entomol.* 104, 1977–1983.
- Birgersson, G., Debarr, G.L., De Groot, P., Dalusky, M.J., Pierce Jr., H.D., Borden, J.H., Meyer, H., Francke, W., Espelie, K.E., Berisford, C.W., 1995. Pheromones in white pine cone beetle, *Conophthorus coniperda* (Schwarz) (Coleoptera: Scolytidae). *J. Chem. Ecol.* 21, 143–167.
- Buckhorn, W.J., 1957. Scheduling of Cutting or Thinning Operations in Immature Stands of Ponderosa Pine to Minimize Damage by the Oregon Pine Ips. PNW-RN-142. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR, 2 pp.
- Burnside, R.E., Kruse, J.J., 2009. Management of White Spruce Slash to Minimize Infestation by the Northern Spruce Engraver Beetle (*Ips perturbatus*) in Interior Alaska. Grant 39986 – Progress and Final Report, 13 pp.
- Burnside, R.E., Holsten, E.H., Fettig, C.J., Kruse, J.J., Schultz, M.E., Hayes, C.J., Graves, A.D., Seybold, S.J., 2011. The Northern Spruce Engraver, *Ips perturbatus*, FIDL 180. U.S. Department of Agriculture, Forest Service, Pacific Northwest Region, Portland, OR, 12 pp.
- Byers, J.A., Wood, D.L., Craig, J., Hendry, L.B., 1984. Attractive and inhibitory pheromones produced in the bark beetle, *Dendroctonus brevicomis*, during host colonization: regulation of inter- and intraspecific competition. *J. Chem. Ecol.* 10, 861–877.
- Byers, J.A., Zhang, Q.-H., Schlyter, G., 1998. Volatiles from nonhost birch trees inhibit pheromone response in spruce bark beetles. *Naturwissenschaften* 85, 557–561.
- Chapin III, F.S., McGuire, D., Ruess, R.W., Walker, M.W., Boone, R.D., Edwards, M.E., Finney, B.P., Hinzman, L.D., Jones, J.B., Juday, G.P., Kasischke, E.S., Kielland, K., Lloyd, A.H., Oswood, M.W., Ping, C., Romanovsky, V.E., Schimel, J.P., Sparrow, E.B., Sveinbjörnsson, B., Valentine, D.W., Van Cleave, K., Verbyla, D.L., Viereck, L.A., Werner, R.A., Wurtz, T.L., Yarie, J., 2006. Summary and synthesis: past and future changes in the Alaskan boreal forest. In: *Alaska's Changing Boreal Forest*, pp. 332–338.
- Chapin III, F.S., Trainor, S.F., Huntington, O., Lovcraft, A.M., Zavaleta, E., Natcher, D.C., McGuire, A.D., Nelson, J.L., Ray, L., Calef, M., Fresco, N., Huntington, H., Rupp, T.S., DeWilde, L., Naylor, R.L., 2008. Increasing wildfire in Alaska's boreal forest: pathways to potential solutions of a wicked problem. *Bioscience* 58, 531–540.
- Dallara, P.L., Seybold, S.J., Meyer, H., Tolasch, T., Francke, W., Wood, D.L., 2000. Semiochemicals from three species of *Pityophthorus* (Coleoptera: Scolytidae): identification and field response. *Can. Entomol.* 132, 889–906.
- DeGomez, T., Fettig, C.J., McMillin, J.D., Anhold, J.A., Hayes, C., 2008. Managing Slash to Minimize Colonization of Residual Leave Trees by *Ips* and Other Bark Beetle Species Following Thinning in Southwestern Ponderosa Pine, AZ1448. University of Arizona, College of Agriculture and Life Sciences, Tucson, AZ, 21 pp.
- Dodds, K.J., 2011. Effects of habitat type and trap placement on captures of bark (Coleoptera: Scolytidae) and longhorned (Coleoptera: Cerambycidae) beetles in semiochemical-baited traps. *J. Econ. Entomol.* 104, 879–888.
- Fettig, C.J., McKelvey, S.R., Huber, D.P.W., 2005. Nonhost angiosperm volatiles and verbenone disrupt response of western pine beetle, *Dendroctonus brevicomis* (Coleoptera: Scolytidae), to attractant-baited traps. *J. Econ. Entomol.* 98, 2041–2048.
- Fettig, C.J., McMillin, J.D., Anhold, J.A., Hamud, S.M., Borys, R.R., Dabney, C.P., Seybold, S.J., 2006. The effects of mechanical fuel reduction treatments on the activity of bark beetles (Coleoptera: Scolytidae) infesting ponderosa pine. *For. Ecol. Manage.* 230, 55–68.
- Gillette, N.E., Munson, A.S., 2009. Semiochemical sabotage: behavioral chemicals for protection of western conifers from bark beetles. In: *The Western Bark Beetle Research Group: A unique collaboration with Forest Health Protection, Proceedings of a Symposium at the 2007 Society of American Foresters Conference, October 23–28, 2007, Portland, Oregon. PNW-GTR-784*. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR, pp. 85–110.
- Gobeil, A.R., 1936. The biology of *Ips perturbatus* Eichhoff. *Can. J. Res.* 14, 181–204.
- Graves, A.D., Holsten, E.H., Ascerno, M.E., Zogas, K.P., Hard, J.S., Huber, D.P.W., Blanchette, R.A., Seybold, S.J., 2008. Protection of spruce from colonization by the bark beetle, *Ips perturbatus*, in Alaska. *For. Ecol. Manage.* 256, 1825–1839.
- Hayes, C.J., DeGomez, T.E., McMillin, J.D., Anhold, J.A., Hoffstetter, R.W., 2008. Factors influencing pine engraver (*Ips pini* Say) colonization of ponderosa pine (*Pinus ponderosa* Dougl. ex. Laws.) slash in northern Arizona. *For. Ecol. Manage.* 255, 3541–3548.
- Hayes, C.J., Hoffstetter, R.W., DeGomez, T.E., Wagner, M.R., 2009. Effects of sunlight and log size on pine engraver (Coleoptera: Curculionidae) reproduction in ponderosa pine slash in Northern Arizona, U.S.A. *Agric. For. Entomol.* 11, 341–350.
- Hermanns, J. 2008. Hazard Fuel Reduction and Bio-energy Projects Coexist in the Community of Tok. Alaska Department of Natural Resources, 3 pp. <<http://www.forestry.alaska.gov/pdfs/08TokFireMitigationSchoolProject.pdf>> (accessed 26.05.12).
- Hindmarch, T.D., Reid, M.L., 2001a. Forest thinning affects reproduction in pine engravers (Coleoptera: Scolytidae) breeding in felled lodgepole pine trees. *Environ. Entomol.* 30, 919–924.

- Hindmarch, T.D., Reid, M.L., 2001b. Thinning of mature lodgepole pine stands increases scolytid bark beetle abundance and diversity. *Can. J. For. Res.* 31, 1502–1512.
- Hinzman, L.D., Viereck, L.A., Adams, P.C., Romanovsky, V.E., Yoshikawa, K., 2006. Climate and permafrost dynamics of the Alaskan boreal forest. In: *Alaska's Changing Boreal Forest*, pp. 39–61.
- Holsten, E.H., 1998. *Ips perturbatus*: a Pest of Managed Stands? R10-TP-77. U.S. Department of Agriculture, Forest Service, Alaska Region, Anchorage, AK, 9 pp.
- Holsten, E.H., Werner, R.A., 1987. Engraver Beetles in Alaska Forests: Brochure. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR, 6 pp.
- Holsten, E.H., Burnside, R.E., Seybold, S.J., 2000. Attractant Semiochemicals of the Engraver Beetle, *Ips perturbatus*, in South-central and Interior Alaska. PNW-RP-529. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR, 9 pp.
- Holsten, E.H., Burnside, R.E., Seybold, S.J., 2001. Verbenone interrupts the response to aggregation pheromone in the northern spruce engraver, *Ips perturbatus* (Coleoptera: Scolytidae), in south-central and interior Alaska. *J. Ent. Soc. British Columbia* 98, 81–86.
- Huber, D.P.W., Gries, R., Borden, J.H., Pierce Jr., H.D., 1999. Two pheromones of coniferous bark beetles found in the bark of nonhost angiosperms. *J. Chem. Ecol.* 25, 805–816.
- Huber, D.P.W., Borden, J.H., Stastny, M., 2001. Response of the pine engraver, *Ips pini* (Say) (Coleoptera: Scolytidae), to conophthorin and other angiosperm bark volatiles in the avoidance of non-hosts. *Agric. For. Entomol.* 3, 225–232.
- Hunt, D.W.A., Borden, J.H., Lindgren, B.S., Gries, G., 1989. The role of autoxidation of α -pinene in the production of pheromones of *Dendroctonus ponderosae* (Coleoptera: Scolytidae). *Can. J. For. Res.* 19, 1275–1282.
- Leufvén, A., Bergström, G., Falsen, E., 1984. Interconversion of verbenols and verbenone by identified yeasts isolated from the spruce bark beetle *Ips typographus*. *J. Chem. Ecol.* 10, 1349–1361.
- Lindgren, B.S., Nordlander, G., Birgersson, G., 1996. Feeding deterrence of verbenone to the pine weevil, *Hylobius abietis* (L.) (Col., Curculionidae). *J. Appl. Entomol.* 120, 397–403.
- Livingston, R.L., 1979. The Pine Engraver *Ips pini* (Say) in Idaho, Life History, Habits, and Management Recommendation. Rept. 79–3. Idaho Department of Lands Report, Coeur d'Alene, ID, 7 pp.
- McCulloch, C.E., Searle, S.R., 2001. Generalized, Linear and Mixed Models. Wiley-Interscience, New York, 325 pp.
- McGuire, A.D., Ruess, R.W., Lloyd, A., Yarie, J., Klein, J.S., Juday, G.P., 2010. Vulnerability of white spruce tree growth in interior Alaska in response to climate variability: dendrochronological, demographic, and experimental perspectives. *Can. J. For. Res.* 40, 1197–1209.
- Nicholls, D., Miles, T., 2009. Cordwood Energy Systems for Community Heating in Alaska – An Overview. PNW-GTR-783. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR, 18 pp.
- Parker, D.L., 1991. Integrated Pest Management Guide: Arizona Five-spined Ips, *Ips lecontei* Swaine, and Pine Engraver, *Ips pini* (Say), in Ponderosa Pine. R3-91-9. U.S. Department of Agriculture, Forest Service, Pacific Southwest Region, Albuquerque, NM, 17 pp.
- Pierce Jr., H.D., De Groot, P., Borden, J.H., Ramaswamy, S., Oehlschlager, A.C., 1995. Pheromones in red pine cone beetle, *Conophthorus resinosae* Hopkins, and its synonym, *C. banksianae* McPherson (Coleoptera: Scolytidae). *J. Chem. Ecol.* 21, 169–185.
- Redmer, J.S., Wallin, K.F., Raffa, K.F., 2001. Effects of host tree seasonal phenology on substrate suitability for the pine engraver *Ips pini*. *J. Econ. Entomol.* 94, 844–849.
- Robertson, I.C., 2000. Reproduction and developmental phenology of *Ips perturbatus* (Coleoptera: Scolytidae) inhabiting white spruce (Pinaceae). *Can. Entomol.* 32, 529–537.
- Sartwell, C., 1970. *Ips pini* Attack Density in Ponderosa Pine Thinning Slash as Related to Felling Date in Eastern Oregon. PNW-RN-131. U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, OR, 8 pp.
- Shetler, G., Turetsky, M.R., Kane, E., Kasischke, E., 2008. Sphagnum mosses limit total carbon consumption during fire in Alaskan black spruce forests. *Can. J. For. Res.* 38, 2328–2336.
- Shepherd, W.P., Huber, D.P.W., Seybold, S.J., Fettig, C.J., 2007. Antennal responses of the western pine beetle, *Dendroctonus brevicomis* (Coleoptera: Curculionidae), to stem volatiles of its primary host, *Pinus ponderosa*, and nine sympatric nonhost angiosperms and conifers. *Chemoecology* 17, 209–221.
- Snyder, C., Schultz, M.E., Lundquist, J., 2008. Forest Health Conditions in Alaska – 2007. R10-PR-18. U.S. Department of Agriculture, Forest Service, Alaska Region, Anchorage, AK, 96 pp.
- Steed, B.E., Wagner, M.R., 2004. Importance of log size on host selection and reproductive success of *Ips pini* (Coleoptera: Scolytidae) in ponderosa pine slash of northern Arizona and western Montana. *J. Econ. Entomol.* 97, 436–450.
- Villa-Castillo, J., Wagner, M.R., 1996. Effect of overstory density on *Ips pini* (Coleoptera: Scolytidae) performance in ponderosa pine slash. *J. Econ. Entomol.* 89, 1537–1545.
- Walsh, J.E., Chapman, W.L., Romanovsky, V., Christensen, J.H., Stendel, M., 2008. Global climate model performance over Alaska and Greenland. *J. Climate* 21, 6156–6174.
- Watson, E.B., 1927. Notes on the hibernation of the spruce bark-beetle, *Ips perturbatus* Eichh., in northern Ontario. *Can. Entomol.* 59, 120–121.
- Werner, R.A., 1988. Recommendations for suppression of an *Ips perturbatus* outbreak in interior Alaska using integrated control. In: *Integrated control of Scolytid Bark Beetles: Proceedings of the IUFRO Working Party and the 17th International Congress of Entomology Symposium*, July 4, 1988, Vancouver, BC. Virginia Polytechnic Institute and State University Press, Blacksburg, VA, pp. 189–196.
- Werner, R.A., 1993. Response of the Engraver Beetle, *Ips perturbatus*, to Semiochemicals in White Spruce Stands of Interior Alaska. PNW-RP-465. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR, 9 pp.
- Werner, R.A., 2002. Effect of Ecosystem Disturbance on Diversity of Bark and Wood-boring Beetles (Coleoptera: Scolytidae, Buprestidae, Cerambycidae) in White Spruce (*Picea glauca* (Moench) Voss) Ecosystems of Alaska. PNW-RP-546. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR, 15 pp.
- Werner, R.A., Holsten, E.H., 1997. Dispersal of the Spruce Beetle, *Dendroctonus rufipennis*, and the Engraver Beetle, *Ips perturbatus*, in Alaska. PNW-RP-501. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR, 8 pp.
- Whitmore, M.C., 1983. The Predators and Parasites Affecting Scolytid Populations from White Spruce in Alaska. Thesis, University of Washington, Seattle.
- Wilkinson, R.G., Hanover, J.W., Wright, J.W., Flake, R.H., 1971. Genetic variation in the monoterpene composition of white spruce. *For. Sci.* 17, 83–90.
- Wolken, J.M., Hollingsworth, T.N., Rupp, T.S., Chapin III, F.S., Trainor, S.F., Barrett, T.M., Sullivan, P.F., McGuire, A.D., Euskirchen, E.S., Hennon, P.E., Beaver, E.A., Conn, J.S., Crone, L.K., D'Amore, D.V., Fresco, N., Hanley, T.A., Kielland, K., Kruse, J.J., Patterson, T., Schuur, E.A.G., Verbyla, D.L., Yarie, J., 2011. Evidence and implications of recent and projected climate change in Alaska's forest ecosystems. *Ecosphere* 2 (124), 1–35.
- Wood, S.L., 1982. The Bark and Ambrosia Beetles of North and Central America (Coleoptera: Scolytidae), A Taxonomic Monograph. Great Basin Naturalist Memoirs. No. 6, Brigham Young University, Provo, UT, 1359 pp.
- Zhang, Q.-H., Schlyter, F., 2004. Olfactory recognition and behavioural avoidance of angiosperm nonhost volatiles by conifer-inhabiting bark beetles. *Agric. For. Entomol.* 6, 1–19.
- 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, 69–80.
- Zhang, Q.-H., Liu, G.-T., Schlyter, F., Birgersson, G., Anderson, P., Valeur, P., 2001. Olfactory response of *Ips duplicatus* to nonhost leaf and bark volatiles in Inner Mongolia, China. *J. Chem. Ecol.* 27, 955–1009.