

Application of Semiochemicals to Assess the Biodiversity of Subcortical Insects following an Ecosystem Disturbance in a Sub-boreal Forest

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Abstract From 2000 through 2003 we used semiochemical-baited traps in northeastern Minnesota, USA, to assess changes in assemblages of subcortical forest insects after a catastrophic wind storm in 1999 and subsequent (1999–2000) fuel-reduction activities (salvage-logging and prescribed-burning). We determined the regional efficacy

of fifteen semiochemical blends (pheromones and kairomones) as attractants for target and non-target subcortical insect species (Coleoptera: Anthribidae, Buprestidae, Cerambycidae, Cleridae, Cucujidae, Curculionidae, Histeridae, Nemonychidae, Salpingidae, Scolytidae, Tenebrionidae, and Hymenoptera: Siricidae). During the four summers,

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we trapped 86,471 subcortical insects (143 species) in baited and unbaited Lindgren funnel traps, and 500 beetles (44 species) in baited and unbaited pitfall traps. We report 23 new state collection records of subcortical insects from Minnesota. Trap catches of subcortical insects were greatest in the wind-disturbed areas 2 years after the event, and declined thereafter. Similar trends were observed for subcortical insects in the burned areas. Both wind-disturbance and burning increased the subcortical insect species richness and diversity on the landscape. The subcortical insect species compositions of the salvaged and burned forest areas differed from those of the undisturbed and wind-disturbed areas. Trap catches of subcortical insects in response to semiochemical treatments also varied with year of sampling and land-area treatment. The greatest diversity of subcortical beetle species was in traps baited with attractants for the scolytids, *Dendroctonus valens* [(+)- α -pinene and (-)- β -pinene] and *Dryocoetes* spp. [*exo*-brevicommin and (-)- α -pinene], perhaps reflecting the generic nature of the baits. The most distinct species compositions were collected in response to the wood-borer and *Dendroctonus simplex* baits, whereas the species compositions in traps with the *D. valens* and *Dryocoetes* spp. baits, and the unbaited funnel trap were the most similar. The variation in trap catch with time and across landscapes suggests that the responses of subcortical insects to semiochemicals are more complex than previously appreciated.

Keywords Anthribidae · Bark beetles · *Betula papyrifera* · Biodiversity · Buprestidae · Cerambycidae · Cleridae · Coleoptera · Curculionidae · *Dendroctonus rufipennis* · *Dendroctonus simplex* · *Dendroctonus valens* · *Dryocoetes autographus* · Histeridae · Host attractants · *Hylurgops rugipennis pinifex* · Ipsdienol · Ipsenol · *Ips grandicollis* · *Ips perroti* · *Ips perturbatus* · *Ips pini* · Kairomones · Minnesota · Natural disturbances · Nemonychidae · Pheromones · *Picea glauca* · Pinenes · *Pinus banksiana* · *Populus tremuloides* · Predators · Salpingidae · Scolytidae · *Sirex behrensii* · Siricidae · Semiochemicals · Tenebrionidae · Wind-disturbance · Woodborers

Introduction

On 4 July 1999, a catastrophic storm with wind derechos (straight-line winds with multiple downbursts) of over 145 km hr⁻¹ in the Superior National Forest (in northeastern Minnesota, USA) resulted in the wind-throw of over 193,000 ha of forestland (USDA Forest Service 2000). This long-duration and extensive wind storm originated in North Dakota, lasted less than 24 h, and traveled over 2,100 km from northern Minnesota into southern Ontario and Quebec, and northern New Hampshire, Vermont, and

Maine (NOAA 2005). In Minnesota, over 85% of the most severe damage (areas with 67–100% tree mortality) occurred in the Boundary Waters Canoe Area Wilderness (BWCAW), where no forest management activity is permitted (see maps in Gandhi et al. 2005). Some damage also occurred along the Gunflint Trail Corridor, which is a heavily transited entry into the BWCAW and an access route to numerous vacation homes and service structures. Such a catastrophic storm was unique both in its extent (193,000 ha), scale of damage (>70% tree mortality in most areas), and long-interval duration (once every 1,000 yr) (Frelich and Lorimer 1991; USDA Forest Service 2000). With dead and downed trees (fuel loads) exceeding 16,000 kg/ha in some of the wind-disturbed areas (Gilmore et al. 2003), there was a strong potential for the occurrence of other natural disturbances such as wildfire, and insect and disease outbreaks. In 1999–2002, in response to these threats to remaining forest stands in this area, the USDA Forest Service reduced the fuel load along the Gunflint Trail Corridor through: (1) salvage-logging (1,100 ha), and (2) prescribed-burning (860 ha).

Subcortical (phloeophagous, xylophagous, and rhizophagous) forest insects are the first to colonize, reproduce, and increase populations in wind-disturbed forested landscapes (Connola et al. 1956; Gardiner 1975; Ayres et al. 1999). These early-successional species colonize the phloem and outer xylem of the tree tissue before it has desiccated completely (Gandhi et al. 2007). In wind-damaged forests, habitats for these species typically include uprooted trees; fallen branches and tree parts (slash); partially damaged, moribund, and living standing trees; and undamaged residual trees [collectively known as coarse-woody debris (CWD)]. Weakened, moribund, and undamaged residual standing trees, which die as a consequence of the aftermath of the storm, provide additional subcortical insect habitat for several years after the wind disturbance. The condition of CWD changes with time due to fermentation of xylem, decay of phloem, bark slough-off, breakage of stems and branches, and accumulation of additional CWD on the forest floor. The diversity and abundance of CWD created by a wind-disturbance provides excellent habitat for subcortical insects, and there is a temporal progression of species that exploit CWD with fresh phloem through those that exploit CWD with drying or decaying xylem. A large number of predators and parasites also are associated with subcortical herbivorous insects (Dahlsten 1970; Ryall 2003). Thus, as the amounts and characteristics of CWD change over time (Ryall and Smith 2005; Wilson and McComb 2005), there will be changes and turnover of associated subcortical insect communities (Weiss 1920; Blackman and Stage 1924; Savely 1939; Wallace 1953).

Historically, through rearing and collecting, workers have described the guilds of subcortical insects associated

with trees such as basswood, *Tilia americana* L. (Townsend 1886); tamarack, *Larix laricina* (Du Roi) K. Koch (Blackman and Stage 1918); shagbark hickory, *Carya ovata* (P. Mill.) K. Koch (Blackman and Stage 1924); shortleaf pine, *Pinus echinata* Mill, loblolly pine, *Pinus taeda* L., white oak, *Quercus alba* L., northern red oak, *Q. rubra* L., southern red oak, *Q. falcata* Michx., black oak, *Q. velutina* Lam., and post oak, *Q. stellata* Wangenh. (Savely 1939); and Scots pine, *Pinus sylvestris* L. (Wallace 1953). More recently, such community level taxonomic characterizations in North America have included insects associated with aspen, *Populus* spp. (Hammond 1997; Hammond et al. 2001); butternut, *Juglans cinerea* L. (Katovich and Ostry 1998); Douglas-fir, *Pseudotsuga menziesii* (Mirbel) Franco, hemlock, *Tsuga* spp. (Endlicher) Carrière, and lodgepole pine, *Pinus contorta latifolia* (Engelmann) Critchfield (Deyrup and Gara 1978); elms, *Ulmus* spp. L. (Hajek and Dahlsten 1985); loblolly and shortleaf pines, *Pinus taeda* and *P. echinata* (Dixon and Payne 1979; Berisford 1980); Monterey pine, *Pinus radiata* D. Don (Ohmart 1981; Ohmart and Voigt 1982); ponderosa pine, *Pinus ponderosa* Laws. (Dahlsten 1970; Stephen and Dahlsten 1976a, b); red pine, *Pinus resinosa* Ait. (Aukema and Raffa 2000, 2005; Aukema et al. 2000a, b, 2004, 2005; Erbilgin and Raffa 2001; Erbilgin et al. 2003); sugar pine, *Pinus lambertiana* Dougl. (Dahlsten and Stephen 1974); and white spruce, *Picea glauca* (Moench) Voss (Whitmore 1982; Gara et al. 1995; Haberkern et al. 2002). In Europe, community level work on subcortical forest insects also has been conducted in beech, *Fagus sylvatica* L. (Schiegg 2001); Norway spruce, *Picea abies* (L.) Karst, and *Pinus sylvestris* (Kaila et al. 1997); and subalpine spruce forests (Wermelinger et al. 2002, 2003; Joensuu et al. 2008).

Semiochemicals are being used increasingly to assess forest insect conservation biology and biodiversity (Svensson et al. 2004; Tolasch et al. 2007; Svensson and Larsson 2008; Larsson and Svensson 2009), and flight traps (with or without lures) are replacing hand collecting or rearing to assess the biodiversity and community ecology of subcortical insects (Ranius and Jansson 2002). Flight and pitfall traps baited with semiochemicals, such as aggregation pheromones and kairomones (Wood 1982a; Chénier and Philogène 1989), also can be used to monitor the diversity and population abundance of early successional subcortical insects following ecological disturbances (Werner 2002). In fact, semiochemicals have been a research and management tool for bark beetles for over 40 years (Wood et al. 1968), especially in western North American forests where these beetles can be devastating (Bedard and Wood 1981; Negrón et al. 2008). In many cases, semiochemicals were first identified from western North American bark beetle species (Silverstein et al. 1966, 1967; Wood et al. 1967; Furniss et al. 1972; Baker et al. 1977; Birch et al. 1980; Bowers et al.

1991; Hobson et al. 1993; Borden et al. 1996; Camacho et al. 1998; Holsten et al. 2000), and baits in other regions of the continent often are based on these research results. In addition to targeting specific species, semiochemicals also can be used to assess the diversity of predators and commensals that exploit the attractants of subcortical insects as host-finding kairomones (Dixon and Payne 1980; Phillips et al. 1988; Chénier and Philogène 1989; Seybold et al. 1992; Aukema and Raffa 2000, 2005; Erbilgin and Raffa 2001).

Presently, little is known about semiochemicals of subcortical insects and their associates in the sub-boreal forests of north-central North America. Studies on the semiochemicals of forest insects across different stand types within a landscape (such as the BWCAW) or over multiple field seasons are rare. Most semiochemical studies have been conducted over only one or two summers, either within relatively homogenous stands (e.g., single species pine stands of similar ages) (Miller and Borden 2003) or concurrently during one season across wide geographic areas (Miller et al. 1997). Finally, few studies have explored the full range of subcortical forest insects by using traps baited with semiochemicals. Most semiochemical studies have focused on either single subcortical species (e.g., Bedard et al. 1980; Borden et al. 1996); their associated predators (e.g., Seybold et al. 1992; Erbilgin and Raffa 2001); or on a small subset of subcortical insect families (e.g., Phillips et al. 1988; Chénier and Philogène 1989; Miller and Rabaglia 2009).

We studied the responses of phloeophagous, xylophagous, and rhizophagous insects and their associates to semiochemical treatments in the context of an ecological disturbance, the severe wind-disturbance event and subsequent management activities in a northeastern Minnesota sub-boreal forest. We targeted Buprestidae, Cerambycidae, and Scolytidae because they are the most economically important subcortical taxa, are early colonizers of CWD, and are crucial to CWD breakdown and nutrient cycling (Craighead et al. 1927; Craighead 1950; Furniss and Carolin 1977; Jacobs 2004). Among the primary subcortical insects, these taxa are the most species-rich and numerically abundant in sub-boreal forests (Dodge 1938; Bright 1976, 1987; Downie and Arnett 1996; Yanega 1996). Our specific research objectives were: 1) to test the efficacy of various known semiochemical treatments to monitor subcortical insects in a sub-boreal forest; and 2) to use trap-catch to document population responses of subcortical insects to a severe wind-disturbance event (>70% tree mortality) and fuel-reduction (salvaging and burning) treatments. We studied these subcortical insects for 4 years because we hypothesized that populations and assemblages of subcortical beetles would track the changing conditions of the CWD in the disturbed stands (Jacobs 2004).

Methods and Materials

Study Sites Subcortical insects and their associates were sampled from 28 sites in the BWCAW, and along the Gunflint Trail Corridor in the Superior National Forest in Cook County, MN, USA (Gandhi 2005; Gandhi et al. 2008). Mean annual temperature of the region is 1–2°C (Baker and Strub 1965), and mean annual precipitation is 65–75 cm (Baker and Kuehnast 1978). This area is located in the Laurentian mixed forest ecological province, northern Superior uplands section, and border lakes subsection of Minnesota (Minnesota Department of Natural Resources 1999). Soils along the Gunflint Trail have been classified primarily as the soil orders Inceptisols and Entisols (Anderson et al. 2001); major cover types in this area are aspen/birch/conifer (ABC) and jack pine, *Pinus banksiana* Lamb. (JP) (Table 1). In general, the ABC sites are on deeper, moist, well-drained till, outwash and lacustrine deposits, and loamy Entisols [Land Type Associations (LTA) 14, 22, 23, 37], whereas the JP sites are on shallow, well-drained till and outwash deposits, and sandy Inceptisols (LTA 21, 23) (USDA Forest Service 2000). The ABC forests originated after clear-cutting, whereas the JP forests originated after a wildfire (M. Theimer, personal communication, USDA Forest Service, Superior National Forest). Forest overstory of the ABC type is composed of trembling aspen, *Populus tremuloides* Michx., paper birch, *Betula papyrifera* Marsh., eastern white pine, *P. strobus* L., red pine, *P. resinosa*, black spruce, *Picea mariana* (P. Mill.) B. S.P., white spruce, *P. glauca*, balsam fir, *Abies balsamea* (L.) P. Mill., northern white cedar, *Thuja occidentalis* L., and tamarack, *L. laricina*. Forest overstory of the JP type is composed of jack pine, *P. banksiana*, and *B. papyrifera*.

Table 1 Attributes of tree species in two forest cover types in the study plots in the Superior National Forest, Cook Co., MN, USA

Stand Attributes ^a	Aspen/ Birch/ Conifer ^b	Jack Pine ^b
Soil pH	5.31±0.05	5.02±0.07
Mean Age (years)	71.33±3.62	75.29±1.64
Total Basal Area (m ² /ha)	22.10±8.24	25.37±6.70
Basal Area (m ² /ha) by Species		
Aspen, <i>Populus tremuloides</i> Michx.	10.95±2.98	2.33±1.50
Jack Pine, <i>Pinus banksiana</i> Lamb.	2.50±1.85	18.17±2.60
Balsam Fir, <i>Abies balsamea</i> (L.) P. Mill.	2.18±0.4	0.67±0.33
Paper Birch, <i>Betula papyrifera</i> Marsh.	5.12±2.23	0.83±0.37
Black Spruce, <i>Picea mariana</i> (P. Mill.) B.S.P.	1.35±0.78	3.37±1.90

^a From Gilmore et al. (2002, 2005, unpublished data) and Johnson (2004)

^b Data are means ± standard error

Adjoining and low-lying areas often contained *L. laricina* and *T. occidentalis* in riparian habitats. Forest understory of the two cover types is characterized by *Corylus cornuta* Marsh., *Vaccinium* spp., *P. tremuloides*, *A. balsamea*, and *P. glauca* (Gilmore et al. 2002, 2005; Johnson 2004).

Experimental Design

Land-Area Treatments During the summer of 2000, we sampled from study sites in the ABC and JP forest cover types, whereas during the summers of 2001–2003, only JP sites were sampled for logistical reasons and because results in 2000 suggested that JP sites had the greatest subcortical insect diversity. In 2000, mature *P. tremuloides* and *Pinus banksiana* trees on these sites had mean ages of 71 years and 73 years, respectively. In 2000, we sampled two sites (replicates) for each of three treatment types [(1) undisturbed forests (control); (2) severely wind-disturbed forests (>70% tree mortality); and (3) wind-disturbed-salvage-logged (salvaged) forests] in each of the two (ABC and JP) cover types for a total of 12 sites. In 2001–2003, we sampled four sites (replicates) for each of the four treatment types [(1) undisturbed, (2) severely wind-disturbed, (3) salvaged, and (4) wind-disturbed-prescribed-burned (burned) forests] in the JP cover type for a total of 16 sites (Gandhi 2005; Gandhi et al. 2008). The wind-disturbed sites were salvaged between the summer of 1999 and the spring of 2000, and burned between the fall of 2000 and the spring of 2001 (Gandhi 2005; Gandhi et al. 2008). The sites were 2–3 ha in size, and located at least 500 m (and often greater distances) away from each other. Salvaging entailed removal of all merchantable and damaged trees except for standing live *P. resinosa*, *P. strobus*, and *T. occidentalis* (USDA Forest Service 2000).

Semiochemical Treatments: Baited Pitfall Traps Rhizophagous insects and their associates were caught with baited pitfall traps that consisted of a 500 ml round plastic container (10.7 cm i.d.) inside a 1.0 l plastic liner buried in the ground (Spence and Niemelä 1994). Propylene glycol (200 ml; recreational vehicle antifreeze, Peak Co., Northbrook, IL, USA) in the plastic container served as killing agent and preservative for trapped beetles (Weeks and McIntyre 1997). The trap was covered with a 100 cm² plywood board suspended 4 cm above the trap to minimize flooding and disturbance by animals. Baits were hung from the plywood board and placed inside the inner cup above the level of propylene glycol. Baits included 4 host attractant solutions: 2% (–)- α -pinene, 2% (+)- α -pinene, 2% (–)- β -pinene (in ethanol), and a 100% ethanol control. The pinenes were purchased from Sigma Aldrich (St. Louis, MO, USA), and all had chemical purities of $\geq 99\%$ and enantiomeric purities of >98%. The ethanol was

purchased from Aaper Alcohol Co. (Shelbyville, KY, USA).

During the summer of 2000, a total of 144 baited pitfall traps were installed in the ABC and JP cover types. There were 12 baited pitfall traps per site with three replicates of each bait treatment placed on a 6 by 2 grid, and separated by >20 m to reduce trap sampling interactions. The 12 traps were each baited with one of the four semiochemical blends. Semiochemical blends were released from wicks inserted in full 15 ml glass vials. When traps were emptied, the location of the trap and its semiochemical bait were not re-randomized within the site, and the baits were not replaced during the summer. In 2000, traps were operated from August to October and emptied every 15–30 d. For logistical reasons, the study was not initiated until August; for biological reasons, May would have been preferable.

During the summers of 2001–2003, the sampling design was changed to include 80 traps distributed over 16 sites, all located in the JP cover type. At each site, 5 pitfall traps baited with the 4 semiochemical blends in ethanol, ethanol alone, and an unbaited control were assigned to 5 sample sub-plots randomly drawn from a grid of 28 sub-plots. When the traps were emptied, the inner cups and the associated baits were re-randomized on the 5 outer cup locations (i.e., among the 5 sub-plots). In 2001 and 2002, the semiochemical blends were released from closed polyethylene bottles at an unknown low release rate (15 ml total volume) [Phero Tech. (now Contech Enterprises) Inc., Delta, BC, Canada]. In 2003, semiochemical blends were released from these polyethylene bottles with a 0.13 cm² hole in the side of the vial cap. The mean (\pm SE) release rates for 15 d in the field for each of the semiochemical blends in 2003 were as follows: (1) (–)- α -pinene: 7.98 \pm 0.23 g; (2) (+)- α -pinene: 7.64 \pm 0.26 g; (3) (–)- β -pinene: 7.24 \pm 0.20 g; and (4) 100% ethanol: 7.48 \pm 0.20 g. Baiting started in May, and baits were replaced in July in 2001 and 2002, and every 2 wk in 2003. In 2001–2003, traps were deployed from May to October and emptied every 15–20 d.

Semiochemical Treatments: Lindgren Funnel Traps Subcortical insects were caught in flight with 16-unit Lindgren funnel traps (Lindgren 1983). The traps were baited on the 8th funnel from the top with semiochemicals that were chosen to elicit responses from the major species of scolytid and woodboring beetles known to be present in this sub-boreal forest (Dodge 1938; Bright 1976; University of Minnesota Insect Collection (UMIC), St. Paul, MN; K.J.K.G., personal observation) (Table 2). The selection of many of the semiochemicals was based on research data accumulated on populations of scolytid and woodboring beetles from western North America (Table 2). A bait for the spruce beetle, *Dendroctonus rufipennis* (Kirby) was employed

initially in 2000 and 2001 in anticipation of potential population increases of this species, but because we trapped far more individuals of the eastern larch beetle, *Dendroctonus simplex* LeConte than *D. rufipennis* in response to this bait, we used a different bait targeting *D. simplex* in 2002 and 2003 (see Discussion for further explanation). During the summer of 2000, a total of 324 funnel traps were installed in the ABC and JP forest cover types. Twenty seven funnel traps were hung on 2.2 m tall iron rebar poles in each site so that the trap collection cup was approximately 0.1 m above the forest floor. The traps were placed on a 7 by 4 grid, separated by >20 m, and were >20 m from forest edges. Traps were each baited with 1 of 8 semiochemical blends, or left unbaited (3 replicates of each semiochemical treatment and control at each site). The collection cup of each trap contained a 4 cm² Dichlorvos-impregnated plastic strip to kill insects. When traps were emptied, the location of the trap and its semiochemical bait were not re-randomized within the site. In 2000, traps were deployed from August to October and emptied every 15–30 d.

During the summer of 2001, the sampling design was altered to include 160 traps distributed over 16 sites located only in the JP cover type. At each site, 10 funnel traps (baited with 9 semiochemical combinations and an unbaited control) were assigned to 10 sample sub-plots randomly drawn from a grid of 28 sub-plots. During the summers of 2002–2003, the sampling design was altered further to include 176 traps distributed over 16 sites in the JP cover type. At each site, 11 funnel traps (baited with 10 semiochemicals and an unbaited control) were assigned to 11 sample sub-plots randomly drawn from a grid of 28 sub-plots. Semiochemical treatments were altered among years 2000, 2001, and 2002–2003 after assessing the trapping efficacy of the baits. Semiochemical baits were replaced each year in July or August. In 2001–2003, when traps were emptied every 15–20 d, the location of the trap and its semiochemical bait were re-randomized among the 10 or 11 sub-plots. In 2001–2003, traps were deployed from May to October and emptied every 15–20 d.

Adult subcortical insects were identified by K.J.K.G. with taxonomic keys (Middlekauff 1960; Linsley 1962a, b, 1963, 1964; Linsley and Chemsak 1972; Nelson 1975; Bright 1976, 1987; Wood 1982b, Triplehorn 1990; Goulet 1992; Chemsak 1996; Downie and Arnett 1996; Yanega 1996; Kovarick and Caterino 2001; Bellamy and Nelson 2002; Optiz 2002; Pollack 2002; Thomas 2002; Turnbow and Thomas 2002) and with the assistance of systematists. Specifically, reference collections of buprestid, cerambycid, clerid, histerid, scolytid, and tenebrionid beetles and siricid wasps were verified by C. Bellamy (California Department of Food and Agriculture, Sacramento) and G. Nelson (College of Osteopathic Medicine, Kansas City, deceased);

Table 2 List of semiochemicals used to target subcortical beetle species in Lindgren funnel traps in 2000–2003, Superior National Forest, Cook Co., MN, USA^a

Target Beetle Species or Families	Semiochemical	Enantiomeric Composition	Load (mg)	Release rate/d	Chemical Purity (%)
<i>Ips grandicollis</i> ^b	Ipsenol ^c	97%(-)	20	240 µg ^d	97
	α-Pinene ^c	98.5%(-)	6,413	200–300 mg ^d	99
<i>Ips perroti</i> ^b	Ipsenol ^c	97%(-)	20	240 µg ^d	97
	Ipsdienol ^c	97%(-)	20	110 µg ^d	93
<i>Ips perroti</i> ^f	Ipsenol ^c	97%(-)	20	240 µg ^d	97
	Ipsdienol ^c	97%(+)	20	110 µg ^d	93
<i>Ips perturbatus</i> ^b	Ipsenol ^c	97%(-)	20	240 µg ^d	97
	Ipsdienol ^c	97%(+)	20	110 µg ^d	93
	<i>cis</i> -Verbenol ^c	83%(-)	20	300–600 µg ^d	94
<i>Ips pini</i> ^b	Ipsdienol ^c	Racemic	20	110 µg ^d	93
	Lanierone ^c	NA	4	10 µg ^d	≥98
<i>Dendroctonus rufipennis</i> ^g	Frontalin ^h	Racemic	300	2.6 mg ⁱ	≥98
	α-Pinene ^j	96%(-)	650	1.5 mg ^k	99
<i>Dendroctonus simplex</i> ^g	1-Methyl-2-cyclohexenol ^c	Racemic	20	1.5 mg ^d	97
	Seudenol ^c	Racemic	20	1.5 mg ^l	99
	α-Pinene ^j	96%(-)	650	1.5 mg ^k	99
<i>Dendroctonus valens</i> ^b	α-Pinene ^c	98.5%(+)	12,870	200–300 mg ^d	99
	β-Pinene ^c	(-)	12,990	200–300 mg ^d	99
<i>Dendroctonus valens</i> ^m Phero Tech Bait	α-Pinene ^c	(+)	4,290	unknown	
	β-Pinene ^c	(-)	4,330	unknown	
	3-Carene ^c	(+)	4,285	unknown	
<i>Dryocoetes</i> spp. ⁿ	<i>exo</i> -Brevicomino ^o	Racemic	243	1.7 mg ⁱ	97
	α-Pinene ^c	98.5%(-)	6,435	200–300 mg ^d	99
Buprestidae, Cerambycidae ^b	Ethanol ^p	NA	120,000	400 mg ^l	≥98
	α-Pinene ^p	96%(-)	170,000	2 g ^l	99

^a All materials and release rates were provided by Phero Tech (now Contech Enterprises) Inc. (Delta, BC, Canada), except for (+)-α-pinene and (-)-β-pinene used for *D. valens*, which were purchased from Sigma Aldrich and formulated in our laboratory. References for the selection of semiochemical attractants are as follows: *Ips grandicollis* (Erbilgin and Raffa 2000); *Ips perroti* (Ayres et al. 2001); *Ips perturbatus* (Holsten et al. 2000); *Ips pini* (Teale et al. 1991); *Dendroctonus rufipennis* (Borden et al. 1996); *Dendroctonus simplex* (Werner et al. 1981); *Dendroctonus valens* (Hobson et al. 1993); and *Dryocoetes* spp. (Camacho et al. 1998)

^b Baits were used in 2000–2003

^c Bubble cap release device

^d At 25°C

^e 15 ml Polyethylene screw-cap bottle release device

^f Bait was used in 2001–2003

^g Bait for *D. rufipennis* was used in 2000 and 2001; bait for *D. simplex* was used in 2002 and 2003

^h 400 µl Polyethylene Eppendorf vial release device

ⁱ At 23°C

^j 1.8 mL Polyethylene Eppendorf vial release device

^k At 21°C

^l At 20°C

^m Bait was used in 2002–2003

ⁿ *Dryocoetes* spp. were sampled with (+/-)-*endo*-brevicomino alone in 2000

^o 250 µl Polyethylene Eppendorf vial release device

^p Ultra high release device

NA- Not Applicable

J. Chemsak (University of California, Berkeley, deceased) and D. Penrose (California Department of Food and Agriculture, Sacramento); W. Barr (University of Idaho, retired) and J. Rifkind (private collector, Valley Village, California); Y. Bousquet (Agriculture Canada, Ottawa); D. Bright (Agriculture Canada, Ottawa, retired); C. Triplehorn (Ohio State University, retired); and J. Luhman (Minnesota Department of Food and Agriculture, St. Paul), respectively. All curculionid beetles were identified by S.J.K (University of Wisconsin) and D. Langor (Canadian Forest Service, Edmonton) (Blatchley and Leng 1916; Kissinger 1964; Fridrich 1965; Warner 1966; Salsbury 2000). Voucher specimens have been deposited at the UMIC, St. Paul, MN and the California Academy of Sciences, San Francisco, CA. The UMIC was also examined during this study for specimens of potential new state record insects that had not been recorded previously in the literature.

Data Handling and Statistical Analyses

Pitfall Traps Since only 500 beetles were caught in the pitfall traps during the summers of 2000–2003, no statistical analyses were performed. Instead, species-lists with a brief interpretation of trends are provided. Such small catches may represent either the inadequacy of the traps or baits or small population sizes in the forest stands.

Funnel Traps: Subcortical Insect Trap Catches Trap catches of early successional subcortical insects (=subcortical insects) were standardized to 15-d intervals [(trap catch/ total number of days that trap was operational) X 15] as the traps were emptied approximately every 2 wk. This standardization accounted for the variable number of days when the traps were operational in the plots. If funnel traps were disturbed for a particular period, catches from that period were excluded from analyses. For data collected in 2000, trap catches were pooled for all subcortical insects over the season, and three-factor analyses of variance (ANOVA) were performed first with the cover type, land-area treatment, and semiochemical treatment as factors (SAS 1999–2001). Data were checked for the required assumptions of constant variance and normality using residual and normality plots. A Goodness-of-Fit test for normal distribution (Kolmogorov-Smirnov) was conducted on the residuals to test the null hypothesis that the data were normally distributed. Data for standardized subcortical insect catches showed non-normality, and were transformed by $\ln(x+1)$, which resulted in normally distributed data. Type III Sum of Squares were used to assess the statistical significance of factors at $\alpha=0.05$. The ANOVA was performed in an iterative manner in which the complete model was analyzed by successive deletions of non-significant higher-order interaction terms, two-way interaction terms, and

main factors. The final model terms that were significant are presented in the tables, and all terms that were omitted as a consequence of the iterative procedure are listed as non-significant (NS). The Ryan-Einot-Gabriel-Welsch (REGW) test with $\alpha=0.05$ was used for pairwise comparisons among treatment means (Day and Quinn 1989). All data were back-transformed before presentation.

For data collected in 2001–2003, split-plot analyses of variance tests were performed for: 1) all subcortical insect species combined; 2) subcortical insect families with $\geq 10\%$ of total catch; and 3) subcortical insect species with $\geq 1\%$ of the total beetle catch by using the PROC MIXED option (SAS 1999–2001). Split-plot analyses were performed because the traps were re-randomized every 15 d; the whole plot factor was the land-area treatment and the two split-plot factors were semiochemical treatment and year. The split-plot analysis of variance test for all subcortical insect species combined was also performed as described above, but excluding the trap catch of the most abundant subcortical insect species. This test was performed to assess the effect of the most abundant species on the total trap catches.

To determine if the responses of males and females of the four most abundant scolytid species were dependent upon the land-area treatment, selected semiochemical treatments, and year (2001–2003), a three- or a two-way ANOVA was performed on the standardized percentage of males trapped in funnel traps. These four species also were relatively easy to separate by sex. To assemble this data set, we determined the sex of 1,937 adults of *D. simplex*, 2,684 *I. grandicollis*, 7,442 *I. perroti*, and 8,811 *I. pini*. Trap catches with < 10 individuals were excluded from these analyses because of the bias in sex ratio from small samples.

Funnel Traps: Subcortical Insect Species Richness Venn diagrams were used to illustrate relationships of species richness (total number of early successional species) among the ABC and JP cover types, and the land-area treatments. In the diagrams, each habitat set is represented by a circle that contains the unique numbers of species; overlapping areas depict numbers of insect species held in common with other cover type and land-area treatment combinations (Langbehn et al. 1972). Venn diagrams were constructed for species richness as follows: 1) 2000 funnel trap catches in the ABC (Fig. 4a) and JP (Fig. 4b) cover types in the three land-area treatments; and 2) 2001–2003 funnel trap catches (pooled over all three seasons) in the JP cover type in the four land-area treatments.

Funnel Traps: Subcortical Insect Species Diversity Two methods (rarefaction and Simpson's diversity index) were used to assess subcortical insect species diversity in funnel trap catches in relationship to the cover type, land-area

treatment, and semiochemical treatment. Rarefaction indices estimate the mean (\pm SE) subcortical insect species diversity (richness and evenness); the technique accounts for differences in trapping effort among habitats and is ideal for catches with variable trapping intervals (Magurran 2004; software developed by Holland 2003). Rarefaction analyses were performed on the following subcortical insect assemblages: 1) 2000 funnel trap catches in the ABC and JP cover types; 2) 2001–2003 funnel trap catches in 4 land-area treatments in the JP cover type; 3) 2000 funnel trap catches with 9 semiochemical treatments (including unbaited control) in the ABC and JP cover types; and 4) 2001–2003 funnel trap catches with 12 (including unbaited control) semiochemical treatments in the JP cover type.

Simpson's diversity index was used to assess species diversity and dominance for land-area and semiochemical treatments (Magurran 2004). The measure was expressed as "diversity" rather than "dominance" to ensure that species diversity increased and dominance decreased with an increasing index value (McCune and Mefford 1999; McCune and Grace 2002).

Funnel Traps: Subcortical Insect Species Composition Subcortical insect species compositions for each land-area treatment, year, and semiochemical treatment for JP stands in 2001–2003 were compared by constructing dendrograms with a similarity percentage scale that was generated by cluster analysis. In this clustering technique, standardized mean funnel trap catches within each treatment-type were analyzed by using the Bray-Curtis Distance method with the group average option (McCune and Mefford 1999; McCune and Grace 2002).

Results

Pitfall Trap Sampling During the summers of 2000–2003, 1,828 pitfall trap samples yielded 500 rhizophagous beetle adults representing 5 families, 34 genera, and 44 species (Supplemental Data Table 1). In 2000, only one species [*Dryocoetes autographus* (Ratzeburg) (Scolytidae)] was trapped in the ABC cover type. In the JP cover type, Curculionidae (73% of the total catch) was the most abundant family followed by Scolytidae (19%), and Cerambycidae (7%). Within each of these respective families, *Hylobius pales* (Herbst) (27%), *Hylurgops rugipennis pinifex* (Fitch) (8%), and *Stictoleptura canadensis canadensis* (Olivier) (2%) were the most abundant. Overall, *H. pales* (27%), *Hylobius radialis* Buchanan (16%), and *Otiorhynchus ovatus* (Linnaeus) (9%) (all Curculionidae) were the most abundant beetle species. Thirty-two rhizophagous beetle species were rare and represented $\leq 1\%$ of the total beetle catch; ten rhizophagous beetle species were

common and represented 1–10% of total beetle catch; and two rhizophagous beetle species were abundant and represented $>10\%$ of the total beetle catch. *Otiorhynchus ovatus* and *Polydrusus sericeus* (Schaller) are exotic species from Europe. Several species of bark beetles [e.g., *Ips grandicollis* (Eichhoff), *Ips pini* (Say), *Dr. autographus*, *Polygraphus rufipennis* (Kirby), and *Dendroctonus simplex* LeConte] generally not associated with the forest floor were caught in these traps.

In 2000–2003, 42% of the beetles were caught in the burned sites followed by lower percentages in the undisturbed (21%), salvaged (21%), and wind-disturbed (16%) sites. The species richness was also highest in the burned sites (26 species). Most of the rhizophagous beetles were caught in the traps baited with ethanol solutions of (+)- α -pinene (33%) followed by traps baited with (–)- α -pinene (26%), (–)- β -pinene (23%), ethanol (11%), and unbaited traps (7%) (Supplemental Data Table 2). The species richness (23 species) was also highest in the traps baited with ethanol solutions of (+)- α -pinene.

Funnel Trap Sampling During the summers of 2000–2003, 3,975 funnel trap samples yielded a total of 86,471 subcortical insect adults representing 12 families, 96 genera, and 143 species (Supplemental Data Tables 3, 4). The majority of subcortical insect species (126) were rare (i.e., each represented $\leq 1\%$ of the total insect catch), 14 subcortical insect species were common (i.e., each represented 1–10% of the total insect catch), and three subcortical insect species were abundant (i.e., each represented $>10\%$ of the total insect catch).

Scolytidae (55% of the total catch) was the most abundant family followed by Cleridae (18%), Buprestidae (13%), and Cerambycidae (10%). Other families such as Anthribidae, Cucujidae, Curculionidae, Histeridae, Nemonychidae, Salpingidae, Siricidae, and Tenebrionidae each represented $<5\%$ of the total catch. Within their respective families, *D. simplex* (35%) (Scolytidae), *Thanasimus dubius* (Fabricius) (65%) (Cleridae), *Buprestis maculativentris* Say (10%) (Buprestidae), and *Monochamus scutellatus scutellatus* (Say) (25%) (Cerambycidae) were the most abundant species. Overall, *D. simplex* (19%) was the most abundant beetle species followed by *T. dubius* (12%), and *I. pini* (10%).

Among families, cerambycid beetles had the greatest species diversity (43 species) followed by curculionid (34 species), scolytid (24 species), and buprestid (21 species) beetles. We also caught 10 species of clerid beetles and 5 species of siricid woodwasps. Among buprestid beetles, *Chrysobothris sexsignata* (Say), *Cypriacis striata* (Fabricius), *Cypriacis sulcicollis* (LeConte), *Phaenops aeneola* (Melsheimer), and *Phaenops drummondi drummondi* (Kirby) are new state records (Downie and Arnett 1996).

Among cerambycid beetles, *Pygoleptura nigrella nigrella* (Say) and *Xestoleptura tibialis* (LeConte) are new state records (Linsley 1962a, b, 1963, 1964; Linsley and Chemsak 1972; Downie and Arnett 1996; Yanega 1996). Among clerid beetles, *Enoclerus muttkowski* (Wolcott), *Enoclerus nigripes rufiventris* (Spinola), *Madoniella dislocatus* (Say), *Thanasimus trifasciatus* (Say), *Thanasimus nubilus* (Klug), *Thanasimus undatulus undatulus* (Say), *Trichodes nutalli* (Kirby), and *Zenodosus sanguineus* (Say) are new state records (Downie and Arnett 1996). Katovich and Ostry (1998) reported that *Z. sanguineus* was collected on the bark of butternut, *Juglans cinerea*, but it was not clear whether the species was collected from Wisconsin or Minnesota. Among histerid beetles, *Paromalus teres* LeConte, *Platysoma coarctatum* LeConte, *Platysoma deficiens* Casey, and *Platysoma lecontei* (Marseul) are new state records (Downie and Arnett 1996). Among salpingid beetles, *Boros unicolor* Say is a new state record (Downie and Arnett 1996), whereas among scolytid beetles, *Ips latidens* (LeConte) is a new regional record for the Great Lakes region in the USA (Dodge 1938; Wood 1982b; Downie and Arnett 1996). Among siricid wasps, *Sirex behrensii* (Cresson), *Urocerus gigas flavicornis* (Fabricius), and *Xeris spectrum* (Linnaeus) are new state records (Smith and Schiff 2002). Among these new records, *C. sulcicollis*, *P. aeneola*, *E. muttkowski*, *E. n. rufiventris*, *T. trifasciatus*, *I. latidens*, and *S. behrensii* were not present in the University of Minnesota Insect Collection, whereas the rest of the species had been collected previously from Minnesota and deposited in the museum, but not reported in the literature (Supplemental Data Table 5).

Subcortical Insect Trap Catches The three-way ANOVA for pooled trap catches of all subcortical insect species for the year 2000 showed that cover type, land-area treatment, and semiochemical treatment were significant main effects in the model (Table 3, Fig. 1). Thirty five percent more subcortical insects were caught in the JP than in the ABC cover type (Fig. 1a). Across both cover types significantly more (20–34%) insects were caught in the salvaged than in the undisturbed and wind-disturbed forests (Fig. 1a). Significantly more subcortical insects of all taxa were caught in response to the *I. pini* bait than to the other baits (Fig. 1b), and significantly more (478–559%) insects were caught in response to the *Dendroctonus rufipennis*, *I. grandicollis*, and *I. perturbatus* (Eichhoff) baits than to the unbaited traps (Fig. 1b).

For all subcortical insect species for 2001–2003, there were significant interactions between year and land-area treatment, and between year and semiochemical treatment (Table 3, Supplemental Data Fig. 1). In general, trap catches were up to 2.5 times greater in 2001 and 2002 than in 2003, except in the undisturbed forests. In 2002, the

D. simplex bait caught more beetles than the rest of the bait-types. In 2001–2003, fifteen subcortical beetle species in order of decreasing catches from funnel traps included *D. simplex*, *T. dubius*, *I. pini*, *I. perroti*, *I. perturbatus*, *B. maculativentris*, *I. grandicollis*, *T. u. undatulus*, *T. nubilus*, *Monochamus s. scutellatus*, *M. mutator* LeConte, *Dr. autographus*, *P. rufipennis*, *Chalcophora virginiensis* (Drury), and *H. r. pinifex* (Table 3). Significant interactions between and among model factors occurred, but varied among the families (Table 3, Supplemental Data Figs. 2, 3 and 4) and species (Table 3, Supplemental Data Figs. 5, 6, 7, 8, 9, 10, 11, 12 and 13). *Ips grandicollis* and *I. perturbatus* had significant three-way interactions among model factors (Table 3), which could not be displayed graphically. In 2001 in burned forests, significantly more *B. maculativentris*, *T. nubilus*, and *P. rufipennis* were caught than in 2002 and 2003; in 2001 and 2002 in salvaged forests, significantly more *C. virginiensis* were caught than in 2003; and in 2001 in wind-disturbed forests, more *M. s. scutellatus*, *I. pini*, and *T. dubius* were caught than in 2002 and 2003. In general, significantly more *D. simplex* (Fig. 2a), *I. pini* (Fig. 2b), *I. perroti* (Fig. 2c), *I. perturbatus* (Fig. 2d), and *I. grandicollis* (Fig. 2e) were trapped in response to their respective baits than to the other semiochemical combinations, although the response of *I. grandicollis* tended to be more generic to the baits that we tested. The predaceous beetle, *T. dubius*, also tended to respond more generally to a variety of the baits that we tested (Fig. 2f), perhaps underscoring its role as a generalist bark beetle predator. *Ips perroti* responded more to the *I. perroti*(–)-ipsdienol bait (Fig. 2c); *H. r. pinifex* (Fig. 2g) to the *D. valens*-Phero Tech and woodborer baits; *T. dubius* to the *D. rufipennis* bait (Fig. 2f); and *Dr. autographus* (Fig. 2h) to the *Dryocoetes* spp. and woodborer baits.

The grand mean percentage of male *D. simplex* trapped in 2001–2003 was 49%. Year was not used as a model factor in the analysis because of low trap catches in years 2001 and 2003. Because of the higher response of *D. simplex* (Fig. 2a), the trap catches analyzed included those responding to the baits targeting *D. simplex*, *I. pini*, and woodborers. The two-way ANOVA for the percentage of male *D. simplex* indicated no significant effect of the interactions of land-area and semiochemical treatments ($F_{(4,35)} = 1.89$, $P=0.141$), or of land-area treatment alone ($F_{(2,35)} = 0.48$, $P=0.625$) or semiochemical treatment alone ($F_{(2,35)} = 3.14$, $P=0.056$).

The grand mean percentage of male *I. pini* trapped in 2001–2003 was 44%. Because of the higher response of *I. pini* (Fig. 2b), the trap catches analyzed included those responding to the baits targeting *I. pini* and *I. perroti*(+)-ipsdienol. The three-way ANOVA for the percentage of male *I. pini* indicated no significant effect of any of the second or third-order interactions ($P>0.5$), of year alone

Table 3 ANOVA model for the pooled funnel trap catches of all subcortical beetle species, four beetle families, and fourteen species with year (YR), land-area treatment (LT), semiochemical treatment (ST), and their interactions as factors, Superior National Forest, Cook Co., MN, USA

Source ^a	YR	LT	ST	YR*LT	YR*ST	LT*ST	YR*LT*ST
All Subcortical Insects 2000 ^b	NA	10.44 _{2,107} <0.001	9.99 _{8,107} <0.001	NA	NA	NS	NA
All Subcortical Insects 2001–2003 ^c	24.84 _{2,3573} <0.001	9.69 _{3,3573} <0.001	8.87 _{11,3573} <0.001	4.36 _{6,3573} <0.001	8.49 _{22,3573} <0.001	NS	NS
Buprestidae ^d	179.55 _{2,3573} <0.001	124.11 _{3,3573} <0.001	NS	64.48 _{6,3573} <0.001	NS	NS	NS
Cerambycidae ^d	75.9 _{2,3573} <0.001	25.86 _{3,3573} <0.001	43.49 _{11,3573} <0.001	13.4 _{6,3573} <0.001	5.25 _{22,3573} <0.001	NS	1.27 _{66,3573} 0.048
Cleridae ^d	4.38 _{2,3573} 0.013	49.83 _{3,3573} <0.001	87.12 _{11,3573} <0.001	7.8 _{6,3573} <0.001	4.36 _{22,3573} <0.001	10.65 _{33,3573} <0.001	NS
Scolytidae ^d	16.95 _{2,3573} <0.001	4.4 _{3,3573} 0.004	8.73 _{11,3573} <0.001	2.26 _{6,3573} 0.035	4.23 _{22,3573} 0.002	1.89 _{33,3573} 0.002	NS
<i>Buprestis maculativentris</i> ^d	49.73 _{2,3573} <0.001	96.48 _{3,3573} <0.001	NS	25.44 _{6,3573} <0.001	NS	NS	NS
<i>Chalcophora virginiensis</i> ^d	44.98 _{2,3573} <0.001	96.19 _{3,3573} <0.001	NS	25.4 _{6,3573} <0.001	NS	NS	NS
<i>Dendroctonus simplex</i> ^d	15.82 _{2,3573} <0.001	NS	9.4 _{11,3573} <0.001	NS	5.05 _{22,3573} <0.001	1.53 _{33,3573} 0.027	NS
<i>Dryocoetes autographus</i> ^d	NS	6.07 _{3,3573} <0.001	27.01 _{11,3573} <0.001	2.51 _{6,3573} 0.02	3.11 _{22,3573} <0.001	3.69 _{33,3573} <0.001	NS
<i>Ips grandicollis</i> ^d	20.45 _{2,3573} <0.001	5.1 _{3,3573} 0.002	62.6 _{11,3573} <0.001	5.84 _{6,3573} <0.001	4.08 _{22,3573} <0.001	NS	1.55 _{66,3573} 0.001
<i>Ips perroti</i> ^d	3.45 _{2,3573} 0.032	5.16 _{3,3573} 0.002	52.79 _{11,3573} <0.001	NS	2.23 _{22,3573} 0.002	5.38 _{33,3573} <0.001	NS
<i>Ips perturbatus</i> ^d	6 _{2,3573} 0.003	9.02 _{3,3573} <0.001	18.99 _{11,3573} <0.001	3.38 _{6,3573} <0.001	4.09 _{22,3573} <0.001	5.45 _{33,3573} <0.001	2.61 _{66,3573} <0.001
<i>Ips pini</i> ^d	4.24 _{2,3573} 0.015	2.77 _{3,3573} 0.04	34.54 _{11,3573} <0.001	2.28 _{6,3573} 0.034	NS	2.49 _{33,3573} <0.001	NS
<i>Monochamus mutator</i> ^d	29.91 _{2,3573} <0.001	10.45 _{3,3573} <0.001	30.22 _{11,3573} <0.001	4.8 _{6,3573} <0.001	3.29 _{22,3573} <0.001	3.73 _{33,3573} <0.001	1.77 _{66,3573} <0.001
<i>Monochamus s. scutellatus</i> ^d	33.64 _{2,3573} <0.001	33.5 _{3,3573} <0.001	7.77 _{11,3573} <0.001	9.06 _{6,3573} <0.001	1.76 _{22,3573} 0.03	NS	NS
<i>Polygraphus rufipennis</i> ^d	15.77 _{2,3573} <0.001	11.2 _{3,3573} <0.001	NS	10.65 _{6,3573} <0.001	NS	NS	NS
<i>Thanasimus dubius</i> ^d	19.23 _{2,3573} <0.001	47.52 _{3,3573} <0.001	102.74 _{11,3573} <0.001	2.6 _{6,3573} 0.016	4.1 _{22,3573} <0.001	12.25 _{33,3573} <0.001	NS
<i>Thanasimus u. undatulus</i> ^d	6.33 _{2,3573} 0.002	60.51 _{3,3573} <0.001	32.59 _{11,3573} <0.001	2.8 _{6,3573} 0.01	2.6 _{22,3573} <0.001	6 _{33,3573} <0.001	NS
<i>Thanasimus nubilus</i> ^d	81.53 _{2,3573} <0.001	47.95 _{3,3573} <0.001	NS	45.81 _{6,3573} <0.001	NS	NS	NS

^a For each table entry, the top number is the *F*-value, the bottom number is the *P*-value, and the subscripts refer to the degrees of freedom for each *F*-value. *NA* Non-applicable in the model; *NS* Non-significant factor in the model

^b The ANOVA model was as follows: $Y_{ijk} = CT_i + LT_j + ST_k + (CT*LT)_{ij} + (CT*ST)_{ik} + (LT*ST)_{jk} + (CT*LT*ST)_{ijk} + \epsilon_{ijk}$ where Y_{ijk} is the observed trap catch for cover type, land-area treatment and semiochemical treatment; i, j, k are the numbers of levels for each factor; and ϵ_{ijk} is the error term (unaccounted variation in the model). Cover type was significant ($F=14.53_{2,107}$, $P=0.002$); none of the second- and third-order interactions with the cover type were significant

^c The ANOVA model was as follows: $Y_{ijk} = LT_i + \eta_i + ST_j + (LT*ST)_{ij} + YR_k + (LT*YR)_{ik} + (ST*YR)_{jk} + (LT*ST*YR)_{ijk} + \epsilon_{ijk}$ where Y_{ijk} is the observed trap catch for land-area treatment, semiochemical treatment and year; i, j, k are the numbers of levels for each factor; η_i is the whole plot level random error term; and ϵ_{ijk} is the split plot level random error term

^d Data from 2001–2003

($F_{(2,106)} = 0.46$, $P=0.634$), of land-area treatment alone ($F_{(3,106)} = 1.19$, $P=0.32$), or semiochemical treatment alone ($F_{(1,106)} = 0.25$, $P=0.615$).

The grand mean percentage of male *I. perroti* trapped in 2001–2003 was 25% (Fig. 3a). Because of the higher

response of *I. perroti* (Fig. 2c), the trap catches analyzed included only those from traps baited with (–)-ipsdienol and (–)-ipsenol. The two-way ANOVA for the percentage of male *I. perroti* indicated significant effects of year ($F_{(2,103)} = 5.01$, $P=0.009$) and land-area treatment ($F_{(3,103)} =$

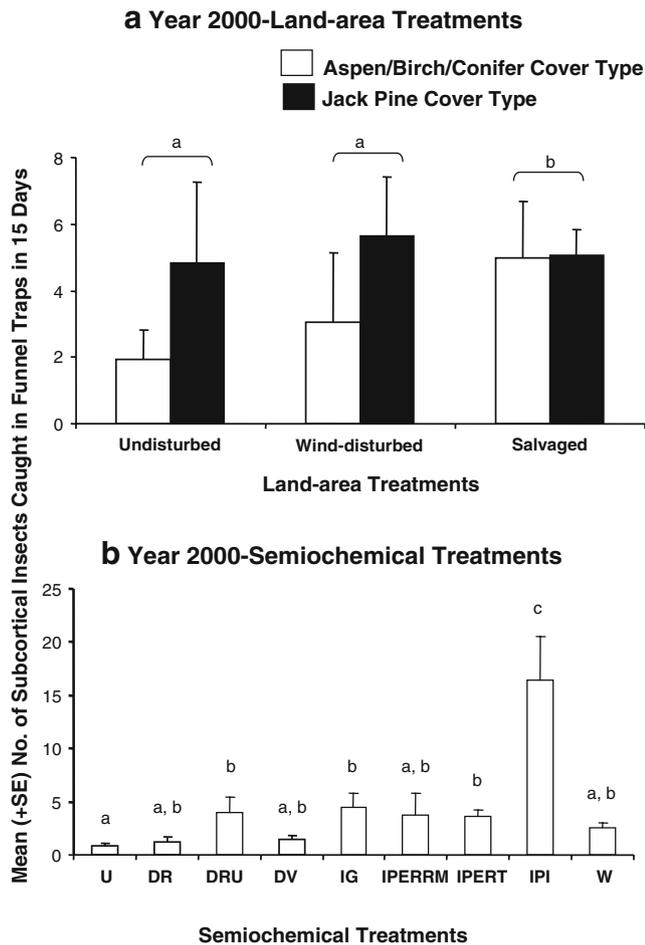


Fig. 1 Mean (+SE) number of subcortical insects per 15 d caught during 2000 in funnel traps in the undisturbed, wind-disturbed, and salvaged plots in the aspen/birch/conifer and jack pine forest cover types (a). Mean (+SE) number of subcortical insects per 15 d caught during 2000 in baited (eight semiochemical lures) or unbaited funnel traps in the aspen/birch/conifer and jack pine cover types (b). Key: U-Unbaited; DR-*Dryocoetes* spp.; DRU-*Dendroctonus rufipennis*; DV-*Dendroctonus valens*; IG-*Ips grandicollis*; IPERRM-*Ips perroti*; IPERT-*Ips perturbatus*; IPI-*Ips pini*; W-Woodborers ($N=18$). Different letters above histogram bars indicate significantly different means (Ryan-Einot-Gabriel-Welsch test, $\alpha=0.05$). In (a) the comparisons were made among land-area treatments pooled across cover types

3.16, $P=0.028$) (Fig. 3a). Across most land-area treatments the percentage of males trapped was higher in 2001 than in 2002 and 2003 (38–50%). The percentage of males trapped was significantly higher in the burned sites than in the rest of the land-area treatments (Fig. 3a).

The grand mean percentage of male *I. grandicollis* trapped in 2001–2003 was 26% (Fig. 3b). Because of the higher response of *I. grandicollis* (Fig. 2e), the trap catches analyzed included only those responding to the bait targeting *I. grandicollis*. The two-way ANOVA for the percentage of male *I. grandicollis* indicated a significant effect of year ($F_{(2,49)} = 10.11$, $P<0.001$) (Fig. 3b). There was no

effect of land-area treatment ($F_{(3,49)} = 0.39$, $P=0.761$) and no interaction between year and land-area treatment ($F_{(6,49)} = 0.83$, $P=0.554$). The percentage of males trapped was significantly higher in 2003 than in 2001 and 2002 (by 50%).

Subcortical Insect Species Richness In 2000, 57 and 67 species of subcortical insects were caught in the ABC and JP cover types, respectively. A comparison of species richness among land-area treatments in the two cover types (Fig. 4) reveals that in 2000 the salvaged forests contained both the greatest total (49 and 51 species) and the most unique insect species (18 and 12 species) when compared with the undisturbed and wind-disturbed forests. In 2000, only 33% and 34% of the insect species were common to all land-area treatments in the ABC and JP cover types, respectively.

In 2001–2003, a total of 140 species of subcortical insects were caught in the JP cover type. A comparison of species richness among land-area treatments reveals that the burned (110 species) and wind-disturbed (106 species) plots contained both the greatest numbers and the most unique insect species (18 and 14 species) (Fig. 5). Fifty three percent to 58% of the subcortical insect species were shared among the four land-area treatments in the JP cover type. The greatest numbers of insect species were shared among the wind-disturbed, salvaged, and burned forests (81 species).

Subcortical Insect Species Diversity Rarefaction analyses of subcortical insect trap catches from 2000 by land-area treatment showed that at a sub-sample size of 400 individuals, the ABC and JP salvaged forests had the greatest estimated mean species diversities (Supplemental Data Fig. 14). Subcortical insect trap catches from 2001–2003 in the JP cover type by land-area treatment showed that at a sub-sample size of 14,000 individuals, the wind-disturbed and burned forests had the greatest estimated mean species diversity (Supplemental Data Fig. 15). Sub-sample sizes of 400 and 14,000 individuals were chosen for 2000 and 2001–2003, respectively, for comparisons across land-area treatments because they were the lowest sub-sample sizes at which a land-area treatment (ABC and JP undisturbed forest areas, respectively) stopped accumulating more species.

Simpson's diversity indices for subcortical insects in 2000 indicated that the salvaged forests of both cover types had the greatest species diversity (Table 4). Simpson's diversity indices for subcortical insects in 2001–2003 indicated that all land area treatments in the JP cover type had similar levels of subcortical insect species diversity, but numerically, the wind-disturbed forests had the greatest species diversity followed closely by the undisturbed, burned, and salvaged forests (Table 4).

Rarefaction analyses of subcortical insect trap catches from 2000 by semiochemical treatment showed that at a

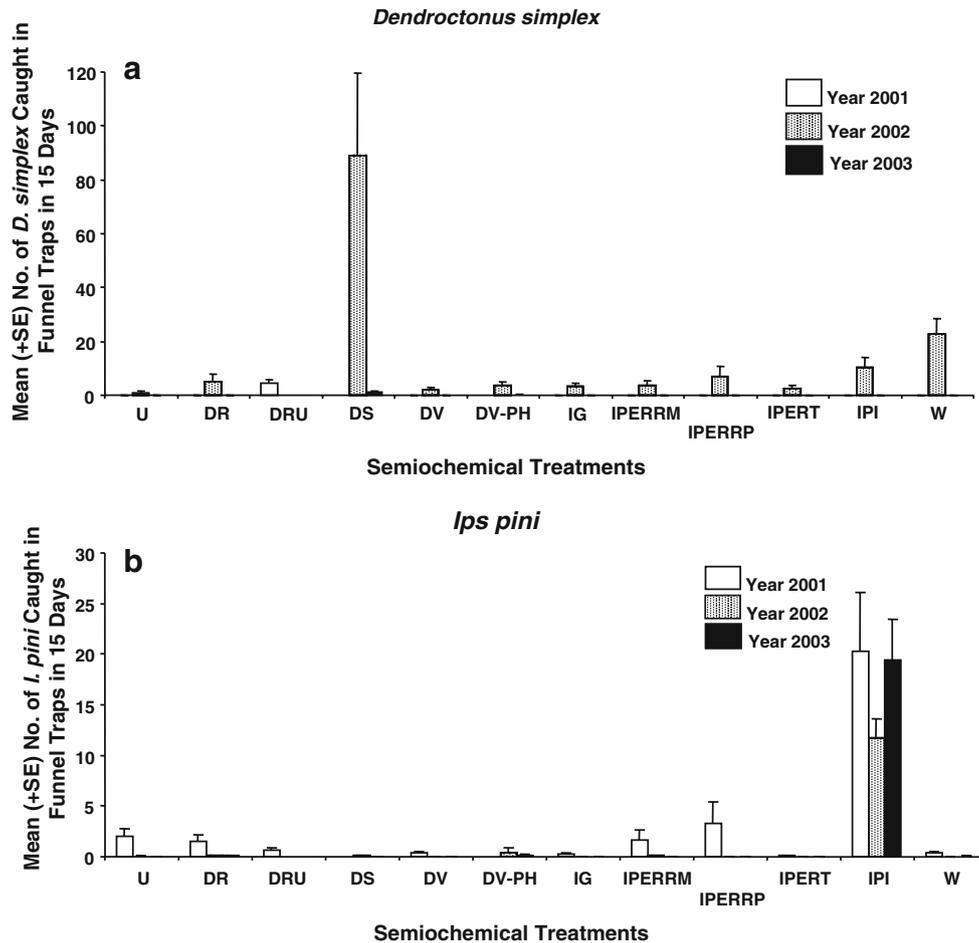


Fig. 2 Mean (+ SE) number of *Dendroctonus simplex* (a), *Ips pini* (b), *Ips perroti* (c), *Ips perturbatus* (d), *Ips grandicollis* (e), *Thanasimus dubius* (f), *Hylurgops rugipennis pinifex* (g), and *Dryocoetes autographus* (h) per 15 d caught during 2001–2003 in baited (11 semiochemical lures) or unbaited funnel traps in the jack pine cover type. Key: U- Unbaited control; DR- *Dryocoetes* spp.; DRU- *Dendroctonus rufipennis* (2001 only); DS- *Dendroctonus simplex* (2002 and 2003 only); DV- *Dendroctonus valens*; DV-PH- *Dendroctonus valens*-Phero Tech (2002 and 2003 only); IG- *Ips*

grandicollis; IPERRM- *Ips perroti*(-)-*Ips*dienol; IPERRP- *Ips perroti*(+)-*Ips*dienol; IPERT- *Ips perturbatus*; IPI- *Ips pini*; W- Woodborers. For 2001, *N* ranges from 103 to 108; for 2002, *N* ranges from 100 to 109; and for 2003, *N* ranges from 86 to 93 for each semiochemical treatment. Apparent response shifts by *D. simplex* (a, 2001–2002); *T. dubius* (f, 2001–2002); and *H. r. pinifex* (g, 2001–2002) resulted as a consequence of the introduction of the experiment of the DS bait (2002); the removal of the DRU bait (2002); and the introduction of the DV-PH bait (2002), respectively

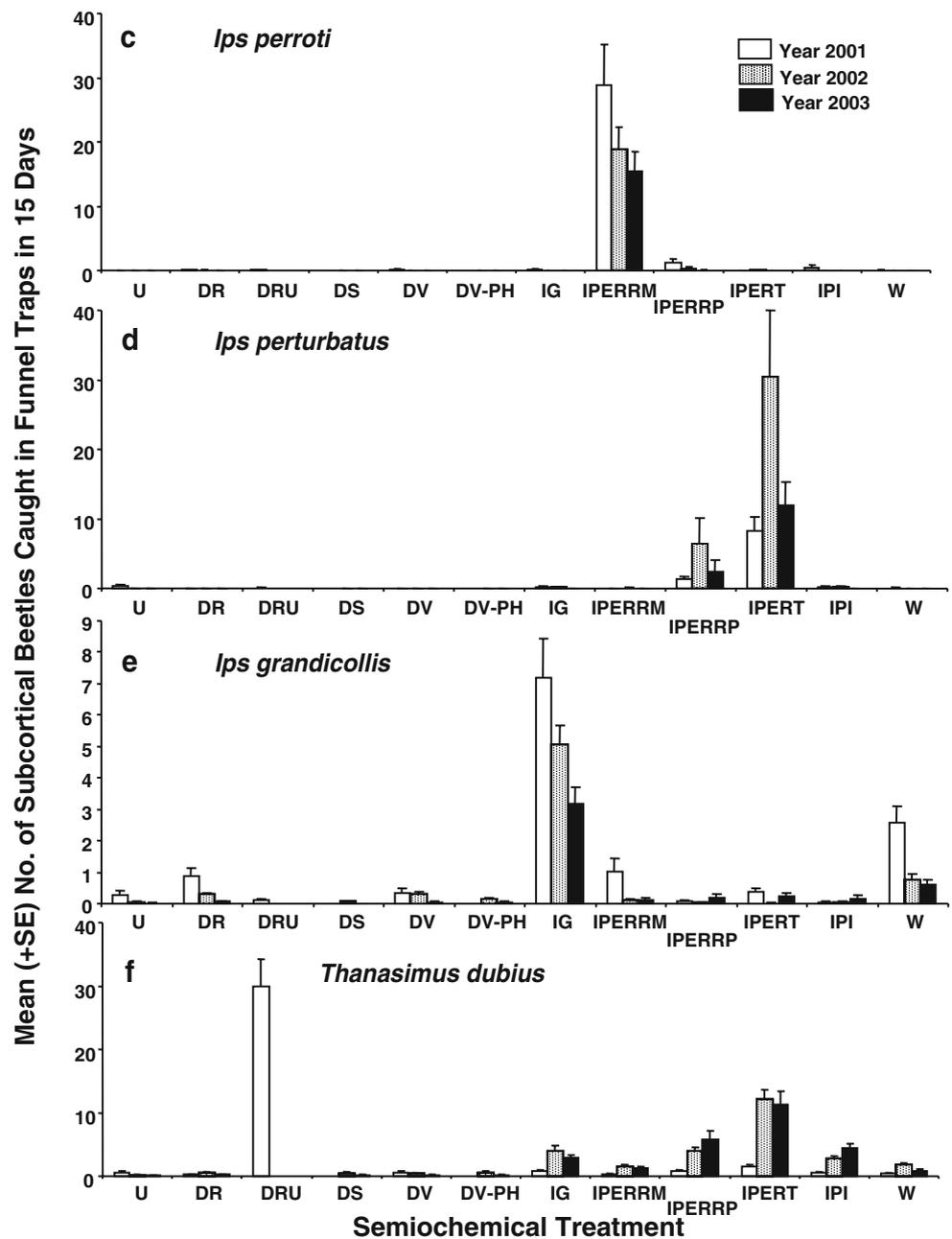
sub-sample size of 80 individuals, the *D. valens* bait elicited the numerically greatest estimated mean species diversity (Supplemental Data Fig. 16). Rarefaction analyses of subcortical insect trap catches from 2001–2003 by semiochemical treatment showed that at a sub-sample size of 1,500 individuals, the *Dryocoetes* spp. bait (Supplemental Data Fig. 17) elicited the numerically greatest estimated mean species diversity. Similar to the results from year 2000, the *I. pini* bait tended to accumulate more species with increasing sample sizes.

Simpson’s diversity indices for subcortical insects in 2000–2003 indicated that the *Dryocoetes* spp. bait elicited the greatest species diversity followed by the *D. valens* and *D. valens*-Phero Tech baits, and woodborer baits, the unbaited trap, and various other baits (Table 5). The species

diversities recorded from traps with the *I. pini* bait, the *I. perroti* (-)-*ips*dienol bait, and the *D. simplex* bait were the lowest, likely reflecting the specificity of these baits.

Subcortical Insect Species Composition The cluster analysis of subcortical insect species composition among JP land-area treatment combinations in 2001–2003 revealed that there were two distinct groups: 1) the 2002 salvaged and burned forests with 90% similarity; and 2) the rest of the land-area treatments over the 3-year period of the study (Fig. 6). There was little similarity in species composition between the 2002 salvaged and burned forests and the rest of the groups. Within the second group, 2001 burned forests were 20%; 2003 salvaged and burned forests (with 85% similarity) and 2001 salvaged forests were 55%

Fig. 2 (continued)



similar to the rest of the group. The undisturbed and wind-disturbed forests clustered together with >65% similarity in species composition. There was a 100% similarity between 2002 undisturbed and wind-disturbed forests.

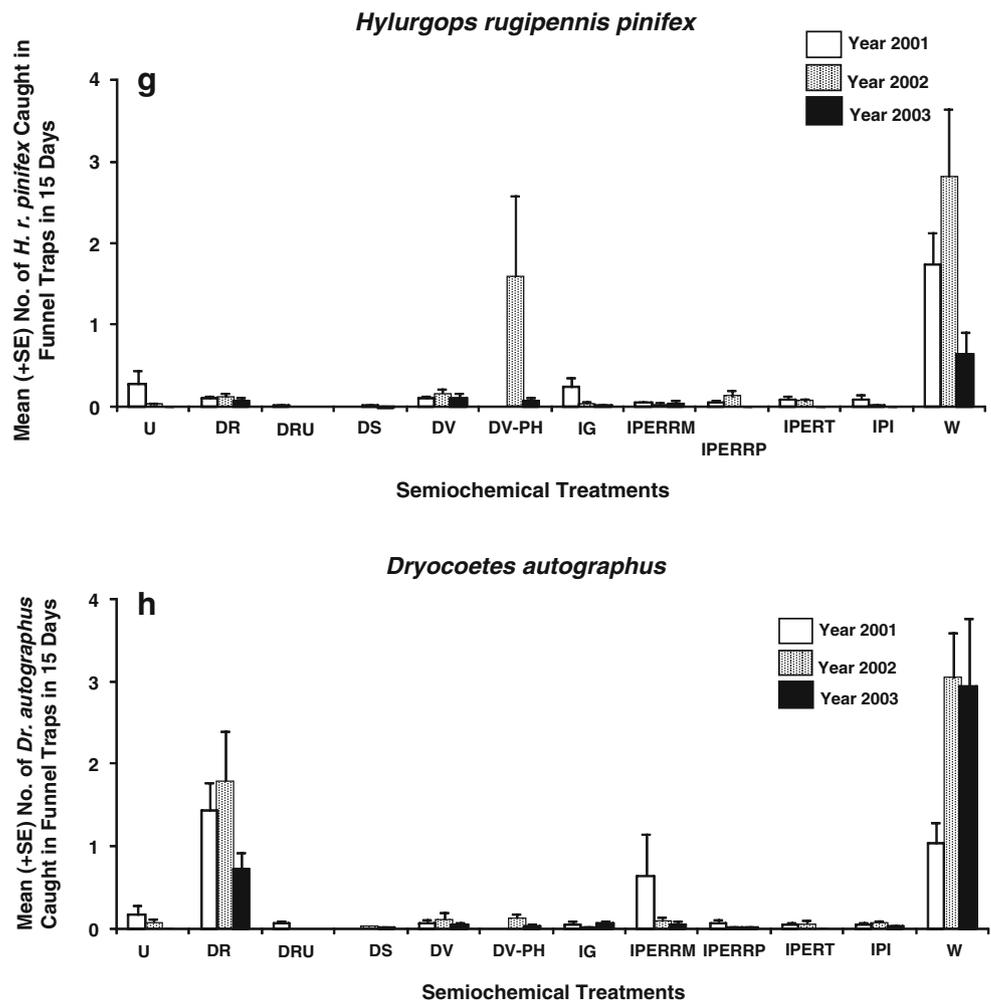
Bray-Curtis cluster analyses of the compositions of subcortical beetle species responding to semiochemical baits in 2001–2003 revealed that the traps baited with attractants for *D. simplex* or woodborers had the most distinct species composition with only 2% similarity with the trap catches to the rest of the baits (Fig. 7). The species compositions responding to the *I. grandicollis* and *I. perroti*-(+)-ipsdienol baits were 85% similar, whereas those to the *D. valens* and

Dryocoetes spp. baits and unbaited traps were 90% similar. There was almost 100% similarity between the trap catches to unbaited traps and the *D. valens*-baited traps.

Discussion

Our study of subcortical forest insect assemblages spanned 4 years with continuous summer trapping on a 120 km² stretch of sub-boreal forest landscape. We collected over 5,000 trap samples with 86,471 rhizophagous and subcortical insects represented by 143 species in baited Lindgren

Fig. 2 (continued)



funnel and pitfall traps. Other studies in North America on subcortical beetles of similar scope are by Hammond (1997) and Hammond et al. (2001) where 40,049 beetles represented by over 250 species were collected in 3 years from aspen, *Populus* spp., stands in north-central Alberta, Canada; and by Jacobs (2004) where 18,374 beetles represented by over 230 species were collected in 3 years from boreal deciduous and coniferous stands in northern Alberta. Neither of these studies used semiochemicals as baits to target key species in the trap catches. Although we caught a greater number of beetles in our traps, we had lower species richness than these other studies on subcortical insects. Possible reasons include: 1) inclusion of late-successional beetle taxa (e.g., Colydiidae, Elateridae, Passalidae, and Staphylinidae) by previous researchers in their analyses in contrast to inclusion of only early-successional taxa in our study (Savely 1939; Gibb et al. 2005); 2) the use of window-traps attached directly to the trees by previous researchers in contrast to baited Lindgren funnel traps hung from poles in our study (e.g., Sverdrup-Thygeson and Birkemoe (2008) found that window traps

hung directly on aspen trees caught more beetles associated with aspen than traps hanging freely); and 3) some of the highly specific semiochemical baits that we used attracted large numbers of target species, but captured far fewer taxa than did unbaited traps or more generically baited traps.

The subcortical insect guild that we have characterized likely originated primarily from jack pine (*P. banksiana*) [e.g., *I. grandicollis*, *I. perroti*, *I. pini*, *Pityogenes plagiatus plagiatus* (LeConte) (all Scolytidae) and *M. s. scutellatus* (Cerambycidae)], with identifiable components from *L. laricina*, *Picea glauca*, *P. resinosa*, and *P. strobus*. For example, *D. simplex*, *Pityokteines sparsus* (LeConte), *P. rufipennis*, and *Scolytus piceae* (Swaine) (all Scolytidae), and *Phymatodes dimidiatus* (Kirby) and *Xylotrechus undulatus* (Say) (both Cerambycidae) have been reared or collected frequently from *L. laricina* (Blackman and Stage 1918; Dodge 1938; Linsley and Chemsak 1997). Similarly, *Crypturgus borealis* Swaine, *D. rufipennis*, *I. perturbatus*, *P. rufipennis*, and *Dryocoetes affaber* (Mannerheim) (all Scolytidae); and *Monochamus* spp. and *Tetropium cinnamopterum* Kirby (both Cerambycidae) have been reared or

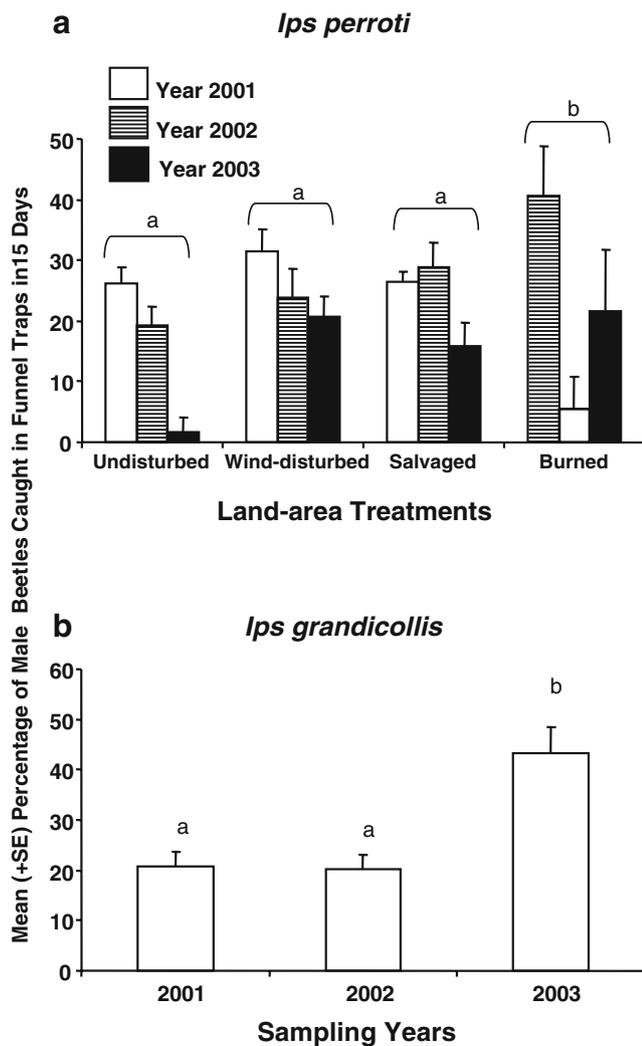


Fig. 3 **a** Percentage male (+ SE) *Ips perroti* per 15 d caught in funnel traps during 2001–2003 in the undisturbed, wind-disturbed, salvaged, and burned plots in the jack pine cover type ($N=104$). **b** Percentage male (+ SE) *Ips grandicollis* per 15 d caught in funnel traps during 2001–2003 in the jack pine cover type ($N=50$). Different letters above histogram bars indicate significantly different means (Ryan-Einot-Gabriel-Welsch test, $\alpha=0.05$). In **(a)** the comparisons were made among land-area treatments pooled across years

collected frequently from *P. glauca* (Dodge 1938; Whitmore 1982; Gara et al. 1995; Linsley and Chemsak 1997; Haberkern et al. 2002). *Ips latidens* and *I. pini* (Scolytidae) occur in *P. strobus* (Dodge 1938; Bright 1976; Wood 1982b; Drooz 1985). Other subcortical taxa such as *D. valens* and *Trypodendron lineatum* (Olivier) (both Scolytidae), as well as most Buprestidae, Cerambycidae, and Siricidae are extremely polyphagous; rearing studies from bark samples or cut logs are needed to establish host relationships.

Compared with subcortical insects caught in funnel traps, we caught few individuals and species of rhizophagous beetles in pitfall traps in 2000–2003. Such a result is

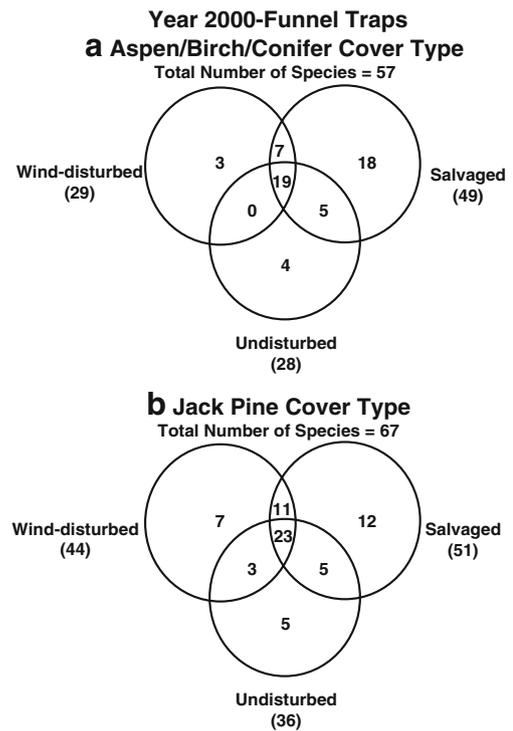


Fig. 4 Venn diagram depicting the total number of subcortical insect species trapped in funnel traps in 2000, and shared by or unique to the undisturbed, wind-disturbed, and salvaged plots in the aspen/birch/conifer **a** and jack pine **b** cover types. Values in parentheses below each land-area treatment refer to the total number of species collected in each habitat

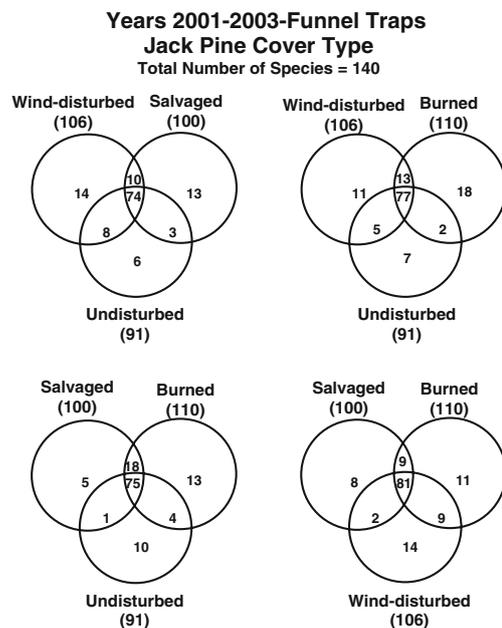


Fig. 5 Venn diagram depicting the total number of subcortical insect species trapped in funnel traps in 2001–2003, and shared by or unique to the undisturbed, wind-disturbed, salvaged, and burned plots in the jack pine cover type. Values in parentheses refer to the total number of species collected in each habitat

Table 4 Species diversity estimates from Simpson's diversity index for subcortical insects caught in funnel traps by land-area treatment in 2000–2003, Superior National Forest, Cook Co., MN, USA

Year	Cover Type	Undisturbed	Wind-disturbed	Salvaged	Burned
2000	Aspen/Birch/Conifer	0.582	0.528	0.742	NA ^a
	Jack Pine	0.679	0.684	0.837	NA ^a
2001–2003	Jack Pine	0.888	0.912	0.884	0.887

^aNA = Not Applicable

unexpected in the wind-disturbed and burned areas where large numbers of windthrown trees with exposed roots were present. This suggests that either the rhizophagous beetles persisted at much lower populations than the stem-colonizing beetles in these forests, or that the baited pitfall traps that we used may not have been the optimal trapping method. In 2000, a high release-rate device was used, and the solution evaporated within a week; in 2001–2002, we used a plastic release device from which ethanol did not elute rapidly (David Wakarchuk, Synergy Semiochemical, personal communication); and in 2003, we used the same plastic release device with a hole in the cap. None of these release devices, especially the one in 2003, seemed to attract large numbers of rhizophagous beetles. In the 2000 field season, which occurred one-year post disturbance and had the highest probability of high populations of rhizophagous insects, the high release from the devices may have rendered our traps effectively unbaited through the latter part of the sampling periods. Nonetheless, other workers have found that sampling rhizophagous insects is problematic; by using baited pitfall traps, Erbilgin et al. (2001) caught only 315 beetles in Wisconsin as compared to 2,624 beetles in Louisiana. They further reported that the baited pitfall traps were more effective than lower stem flight traps (Klepzig et al. 1991) in capturing rhizophagous beetles in Wisconsin than in Louisiana. There appear to be regional differences in both the population levels and responses of rhizophagous beetles to trap-type, which might further affect techniques for monitoring in sub-boreal forests. Rhizophagous beetles generally are difficult to sample and observe in the forest due to their cryptic life-stages. Their larvae are associated with roots and adults hide in the forest litter layer (Lynch 1984; Drooz 1985). Other possible methods to sample rhizophagous beetles include the use of insect emergence cages for infested roots, bark peeling of roots, and placement of pitfall traps directly in and around downed trees.

Effects of Semiochemical Treatments on Subcortical Insects

Overall Variability The effects of semiochemical treatments on subcortical insect flight responses generally were dependent upon the year of sampling and land-area treatments. Such high variability may be a reflection of the rapid

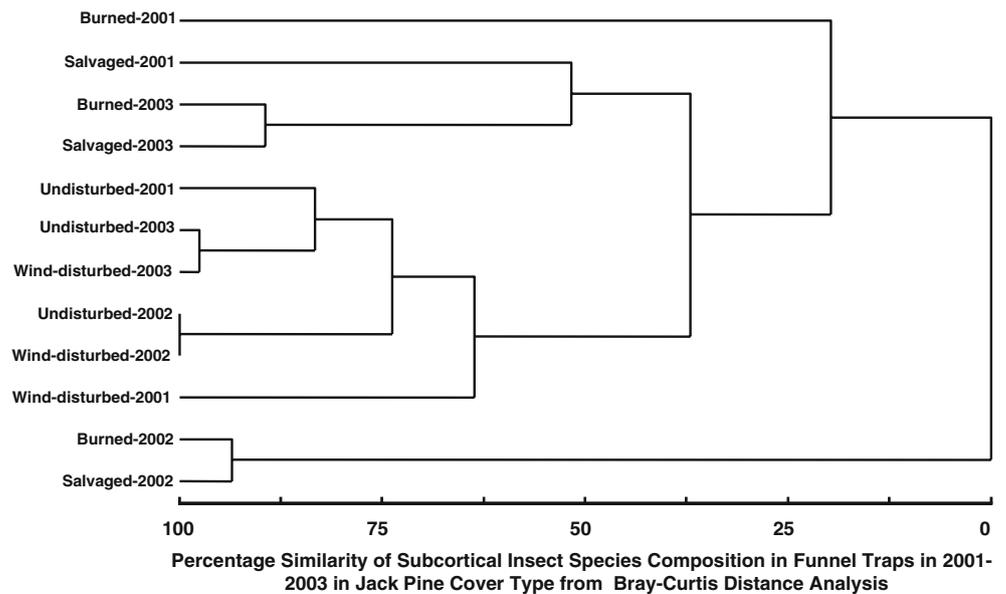
turnover of subcortical insect communities within the disturbed habitats, and the associated large volume of semiochemical signaling by numerous species present at any given time. For example, semiochemicals of some species of scolytid beetles may interfere with the behavioral responses of related and/or competing species (e.g., allomones) (Wood et al. 1967; Birch and Wood 1975; Furniss and Livingston 1979; Borden et al. 1992; Miller and Borden 1992). Other possible reasons for the variable responses include: 1) high population levels of dominant subcortical species at the time of sampling (*see* next paragraph); and 2) the effects of local physical factors such as forest structure and weather conditions, whose effects on responses to semiochemicals are less well understood (Thistle et al. 2004). For studies conducted within a single habitat and over a short period of time, there is the potential to underestimate the variability of the responses of subcortical insects to semiochemicals.

Subcortical Insect Trap Catches Total catches of all subcortical insects were highest in response to the *D. simplex* bait, especially in 2002 in the burned areas. This trend may reflect high population levels of *D. simplex*, and

Table 5 Species diversity estimates from Simpson's diversity index for subcortical insects caught in funnel traps by semiochemical treatment in 2000–2003, Superior National Forest, Cook Co., MN, USA

Semiochemical Baits	Simpson's index
<i>Dryocoetes</i> spp.	0.935
<i>Dendroctonus valens</i>	0.929
<i>Dendroctonus valens</i> -Phero Tech	0.920
Woodborers	0.919
Unbaited	0.915
<i>Ips perroti</i> (+)-ipsdienol	0.904
<i>Ips grandicollis</i>	0.873
<i>Ips perturbatus</i>	0.731
<i>Dendroctonus rufipennis</i>	0.640
<i>Ips pini</i>	0.613
<i>Ips perroti</i> (-)-ipsdienol	0.583
<i>Dendroctonus simplex</i>	0.165

Fig. 6 Dendrogram of the percentage similarity of subcortical insect species trapped in funnel traps in 2001–2003 in the undisturbed, wind-disturbed, salvaged, and burned plots in the jack pine cover type

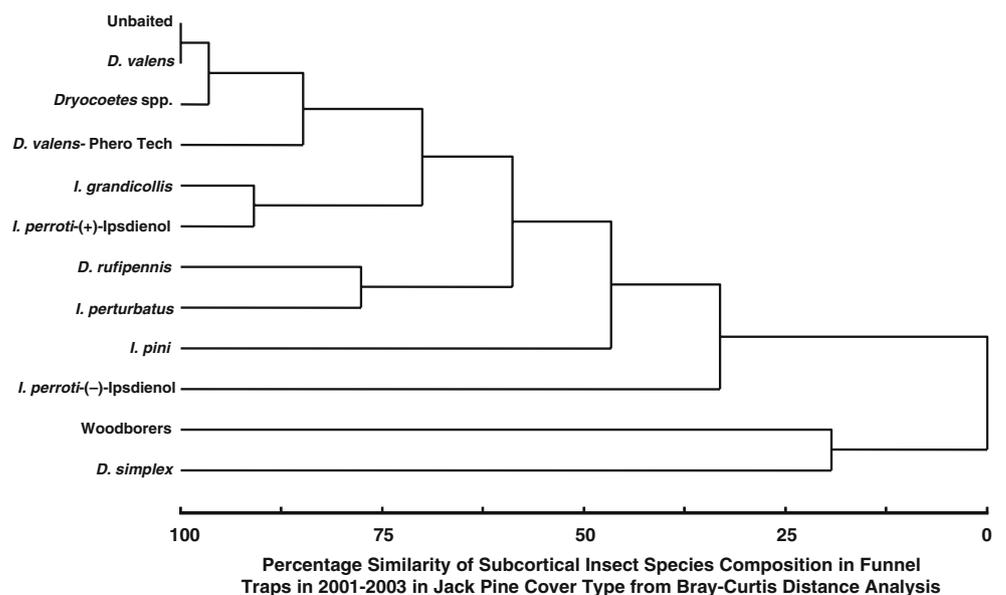


may account for a delayed response observed for all scolytid beetles. The greatest numbers of scolytids were also caught in response to the *D. simplex* bait in 2002 in the burned areas. This overall trend was driven by catches of *D. simplex*, which was the primary scolytid caught during this field season, and is the only native bark beetle that colonizes and kills tamarack and exotic larches in North America (Langor and Raske 1987; Seybold et al. 2002). In recent years, this species has shown an increase in activity, causing >75% mortality of tamarack trees in some areas of northern Minnesota (Albers 2005).

More predatory checkered beetles (Cleridae) were caught in response to the *D. rufipennis* bait than to the rest of the baits. This was true especially in 2001 in the wind-

disturbed forests. The dominant clerid was *T. dubius*, a major predator of *I. pini* in the Great Lakes region (Schenk and Benjamin 1969), and of southern pine beetle, *Dendroctonus frontalis* Zimmermann, in the southern U.S. (Thatcher and Pickard 1966; Berisford 1980). The *D. rufipennis* bait initially was employed in 2000 and 2001 in anticipation of potential population increases of *D. rufipennis*, whose western North American populations respond to wind disturbances (Nelson 1950; Graham 1952; Schmid and Frye 1977; Holsten et al. 1999; Gandhi et al. 2007). However, the commercially available *D. rufipennis* bait was ineffective for attracting eastern populations of *D. rufipennis* in this study and in other studies in northern Minnesota (Seybold et al., unpublished data). We also

Fig. 7 Dendrogram of the percentage similarity of subcortical insect species trapped in funnel traps in 2001–2003 in response to eleven semiochemicals and an unbaited control trap in the jack pine cover type



caught more individuals of *D. simplex* than of *D. rufipennis* in response to this bait in 2001, and thus, we used the *D. simplex* bait in the subsequent years of the study. Mizell et al. (1984) found that *T. dubius* responded positively to frontalin, ipsdienol, and α -pinene. Vité and Williamson (1970) and Dixon and Payne (1980) also found that *T. dubius* was attracted to frontalin, an aggregation pheromone of *D. frontalis*. Similar results were found by Haberkern and Raffa (2003), where *T. dubius* and *Enoclerus nigrifrons* (Say) were attracted to the commercial *D. rufipennis* bait deployed in traps in *P. resinosa* stands in Wisconsin. This suggests that *T. dubius* is a generalist predator of scolytid beetles in both *Pinus* and *Picea* stands.

As expected, *I. pini* was caught in greater numbers in the *I. pini*-pheromone-baited traps, especially in the year 2002. There is geographic variation in the production and response of populations of *I. pini* to various enantiomeric blends of ipsdienol (Lanier et al. 1980; Birch et al. 1980; Seybold et al. 1995). In western populations, *I. pini* is attracted to 97% (-)-ipsdienol and is inhibited by (+)-ipsdienol (Birch et al. 1980). However, in eastern populations, *I. pini* is attracted to a racemic mixture of ipsdienol (Lanier et al. 1980). The responses of *I. pini* to the enantiomers of ipsdienol have been reported from other North American locations (Raffa and Klepzig 1989; Herms et al. 1991). In northern Minnesota, (+/-)-ipsdienol along with lanierone would be an effective pheromone to monitor the populations of *I. pini* (Teale et al. 1991; Seybold et al. 1992, 1995; Miller et al. 1997).

In 2000, we targeted *I. perroti* by using the combination of (+)-ipsdienol and (-)-ipsenol. However, this bait caught very few *I. perroti*. In 2001–2003, we also tested the combination of (-)-ipsdienol and (-)-ipsenol to target this species. Nearly twice as many *I. perroti* were caught in response to this combination, especially in the undisturbed and wind-disturbed forests. Ayres et al. (2001) reported that populations of *I. perroti* in Wisconsin red pine (*P. resinosa*) forests were attracted to a racemic mixture of ipsdienol and ipsenol. We tested only the pure enantiomers of ipsdienol (and not the racemate) in combination with ipsenol. Our results suggest that (-)-ipsdienol and (-)-ipsenol are effective baits for monitoring *I. perroti* in northern Minnesota.

In 2000, we used *endo*-brevicomin as an attractant to target species of bark beetles in the genus *Dryocoetes*, but we caught only a few specimens of *Dryocoetes* spp. Therefore, in 2001–2003, we used racemic *exo*-brevicomin and (-)- α -pinene (Camacho et al. 1998). No previous research had been conducted on *Dryocoetes* spp. pheromone biology in eastern North America, so we used these western model systems as our best-guess strategy for monitoring biodiversity. Although there was some attraction of *Dr. autographus* to the bait with *exo*-brevicomin, the

greatest response by this species was to the woodboring beetle bait, especially in the wind-disturbed forests. Williams and Borden (2004) reported that *Dr. autographus* in British Columbia was most attracted to racemic and (+)-*exo*-brevicomin. Kohnle and Vité (1984) also found that European populations of *Dr. autographus* produce *exo*- and *endo*-brevicomin. The only semiochemical component common between the *Dryocoetes* spp. and woodboring beetle bait was (-)- α -pinene, which was released at an 18-fold higher rate in the latter bait. Camacho et al. (1998) reported similar results for *Dr. confusus* Swaine where (-)- α -pinene improved the response to *exo*-brevicomin in the field. (-)- α -Pinene may be more attractive to *Dr. autographus* than *exo*- or *endo*-brevicomin in our eastern sub-boreal populations.

In 2001–2003, more *Hylurgops r. pinifex* (Scolytidae) were caught in the *D. valens*-Phero Tech and woodboring beetle baits, primarily in the undisturbed and wind-disturbed forests. Very little information is available on the chemical ecology of this species. The common component between *D. valens*-Phero Tech and the woodboring beetle bait is α -pinene. The European species, *H. palliatus* Gyllenhal, was more attracted to ethanol than to host monoterpenes including (+/-)- α -pinene, (+)-3-carene, and terpinolene (Volz 1988; Byers 1992). In contrast, Schroeder and Lindelow (1989) reported that *H. palliatus* was attracted to the combination of both ethanol and α -pinene. Thus, α -pinene may be one of the attractant components for the species in the genus *Hylurgops*.

Among the most abundant subcortical beetles, *B. maculativentris*, *C. virginianensis*, and *P. rufipennis* did not show any response to semiochemical treatments. Both *B. maculativentris* and *C. virginianensis* (buprestid species) may respond to the general odors produced by dead and dying tree hosts (see also Crook et al. 2008). However, Chénier and Philogène (1989) reported a lack of response of buprestid beetles to ethanol and monoterpenes in central Ontario, and they suggest that visual cues may be more important in finding hosts. Similarly, Montgomery and Wargo (1983) reported a lack of response of buprestid beetles to ethanol in Connecticut. Male *P. rufipennis* (Scolytidae) produces an aggregation pheromone while feeding on *Picea glauca* trees in British Columbia (Bowers and Borden 1990), identified as 3-methyl-3-buten-1-ol (Bowers et al. 1991). *Polygraphus rufipennis* also was attracted to a *Dryocoetes* spp. bait in *P. resinosa* stands in Wisconsin (Haberkern and Raffa 2003). In our study, it was caught in the second highest numbers in the *Dryocoetes* spp. bait, but in similar numbers in the unbaited funnel trap. These disparate regional results suggest further work on the semiochemicals of *P. rufipennis* is needed.

Overall, attractants for *I. perroti*, *I. pini*, and *D. simplex* were the most useful baits in trapping their respective target

beetles. *Ips grandicollis* and *I. perturbatus* also responded to their respective target baits at a higher level than to any other semiochemical treatments, but *I. grandicollis* and *T. dubius* tended to be semiochemical generalists when compared with the responses of *I. perroti* and *I. pini* to the spectrum of semiochemicals that we tested (Fig. 2). The *D. valens*, *D. valens*-Phero Tech, *Dryocoetes* spp., and wood-boring beetle baits were the least efficient in capturing their target beetle species in the sub-boreal forests. *Dendroctonus valens* does not have a known pheromone but it is attracted to (+)- α -pinene, (-)- β -pinene, and (+)-3-carene (host kairomones) in western populations (Hobson et al. 1993; White and Hobson 1993), and to (-)- α -pinene, ipsdienol, and lanierone in eastern populations (Erbilgin and Raffa 2000). We did not find a similar attraction of *D. valens* to ipsdienol and lanierone, thus suggesting that more research needs to be conducted on the semiochemical attractants for this species.

Some species of cerambycid beetles showed a trend of greater attraction to the woodboring beetle bait. Cerambycid beetles have a general attraction to host kairomones and scolytid pheromones, although some short-range sex-pheromones also have been isolated (Allison et al. 2004). The presence of higher concentrations of plant volatiles present in the disturbed forest stands may have interrupted attraction of some beetle species to their respective baits or provided competing sources of attraction. Subcortical species with a primary attraction to host attractants may be difficult to trap and monitor with baited funnel traps in disturbed forests due to olfactory competition with large amounts of damaged and moribund trees.

Subcortical Insect Richness and Diversity The greatest diversity of subcortical insect was observed in response to the *D. valens* and *Dryocoetes* spp. baits. Both of these baits had monoterpenes that may have acted as a general attractant for subcortical insects. It also is likely that other bait types with pheromone components may have deterred non-target subcortical insect species. *Dendroctonus valens* and *Dryocoetes* spp. baits, although not as effective in capturing their target species, may have greater efficacy in capturing a broader spectrum of subcortical species in a sub-boreal forest. The lowest biodiversity was recorded from traps baited with lures for *I. pini*, *I. perroti*, and *D. simplex*, perhaps reflecting the specificity of these baits.

Subcortical Insect Species Composition Cluster analyses of subcortical insect species composition among the semiochemical baits in 2001–2003 revealed that woodborer and *D. simplex* baits elicited the most distinct species composition (there was only 2% similarity with the rest of the bait types). Such differences could be attributed to the efficacy of the woodborer and *D. simplex* baits in attracting their target beetles, and their associated subcortical insects

(Table 5). This result also indicates that subcortical insect species that responded to the woodborer and *D. simplex* baits may differ from those that responded other bait types. The species composition of subcortical insects that responded to the *I. grandicollis* and *I. perroti* baits clustered together with 85% similarity. As these baits had (-)-ipsenol in common, this pheromone component may have the capacity to attract similar subcortical species. The species assemblages that responded to the *D. valens* and *Dryocoetes* spp. baits, and the unbaited traps clustered together with >85% similarity, which suggests that the *D. valens*- and *Dryocoetes* spp.-baited traps acted almost like unbaited funnel traps. These two baits and the unbaited trap caught both the greatest numbers of similar, though not identical, subcortical species.

Effects of Land-Area Treatments on Subcortical Insects

Subcortical Insect Trap Catches From 2000–2003, total insect catches between the wind-disturbed and undisturbed forest plots generally were similar. However, in 2001 we caught approximately 2.5-fold more subcortical insects in the wind-disturbed than in the undisturbed areas. Thus, the trap catches of subcortical insects were high 2 years after the wind storm (in 2001), but then they declined. Possible reasons for the decline of early-successional subcortical insect flight activity with time are: increasing populations of insect (Ryall 2003; Ryall et al. 2006) and avian (Baldwin 1968; Fayt et al. 2005) natural enemies (Ryall and Smith 2001); greater inter- and intra-specific competition (Robins and Reid 1997); lower availability and quality of CWD as habitat on the disturbed landscape (Wallace 1953; Wickman 1965; Jacobs 2004); and/or rapid salvaging of other downed material on the landscape (USDA Forest Service 1962, 1965). Similar results were reported for the activity of *I. pini* in ice-damaged *P. resinosa* stands in Ontario where beetle activity declined markedly 2–4 years after the storm (Ryall et al. 2006), and for the activity of *Dendroctonus brevicornis* LeConte in wind-damaged stands in California where beetle activity declined 2 years after the storm (Miller 1928). Populations of *Ips typographus* (L.) and other subcortical beetles peaked 2 years after a wind storm (Vivian) in Switzerland (Wermelinger et al. 1999) and after another wind storm (Lothar) in 1999 in France (Nageleisen 2001). In contrast, after the storm in France, ambrosia beetles (Scolytidae) in the windthrow gaps of a hardwood forest did not increase subsequently in abundance when compared to undisturbed forest areas (Bouget and Noblecourt 2005). Thus, responses of subcortical beetles to wind storms may be taxon specific, and may vary across forest types.

In 2001 and 2002, similar numbers of all subcortical insects were caught in funnel traps in the wind-disturbed and burned forests. However, in 2003, the trap catches of

subcortical insects were lower in the salvaged and burned areas as compared to the wind-disturbed sites. This suggests that although burning initially retained similar or higher numbers of insects than the wind-disturbed areas, flight activity of subcortical insects decreased 4 years after the wind storm in the areas where two disturbances were combined. One explanation for this effect is that the wind-disturbed sites continued to provide food for the beetles (i.e., residual and leaning trees continued to die into the fourth year after the storm). In the burned or logged areas, the residual trees did not die (or there were few residual trees). Alternatively, olfactory cues from the burning and/or logging may have attracted subcortical insects into these treatment sites in 2001 and 2002, but perhaps because of an absence or paucity of host material from the treatments, the insects were lured into traps rather than colonizing and reproducing in the woody debris. Werner (2002) reported that in *P. glauca* stands in Alaska, both clear-cutting and burning increased the populations of subcortical scolytid, buprestid, and cerambycid beetles during the first year after the land-area treatments. Populations of these Alaskan subcortical beetles declined to the pre-disturbance level 5–10 years later. In our study, the decline following the disturbances may have occurred on an even shorter time scale. In black spruce, *Picea mariana*, stands in Quebec, Boulanger and Sirois (2007) described two phases of subcortical insect colonization of trees after burning. The first phase occurs shortly (up to 1 year) after tree death from the fire. Insect populations decline for several years after this phase, but then increase again during the second phase when dead trees fall to the ground and are colonized by fungivorous and saprophagous subcortical insects. Our study likely did not continue long enough to capture this second phase of population increase, nor did we attempt to capture saprophages.

At the family level, flight-activity responses of subcortical insects to forest disturbances also varied with the year of sampling. In 2002, scolytid beetles responded in greater numbers in salvaged and burned as compared to undisturbed forest areas. In contrast, in 2001, clerid and buprestid beetles responded in greater numbers in all land-area treatments as compared to undisturbed forest areas. We hypothesize that the response of scolytid populations showed a lag-period because they may have originated and slowly increased in numbers from within the disturbed stands (Wermelinger et al. 2002). We also observed limited colonization of downed trees in summer 1999 and spring 2000 by scolytids (K.J.K.G. and S.J.S., personal observations). Buprestid beetles in the disturbed stands may have originated from immigration from other stands as a response to the increased amounts of CWD, and/or from within the stand as they generally take 2 years to develop (Bright 1987). Greater populations of clerid beetles present

in 2001 likely were due to their strong attraction to frontalin in the *D. rufipennis* bait, which was used only in this year, and to the increased prey populations after the disturbance event (see next paragraph).

At the species level, in 2001, *I. pini*, *T. dubius*, and *M. s. scutellatus* increased their flight activity in the wind-disturbed and burned areas, and *B. maculativentris*, *T. nubilus*, and *P. rufipennis* showed similar flight activity in the burned areas. However, abundance declined 4 years after the storm. Thus, these species responded positively for a short-time to a compound disturbance on the landscape (i.e., wind followed by burning). In contrast, other species such as *C. virginiensis* and *Dr. autographus* did not increase in numbers in either the wind-disturbed or the burned areas, indicating that these species either do not always respond to the increased amounts of CWD on the landscape or that there may be greater negative pressure from competition, predators, and parasites in disturbed stands.

Among the Scolytidae, relatively more males of *I. perroti* were caught in 2001 than in 2002–2003, whereas for *I. grandicollis* relatively more males were caught in 2003 than in 2001–2002. In 2001, a greater percentage of male *I. perroti* were caught in the burned forests than in the rest of the land-area treatments. We found similar numbers of male and female *I. perroti* emerging from *P. banksiana* trees (Gandhi 2005), so we expected an equal sex-ratio in the flight response of *I. perroti* to the semiochemical-baited traps. Possible reasons for a skewed sex ratio include differential mortality of the sexes (Cameron and Borden 1967) (across land-area treatments and years) or a differential attraction of the sexes to traps in the various land-area treatments.

Subcortical Insect Richness and Diversity In Minnesota there were reportedly 23 species of buprestids (Downie and Arnett 1996), 275 species of cerambycids (Downie and Arnett 1996; Yanega 1996), one species of histerid (Downie and Arnett 1996), 64 species of scolytids (Dodge 1938; Wood 1982b), and 4 species of siricids (Smith and Schiff 2002). Our field study and concurrent museum survey established new Minnesota state records for 23 subcortical insect species in six families: *C. sexsignata*, *C. striata*, *C. sulcicollis*, *P. aeneola*, and *P. d. drummondi* (Buprestidae); *P. n. nigrella* and *X. tibialis* (Cerambycidae); *E. muttkowski*, *E. n. rufiventris*, *M. dislocatus*, *T. trifasciatus*, *T. nubilus*, *T. u. undatulus*, *T. nutalli*, and *Z. sanguineus* (Cleridae); *P. teres*, *P. coarctatum*, *P. deficiens*, and *P. lecontei* (Histeridae); 5) *I. latidens* (Scolytidae); and *S. behrensii*, *U. g. flavicornis*, and *X. spectrum* (Siricidae). The University of Minnesota Insect Collection specimens of previously unreported subcortical species in Minnesota were collected as early as 1894, and in the case of *T. nutalli*, were distributed in as many as 21 counties. In most cases, these specimens represented native fauna from local vegetation. In our field

study, the taxa were also derived primarily from the native fauna present in the sub-boreal Minnesotan forests. However, both *P. d. drummondi* and *P. n. nigrella* have been reported recently from western larch (*Larix occidentalis* Nutt.) logs imported to central Minnesota from Montana (Dodds et al. 2004). Regional distributions of most insects we collected suggest they are native in northeastern Minnesota. For example, *Chrysobothris sexsignata*, *E. n. rufiventris*, and *T. nutalli* occur in *P. resinosa*, *P. banksiana*, and *P. strobus* stands in the adjacent province of Ontario, Canada (Chénier and Philogène 1989), and *I. latidens* occurs in Ontario in *P. strobus* (Bright 1976). *Enoclerus mutkowskii*, *E. nigripes*, *T. undatulus*, and *Z. sanguineus* occur in stands of *P. resinosa* in the adjacent state of Wisconsin (Aukema and Raffa 2000, 2005; Aukema et al. 2000a, b, 2004, 2005; Erbilgin and Raffa 2001; Erbilgin et al. 2003) and *Z. sanguineus* may be associated with a hardwood tree (butternut), *J. cinera*, in Wisconsin (Katovich and Ostry 1998).

Sirex behrensii is a woodwasp primarily found in western North America, but it was recently collected in Ohio, where it was found emerging from imported lumber (Smith and Schiff 2002; D. Smith, personal communication). Hence, either the range of this species is more extensive than previously thought, or it has also been introduced to the forests of Minnesota. It is important to note that this species erroneously has been reported to occur in Virginia and Florida (Smith and Schiff 2002: 178; D. Smith, personal communication).

In 2001–2003, the wind-disturbed forest areas in Minnesota had greater species richness and diversity than the undisturbed areas. Wind storms provide a sudden and localized increase in CWD, which may provide habitat for subcortical insect species (Bouget and Duelli 2004; Gandhi et al. 2007). After windstorm Vivian in Switzerland, there was also an increase in the species richness of scolytid and cerambycid beetles in wind-disturbed areas as compared to the cleared wind-disturbed sites (Wermelinger et al. 2002, 2003). In our study, species richness and diversity were greater in burned areas than in salvaged areas, which suggests that greater numbers of beetle species were attracted to the recently burned, larger-sized pieces of CWD (Gilmore et al. 2003), and to fire-damaged and dead residual trees. There is evidence that fire-damaged trees produce greater amounts of ethanol and, therefore, attract greater numbers of subcortical beetles than do undamaged trees (Santoro et al. 2000; Kelsey and Joseph 2003). Although burning eventually results in lowered population levels of early-successional subcortical beetles, it may actually result in a greater species richness and diversity on the sub-boreal landscape (Santoro et al. 2000). It presently is unclear whether prescribed burning will retain similar species diversity to that of naturally burned forests,

as there may be inherent differences in the amounts and types of CWD in the two disturbed habitats.

Subcortical Insect Composition Analysis of our data from 2001–2003 on species composition indicated that the assemblages from undisturbed and wind-disturbed forests clustered together, whereas the assemblages from salvaged and burned forests also clustered together. Although the wind-disturbance event created regional habitats for species diversity, as has been reported for European forests (Wermelinger et al. 2002, 2003), there is a closer resemblance of the species composition of the undisturbed to the wind-disturbed forest (Bouget and Noblecourt 2005), and of the salvaged to the burned forest. This suggests that the salvaged and burned forests are being colonized by species of subcortical insects different from those that colonize the undisturbed and wind-disturbed forests. Such trends also could be attributed to the similar types (e.g., leaning trees), though different amounts, of CWD present in the undisturbed and wind-disturbed forests, and to the compounded disturbances in the salvaged and burned forests. As in the case with ground beetle assemblages (Gandhi 2005; Gandhi et al. 2008), the fuel-reduction treatments after a wind-disturbance event may have the potential to alter succession of subcortical insects. At present, it is unclear whether the species compositions of the subcortical insects in undisturbed and wind-disturbed forests will become similar to those of the salvaged and burned forests with time; longer term sampling would be necessary to address this question.

Conclusions

In summary, in 2000, we trapped one-third more subcortical insects in jack pine than in aspen/birch/conifer stands. In 2001–2003, we trapped only in the jack pine cover type, and the insect responses to land-area treatments (wind disturbance, salvage-logging, and prescribed-burning) varied with year of sampling and semiochemical treatment. Trap catches of all subcortical insects were three-times greater in 2001–2002 than in 2003, suggesting that these insects were most abundant in the wind-disturbed areas 2 years after the storm event, and then declined. In 2001, approximately 2.5-fold more subcortical insects of all taxa were trapped in wind-disturbed areas than in undisturbed areas. In 2001–2002, trap catches of beetles such as *I. pini*, *M. scutellatus scutellatus*, and *T. dubius* were similar in the wind-disturbed and burned forests. In 2003, catches of these species in the burned forests were reduced in half relative to prior years.

In 2000, salvaged forest areas had the highest species richness and diversity, whereas in 2001–2003, wind-

disturbed forest areas had the highest species richness and diversity. Both wind disturbance and burning increased the subcortical insect species richness and diversity on the landscape. We provide new state records for 23 subcortical insect species in Minnesota, which underscores the efficacy of semiochemicals as tools for determining regional biodiversity. Species compositions of subcortical insects in the undisturbed and wind-disturbed forests were distinct from those of the salvaged and burned forests. Although prescribed-burning could be an effective tool to increase species diversity in the landscape, it could result in different species composition over time.

Trap catches of subcortical insects in response to semiochemical treatments also varied with year of sampling and land-area treatment. Such variability with year has been reported before in the case of *I. pini* and *T. dubius* (see Raffa and Klepzig 1989 vs. Herms et al. 1991). During 2002, relatively high population levels of *D. simplex* dominated the response of all subcortical insects as its attractant [(+/-)-seudenol and (-)- α -pinene] elicited catches of four- to five-times more insects than the other treatments. In general, the predaceous checkered beetle, *T. dubius*, responded the most to traps baited with the attractant for *D. rufipennis* [(+/-)-frontalin, (+/-)-1-methyl-2-cyclohexenol, and (-)- α -pinene]; *I. perroti* responded most to (-)-ipsdienol and (-)-ipsenol; *I. pini* the most to (+/-)-ipsdienol and lanierone; *Dr. autographus* the most to a woodborer (i.e., buprestid, cerambycid, and siricid) attractant [ethanol and (-)- α -pinene]; and *H. rugipennis pinifex* mostly to the Phero Tech *D. valens* [(+)- α -pinene, (-)- β -pinene, and (+)-3-carene] and woodborer attractants. The greatest diversity of subcortical beetle species was in traps baited with attractants for *D. valens* [(+)- α -pinene and (-)- β -pinene] and *Dryocoetes* spp. [*exo*-brevicommin and (-)- α -pinene] perhaps reflecting the generic nature of the baits. The most distinct species compositions were collected in response to the woodborer and *D. simplex* baits, whereas the species compositions in traps with the *D. valens* and *Dryocoetes* spp. baits, and the unbaited funnel trap were the most similar. Our 4-year study across various landscapes suggests that the responses of subcortical insects to semiochemicals are more complex than previously appreciated, and that future researchers should anticipate species variation in space and time.

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