Selective manipulation of predators using pheromones: responses to frontalin and ipsdienol pheromone components of bark beetles in the Great Lakes region

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Abstract

1 One proposed approach to improving biological control of bark beetles (Coleoptera: Scolytidae; alt. Curculionidae: Scolytinae) is to manipulate predator movement using semiochemicals. However, selective manipulation is impeded by attraction of both predators and pests to bark beetle pheromones.

2 The primary bark beetle affecting pine plantations in Wisconsin, U.S.A., is the pine engraver, *Ips pini* (Say). Other herbivores include *Ips grandicollis* (Eichhoff) and *Dryophthorus americanus* Bedel (Curculionidae). The predominant predators are the beetles *Thanasimus dubius* (Cleridae) and *Platysoma cylindrica* (Histeridae).

3 We conducted field assays using two enantiomeric ratios of ipsdienol, and frontalin plus α-pinene. Ipsdienol is the principal pheromone component of *I. pini*, and frontalin is produced by a number of *Dendroctonus* species. α-Pinene is a host monoterpene commonly incorporated into commercial frontalin lures.

4 *Thanasimus dubius* was attracted to frontalin plus α-pinene, and also to racemic ipsdienol. By contrast, *I. pini* was attracted to racemic ipsdienol, but showed no attraction to frontalin plus α-pinene. *Platysoma cylindrica* was attracted to 97%-(–)-ipsdienol and, to a lesser extent, racemic ipsdienol, but not to frontalin plus α-pinene. *Ips grandicollis* was attracted to frontalin plus α-pinene but not to ipsdienol. *Dryophthorus americanus* was attracted to both ipsdienol and frontalin plus α-pinene.

5 This ability to selectively attract the predator *T. dubius* without attracting the principal bark beetle in the system, *I. pini*, provides new opportunities for research into augmentative biological control and basic population dynamics. Moreover, the attraction of *T. dubius*, but not *P. cylindrica*, to frontalin plus α-pinene creates opportunities for selective manipulation of just one predator.

6 Patterns of attraction by predators and bark beetles to these compounds appear to reflect various degrees of geographical and host tree overlap with several pheromone-producing species.

Keywords Aggregation pheromone, biological control, *Dendroctonus frontalis*, *Dendroctonus rufipennis*, interspecific competition, *Ips grandicollis*, *Ips pini*, kairomone, *Platysoma cylindrica*, *Thanasimus dubius*.

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Introduction

Chemical signalling is essential to the reproductive ecology of bark beetles (Coleoptera: Scolytidae; alt. Curculionidae: Scolytinae), with aggregation pheromones playing crucial roles in mate recruitment, resource procurement and host tree partitioning (Wood, 1982a). Chemical signalling also

affects their population dynamics through interspecific exploitation. Competitors exploit these signals as synomones to locate suitable resources (Billings & Cameron, 1984; Poland & Borden, 1998; Ayres *et al.*, 2001), and predators exploit them as kairomones to locate prey (Vité & Williamson, 1970; Turnbow & Franklin, 1981; Wood, 1982a; Mizell *et al.*, 1984; Poland & Borden, 1997; Haynes & Yeargan, 1999). These predators are typically habitat specialists in that they feed almost entirely within trees colonized by bark beetles, but are often feeding generalists in that they respond to the pheromones of several bark beetle species and also feed on much of the fauna within beetle-killed trees (Erbilgin & Raffa, 2001a).

Several authors have proposed reducing the economic damage caused by bark beetles by using semiochemicals to attract predators to incipient outbreaks (Richerson *et al.*, 1980; Chatelain & Schenk, 1984; Borden, 1989). Similarly, attracting predators away from pheromones used during trap-out removal could conserve natural enemies. A major problem hindering both of these augmentative and conservation approaches to biological control is that the same compounds that attract predators also attract the bark beetle pests (Billings, 1985; DeMars *et al.*, 1986).

In previous work, we demonstrated differential attraction between the principal bark beetle pest in the Great Lakes region, the pine engraver *Ips pini* (Say), and its predominant predators, *Thanasimus dubius* (F.) (Coleoptera: Cleridae) and *Platysoma cylindrica* (Paykull) (Coleoptera: Histeridae), by using various enantiomeric ratios of ipsdienol (2-methyl-6-methylene-2,7-octadien-4-ol) (Aukema *et al.*, 2000a; Aukema *et al.*, 2000b), release rates of lanierone (2-hydroxy-4,4,6-trimethyl-2,5-cyclohexadien-1-one) with ipsdienol (Aukema & Raffa, 2000), and ratios of α-pinene to ipsdienol (Erbilgin *et al.*, 2003). However, each of these approaches yielded only partial specificity: both predator species and *I. pini* were attracted to the various treatments. Hence, additional knowledge of the behavioural specificity of predators is needed to improve our understanding of their role in bark beetle population dynamics and their potential for biological control (Miller *et al.*, 1987).

Thanasimus dubius and *P. cylindrica* are among the most common predators of bark beetles in North America. *Thanasimus dubius* occurs from Texas east to North Carolina, north to Minnesota, Ontario and Quebec, and west through the Rocky Mountains and Alaska (Savely, 1939; Thomas, 1955; Furniss & Carolin, 1977; Reeve *et al.*, 1980; Gara *et al.*, 1995; Bentz & Munson, 2000; Santoro *et al.*, 2001). In the southern U.S.A., *T. dubius* is the most abundant predator of the southern pine beetle *Dendroctonus frontalis* Zimmermann (Thatcher & Pickard, 1966; Cronin *et al.*, 2000), and exploits its aggregation pheromone component frontalin (Dixon & Payne, 1979). In the western U.S.A. and Canada, *T. dubius* is a major predator of the spruce beetle *D. rufipennis* (Kirby), which similarly produces frontalin as its principal aggregation pheromone component (Gries *et al.*, 1988; Gara *et al.*, 1995; Bentz & Munson, 2000). *Thanasimus dubius* also attacks *D. simplex* LeConte (Langor, 1991; Seybold *et al.*, 2002), which

occurs throughout eastern North America, including the Great Lakes region, the western Canadian provinces and Alaska. *Dendroctonus simplex* similarly produces frontalin (Barkawi *et al.*, 2003).

Platysoma cylindrica is widely distributed throughout the east from Ontario to Florida and west to Minnesota (Moser *et al.*, 1971; Ayres *et al.*, 1999; Bousquet & LaPlante, 1999; Mazur, 1999; Erbilgin & Raffa, 2002). It is an abundant predator in trees infested with *Ips* spp. and/or *D. frontalis* in the southern U.S.A. (Moser *et al.*, 1971). The beetle has been observed arriving at trees that were colonized by *D. frontalis* alone (Moore, 1972), which suggests a potential attraction to frontalin similar to *T. dubius*. However, *D. frontalis* produces additional compounds (Grosman *et al.*, 1997), which could also be the basis for attraction.

Ips pini is distributed across the pine forests of the northern U.S.A. and Canada, southward through the Appalachian and Rocky Mountains to Georgia and Mexico, respectively (Furniss & Carolin, 1977; Wood, 1982b; Drooz, 1985; Cognato *et al.*, 1999; Furniss *et al.*, 2002). The eastern five-spined ips *I. grandicollis* (Eichhoff) demonstrates substantial overlap with *I. pini*, but has a generally more eastern and southern distribution. Often termed the 'southern pine engraver' (Drooz, 1985), it is distributed throughout the southeastern U.S.A., Mexico and Central America, north to Saskatchewan and Quebec (Wood, 1982b; Gandhi & Seybold, 2002). It has not been reported in the Rocky Mountains. In the Great Lakes region, these *Ips* spp. are most commonly associated with jack pine *Pinus banksiana* Lamb, red pine *P. resinosa* Aiton and white pine *P. strobus* L. (Schenk & Benjamin, 1969; Klepzig *et al.*, 1991). *Ips pini* is more strongly associated with mortality to red pines than is *I. grandicollis* (Klepzig *et al.*, 1991; Erbilgin & Raffa, 2002). The predominant predators of *Ips* spp. in the Great Lakes region are *T. dubius* and *P. cylindrica*, which exert high mortality in laboratory assays (Aukema *et al.*, 2004a; Aukema & Raffa, 2004), and show evidence of density dependence at the stand level (Erbilgin *et al.*, 2002). There is also evidence that *I. grandicollis* can reduce *I. pini* populations through competition (Ayres *et al.*, 2001; Erbilgin *et al.*, 2002). The principal components of the aggregation pheromones of *I. pini* and *I. grandicollis* are ipsdienol and ipsenol, respectively (Wood, 1982a).

A recent study of spruce (*Picea*) stands in the Great Lakes region demonstrated that *T. dubius* is strongly attracted to frontalin plus α-pinene, but no *P. cylindrica* were captured (Haberkern & Raffa, 2003). Because no confirmed *P. cylindrica* attractants were included, it was not possible to distinguish whether or not *P. cylindrica* were present in these stands or whether populations in the Great Lakes region are attracted to frontalin. Similarly, the relative attraction of *T. dubius* to frontalin plus α-pinene vs. ipsdienol remains unknown.

The aim of the present study was to evaluate the responses of predators and bark beetles to semiochemicals that may provide selectivity in the Great Lakes region. We evaluated responses to frontalin and two enantiomeric combinations of ipsdienol.

Materials and methods

This experiment was conducted in a 50-year-old *P. resinosa* plantation in central Wisconsin (43°33′N, 89°51′W). We deployed blocks of four 12-funnel flight traps (Lindgren, 1983) in a square arrangement, with 10 m between traps. We deployed 15 blocks throughout the plantation, with a minimum of 100 m between blocks.

Three of the four traps in each square received a distinct pheromone treatment, with the fourth being a blank control. The synthetic pheromone lures were 50%-(–)-ipsdienol, 97%-(–)-ipsdienol, and 50%-(–)-frontalin plus 94%-(–)-α-pinene (Phero Tech Inc., Delta, British Columbia). α-Pinene synergizes the responses of *D. frontalis* and *D. rufipennis* to frontalin (Furniss *et al.*, 1976; Payne *et al.*, 1978). Ipsdienol was dispensed from polyvinyl chloride, bubble-cap lures with release rates of 110 μg/day at 25 °C in a 1,3-butanediol carrier solvent. Frontalin (>99% purity) and α-pinene (>99% purity) were dispensed from 400 μL polyethylene Eppendorf tube and 1.8 mL polyethylene bottles with release rates of 2.6 mg and 1.5 mg/day (400 mL) at 23 °C, respectively. Destruction of trap contents by predators was prevented by placing a 2 × 2 cm piece of Revenge bug strip (18.6% 2–2-dichlorovinyl dimethyl phosphate; Roxide International, Inc., New Rochelle, New York) in each collection cup. The traps were sampled twice weekly for 4 weeks, from 24 June to 19 July 2002. In summary, this protocol yielded $n = 15$ blocks × 8 sample periods = 120 collections for each of the four treatments.

We performed analysis of variance on each insect species for which more than 20 individuals were captured. Data were analysed according to a split plot design using SAS PROC MIXED (Littrell *et al.*, 1996). The experimental unit was the total number of insects per sample period per trap. Block was modelled in the whole plot, with treatment, sample period and their interaction in the subplot. Modelling sample period in the subplot controlled for small differences in weather and sample period duration (3 or 4 days) (Gray, 2002). Block and block × treatment interaction were considered random effects. Data were square-root transformed before analysis to reduce heteroscedasticity because response variables tended to be Poisson-distributed insect counts. The suitability of resultant models was judged by visual inspection of their residual plots. Where significant treatment effects occurred ($\alpha = 0.05$), differences were separated by pairwise *t*-tests on least squared means (Carmer & Swanson, 1973). Raw means are used for data presentation.

Results

We captured more than 25 species totalling 3040 insects (Table 1). Of these, 14 species and/or families were predators/nonwoodboring herbivores, which accounted for 65.3% of the insects captured. The most abundant predators were *T. dubius* ($n = 1067$) and *P. cylindrica* ($n = 339$). Herbivores comprised the remaining 34.7% of the insects captured. The most abundant bark beetles were *I. pini* and *I. grandicollis*, which comprised 93.0% of all bark beetles. Overall, the most abundant herbivore was *Dryophthorus*

americanus Bedel (Coleoptera: Curculionidae) ($n = 421$). Trap catches were relatively uniform throughout the experiment, although significantly more insects were captured at the end of June (sample period effect: $F_{7,392} > 2.03$; $P < 0.05$ for all species reported below). Similarly, there was a significant sample period × treatment interaction ($F_{21,392} > 1.58$; $P < 0.05$ for all species reported below).

Thanasimus dubius showed significant attraction to frontalin plus α-pinene and 50%-(–)-ipsdienol (Fig. 1) ($F_{3,42} = 81.91$; $P < 0.0001$). The highest numbers of *T. dubius* were captured in traps baited with frontalin plus α-pinene, where there were 12.6-fold more than in traps baited with 50%-(–)-ipsdienol. The number of *T. dubius* captured in unbaited traps or traps baited with 97%-(–)-ipsdienol was not significantly different from zero.

Platysoma cylindrica also demonstrated clear preferences for specific lures (Fig. 1) ($F_{3,42} = 50.93$; $P < 0.0001$). By contrast to *T. dubius*, *P. cylindrica* were not significantly attracted to frontalin plus α-pinene. The majority (54.3%) were captured in traps baited with 97%-(–)-ipsdienol. Similar to *T. dubius*, they were also attracted to 50%-(–)-ipsdienol. Another *Platysoma* species, *P. parallelum* (Say), also demonstrated differential attraction to the lures ($F_{3,43} = 12.69$; $P < 0.0001$). *Platysoma parallelum* was also attracted to 97%-(–)-ipsdienol (0.15 ± 0.04 SE) and 50%-(–)-ipsdienol (0.22 ± 0.05), but not to frontalin plus α-pinene (0.02 ± 0.01), relative to controls (0.02 ± 0.01). No other predators demonstrated significant responses to the treatments.

Among herbivores, three species demonstrated significant responses: *I. grandicollis* ($F_{3,43} = 62.76$; $P < 0.0001$), *I. pini* ($F_{3,43} = 37.26$; $P < 0.0001$) and *D. americanus* ($F_{3,43} = 3.10$; $P = 0.0367$). *Ips grandicollis* was attracted to frontalin plus α-pinene (Fig. 2). By contrast, *I. pini* was attracted to 50%-(–)-ipsdienol, but not to frontalin plus α-pinene. The numbers of *I. grandicollis* and *I. pini* captured at traps baited with other pheromone components were not significantly different from those in unbaited controls. *Dryophthorus americanus* demonstrated a preference for frontalin plus α-pinene relative to the control. Moderate numbers were also found in the ipsdienol-baited traps.

Discussion

These results demonstrate that frontalin plus α-pinene can selectively attract the predator *T. dubius* in red pine plantations without attracting the predominant bark beetle pest, *I. pini*. This could prove useful in the future research of the population dynamics of bark beetles, in which a major area of interest is the relative contribution of bottom-up vs. top-down regulation (Turchin *et al.*, 1991). Previously, methods for conducting manipulated experiments have been restricted by the attraction of both predators and prey to common signals (Aukema *et al.*, 2004b). These results support the feasibility of conducting controlled top-down studies in the field, and/or manipulating predator populations for purposes of augmentative biological control. The potential utility of such studies and manipulations is further supported by observations that red pine mortality to *I. pini*

Table 1 Total number of insects caught in field assays in *Pinus resinosa* plantation, central Wisconsin in 2002

Feeding guild	Family	Insect	Total[a]
Herbivores (34.7%)			1054
	Scolytidae	*Dendroctonus valens* LeConte	16
		Ips grandicollis (Eichhoff)	97
		Ips pini (Say)	287
		Males (*n* = 143)	
		Females (*n* = 144)	
		Ips perroti (Swaine)	4
		Orthotomicus caelatus (Eichhoff)	9
	Curculionidae	*Dryophthorus americanus* Bedel	421
		Stenoscelis brevis (Boheman)	167
	Buprestidae	Metallic wood-boring beetles	17
	Cerambycidae	Longhorn beetles[b]	34
	Siricidae	*Tremex columba* (L.)	2
Predators/other (65.3%)			1986
	Cleridae	*Enoclerus nigrifrons* (Say)	10
		Enoclerus nigripes (Say)	19
		Thanasimus dubius (F.)	1067
		Thanasimus undulatus (Say)	37
		Zenodosus sanguineus (Say)	20
	Histeridae	*Platysoma cylindrica* (Paykull)	339
		Platysoma parallelum (Say)	49
	Carabidae	*Plochionus pallens* (F.)	244
	Cucujidae	Flat bark beetles	31
	Staphylinidae	Rove beetles	17
	Tenebrionidae	*Corticeus parallelus* (Melsheimer)	40
	Trogositidae	*Grynocharis quadrilineata* (Melsheimer)	2
		Tenebroides marginatus Beauvois	99
		Tenebroides collaris Sturm	12

[a]Eight collection periods of 3–4 days in duration.
[b]Predominantly *Monochamus titillator* (F.); few *Orthosoma brunneum* (Forster).

tends to be highly clustered (Klepzig *et al.*, 1991; Erbilgin & Raffa, 2003), and that this mortality is highest where predator–prey associations are spatially and temporally disparate (Raffa, 1991; Erbilgin & Raffa, 2002). However, achieving meaningful control in the field will depend on predator functional and numerical responses across various conditions (Weslien, 1994; Reeve, 1997; Aukema & Raffa, 2002; Aukema & Raffa, 2004; Aukema *et al.*, 2004a; Aukema *et al.*, 2005).

Any use of semiochemically-based predator augmentation must be weighed against the risk of attracting additional bark beetles. Other species known to either produce or be attracted to frontalin (or frontalin plus α-pinene) in the Great Lakes region include the larch beetle *D. simplex*, the spruce beetle *D. rufipennis*, the recently introduced Douglas fir beetle *D. pseudotsugae* Hopkins (Barkawi *et al.*, 2003) and *I. grandicollis* (Fig. 2). However, the first three do not attack pines, and unsurprisingly, were not captured in our experiment. *Dendroctonus valens* LeConte, which is not known to produce adult pheromones, but inhabits pines, was similarly not attracted to frontalin plus α-pinene (Table 1). The response of *I. grandicollis* is more problematic. This beetle can be associated with tree mortality under conditions of severe stress (Conner & Wilkinson, 1983), but it is also a competitor with *I. pini* (Ayres *et al.*, 2001). Additional research on the combined and interacting

effects of predation and competition on bark beetle population dynamics is needed to resolve this issue.

By contrast to *T. dubius*, *P. cylindrica* is not attracted to frontalin plus α-pinene. Complementary no-choice experiments, containing only frontalin plus α-pinene and controls, also demonstrated no attraction (Haberkern & Raffa, 2003). Unlike *T. dubius*, *P. cylindrica* appears to specialize on bark beetles colonizing *Pinus* spp. It is not attracted to sympatric bark beetles colonizing *Picea* logs, or their synthetic pheromones (Haberkern *et al.*, 2002; Haberkern & Raffa, 2003). Furthermore, *P. cylindrica* does not attack *I. pini* when they colonize downed *Picea* (Haberkern *et al.*, 2002), even though it is highly attracted to the pheromone produced by *I. pini* (Raffa & Klepzig, 1989; Aukema *et al.*, 2000a) (Fig. 1). Restriction of prey use to pines may be one mechanism by which *P. cylindrica* reduces interference with *T. dubius* at the whole-tree and stand levels, in addition to temporal, behavioural and spatial processes that enhance within-tree separation (Aukema *et al.*, 2004a).

Attraction by *T. dubius* to both frontalin plus α-pinene and 50%-(−)-ipsdienol, or ipsdienol plus α-pinene (Erbilgin & Raffa, 2001a; Erbilgin & Raffa, 2001b; Erbilgin *et al.*, 2003), indicates an ability of *D. frontalis*, *D. rufipennis*, *D. simplex* and *I. pini* to exploit pheromones. This predator extends throughout the full range of all four species
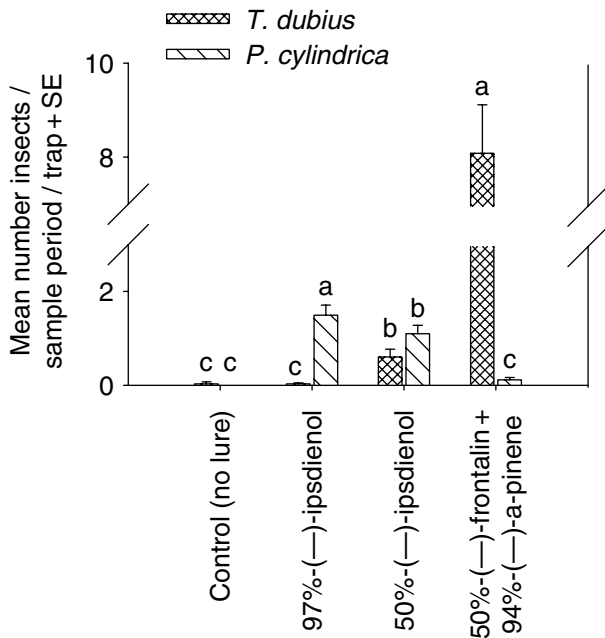
Figure 1 Mean ± SE number of bark beetle predators, *Thanasimus dubius* and *Platysoma cylindrica*, responding to various synthetic pheromone lures per 3- or 4-day sample period in behavioural choice field trial in red pine plantation in Wisconsin, U.S.A. in 2002, for $n = 15$ blocks × 8 sample periods = 120 collections. Different letters within a species indicate significantly different responses using $\alpha = 0.05$.

Figure 2 Mean ± SE number of herbivores *Ips pini*, *Ips grandicollis*, and *Dryophthorus americanus* responding to various synthetic pheromone lures per 3- or 4-day sample period in behavioural choice field trial in red pine plantation in Wisconsin, U.S.A. in 2002, for $n = 15$ blocks × 8 sample periods = 120 collections. Different letters within a species indicate significantly different responses using $\alpha = 0.05$.

(Thatcher & Pickard, 1966; Gara *et al.*, 1995; Aukema *et al.*, 2000b; Bentz & Munson, 2000; Cronin *et al.*, 2000; Ayres *et al.*, 2001; Kennedy & McCullough, 2002; Haberkern & Raffa, 2003). The most parsimonious explanation for attraction to frontalin plus α-pinene in the Great Lakes region is the geographical and temporal overlap of *T. dubius* with the three northern bark beetles, as opposed to its strong association with *D. frontalis* in the south. Wisconsin forests are approximately 700 km north of the range of *D. frontalis* (Drooz, 1985; Rabaglia & Valenti, 2003; Rabaglia, 2003), and are separated by agricultural fields, native prairies, deciduous woodlots and cities, with only occasional windbreak and landscape pines that were planted after European settlement as possible links. This barrier greatly exceeds the dispersal capability of *T. dubius* (Cronin *et al.*, 2000), so northern and southern populations probably have extremely restricted gene flow. An alternative, but less plausible explanation is that attraction to frontalin reflects a historical association when *P. banksiana* and *Picea* spp. extended southward to 34° N latitude and perhaps overlapped *D. frontalis* populations, although that overlap ended approximately 19000–16300 years BP (Delcourt, 1979; Delcourt & Delcourt, 1985).

The higher attraction by *T. dubius* to frontalin plus α-pinene than to either ipsdienol (Fig. 1) or ipsdienol plus α-pinene (Erbilgin & Raffa, 2001b) was unexpected, given the much higher populations of *I. pini* than *D. rufipennis* or *D. simplex*, the greater abundance of *Pinus* spp. than *Picea*
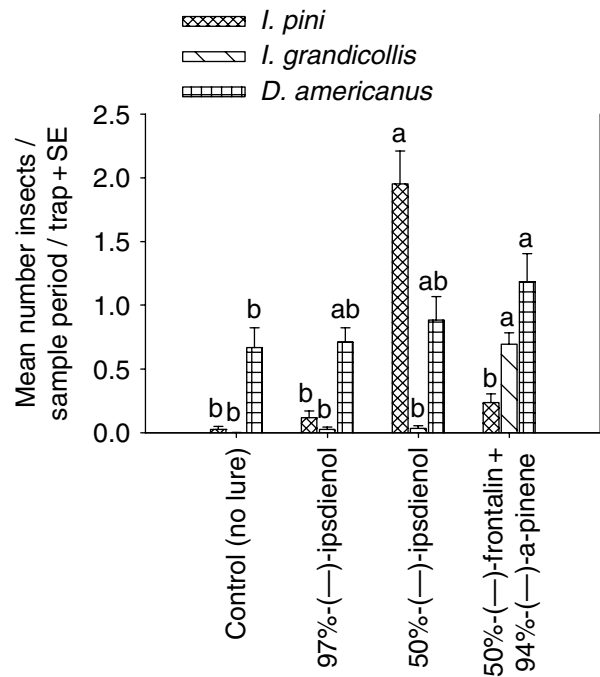
or *Larix* in Wisconsin, and the location of this study 200 km south of natural *Picea* forests. This could reflect the higher release rate of frontalin than ipsdienol, the previous domination of the Great Lakes region by *Picea* as recently as 1000 years ago (Wright, 1964; Wright, 1968), or other unknown causes.

The degree of cross attraction among herbivores likewise appears related to geographical and host-tree overlap. *Ips grandicollis* shares a broad geographical range with *D. frontalis* (Conner & Wilkinson, 1983), and several host pines, such as *P. elliottii* Engelm., *P. palustris* Mill., *P. echinata* Mill., *P. oocarpa* Schiede ex Schlectendahl and *P. taeda* L. (Svihra *et al.*, 1980; Wood, 1982b; Conner & Wilkinson, 1983; Flamm *et al.*, 1993; Haack & Paizschwartz, 1997; Clarke *et al.*, 2000). *Ips grandicollis* is strongly cross-attracted to frontalin (Fig. 2) (Birch *et al.*, 1980; Svihra *et al.*, 1980; Smith *et al.*, 1990), but *I. pini* showed no attraction (Fig. 2). All choice tests include the possibility of masking effects (i.e. that attraction by *I. pini* to frontalin plus α-pinene might be obscured by the presence of ipsdienol) although, as with *P. cylindrica*, this seems unlikely because complementary no-choice experiments containing only frontalin plus α-pinene and controls also demonstrated no attraction (Haberkern & Raffa, 2003). Unlike *I. grandicollis*, overlap of *I. pini* with *D. frontalis* is highly restricted, including only the southern Appalachian mountains and possibly the south-western U.S.A. (Wood, 1982b). This

narrow geographical overlap is further tempered by host differences. In the southern Appalachian mountains, *I. pini* primarily breed in *P. strobus*, which *D. frontalis* avoid except under extreme conditions (Drooz, 1985). In the south-western U.S.A., they are reported to co-occur in ponderosa pine *P. ponderosa* Dougl. ex Laws (Wood, 1982b), but the purported *D. frontalis* may actually be *D. brevicomis* LeConte (Sanchez-Martinez & Wagner, 2002). *Ips pini* show geographical overlap with *D. simplex* and *D. rufipennis*, but rarely colonize *Larix* spp. (Clemens, 1916; Gandhi & Seybold, 2002) or *Picea* (Bright, 1976). The attraction of *D. americanus* to pheromones of *D. frontalis*, *D. rufipennis* and *I. pini* may similarly reflect its association with bark beetle-killed trees throughout the eastern and midwestern U.S.A. (O'Brien & Wibmer, 1982; Drooz, 1985; Downie & Arnett, 1996). The biology of *D. americanus* is not well understood, but it has been observed arriving at trees colonized by *I. pini* (Aukema *et al.*, 2004b).

The extent to which selective manipulation of predators can be achieved for purposes of research or biological control in other systems is unclear. However, based on our results, it is possible to suggest the circumstances where success would be most likely: (i) A pest species overlaps geographically with other bark beetles that produce a different pheromone. This increases the likelihood of a predator responding to a second kairomone in addition to that produced by the target pest. (ii) The various bark beetles occur in different host species habitats. This increases the likelihood of finding a pheromone that would not attract damaging beetles into a stand. (iii) An important native predator overlaps these habitats and exploits the various chemical signals produced by multiple prey. For purposes of utility, this predator must show the requisite geographical, prey, and plant species overlaps, and show strong functional and numerical responses. Such circumstances may prove to be rare outside the Great Lakes region, although it should be kept in mind that new accidental introductions both within and between continents are constantly expanding bark beetle distributions.

References

Aukema, B.H. & Raffa, K.F. (2000) Chemically mediated predator-free space: herbivores can synergize intraspecific communication without increasing risk of predation. *Journal of Chemical Ecology*, **26**, 1923–1939.

Aukema, B.H. & Raffa, K.F. (2002) Relative effects of exophytic predation, endophytic predation, and intraspecific competition on a subcortical herbivore: consequences to the reproduction of *Ips pini* and *Thanasimus dubius*. *Oecologia*, **133**, 483–491.

Aukema, B.H. & Raffa, K.F. (2004) Does aggregation benefit bark beetles by diluting predation? Links between a group-colonization strategy and the absence of emergent multiple predator effects. *Ecological Entomology*, **29**, 129–138.

Aukema, B.H., Dahlsten, D.L. & Raffa, K.F. (2000a) Exploiting behavioral disparities among predators and prey to selectively remove pests: maximizing the ratio of bark beetles to predators removed during semiochemically based trap-out. *Environmental Entomology*, **29**, 651–660.

Aukema, B.H., Dahlsten, D.L. & Raffa, K.F. (2000b) Improved population monitoring of bark beetles and predators by incorporating disparate behavioral responses to semiochemicals. *Environmental Entomology*, **29**, 618–629.

Aukema, B.H., Clayton, M.K. & Raffa, K.F. (2004a) Density-dependent effects of multiple predators sharing a common prey in an endophytic habitat. *Oecologia*, **139**, 418–426.

Aukema, B.H., Richards, G.R., Krauth, S.J. & Raffa, K.F. (2004b) Species assemblage arriving at and emerging from trees colonized by *Ips pini* in the Great Lakes region: partitioning by time since colonization, season, and host species. *Annals of the Entomological Society of America*, **97**, 117–129.

Aukema, B.H., Clayton, M.K. & Raffa, K.F. (2005) Modeling flight activity and population dynamics of the pine engraver, *Ips pini*, in the Great Lakes region: effects of weather and predators over short time scales. *Population Ecology*, **47**, 61–69.

Ayres, M.P., Lombardero, M.J., Ayres, B.D. & Antoro, A.E. (1999) *The Biology and Management of Bark Beetles in Old Growth Forests of Itasca State Park*. Great Lakes Institute for Pine Ecosystems Research, Colfax, Wisconsin.

Ayres, B.D., Ayres, M.P., Abrahamson, M.D. & Teale, S.A. (2001) Resource partitioning and overlap in three sympatric species of *Ips* bark beetles (Coleoptera: Scolytidae). *Oecologia*, **128**, 443–453.

Barkawi, L.S., Francke, W., Blomquist, G.J. & Seybold, S.J. (2003) Frontalin: *de novo* biosynthesis of an aggregation pheromone component by *Dendroctonus* spp. bark beetles (Coleoptera: Scolytidae). *Insect Biochemistry and Molecular Biology*, **33**, 773–788.

Bentz, B.J. & Munson, A.S. (2000) Spruce beetle population suppression in northern Utah. *Western Journal of Applied Forestry*, **15**, 122–128.

Billings, R.F. (1985) Southern pine bark beetles and associated insects: effects of rapidly-released host volatiles on response to aggregation pheromones. *Zeitschrift für Angewandte Entomologie*, **99**, 483–491.

Billings, R.F. & Cameron, R.S. (1984) Kairomonal responses of Coleoptera, *Monochamus titillator* (Cerambycidae), *Thanasimus dubius* (Cleridae), and *Temnochila virescens* (Trogositidae), to behavioral chemicals of southern pine bark beetles (Coleoptera: Scolytidae). *Environmental Entomology*, **13**, 1542–1548.

Birch, M.C., Svihra, P., Paine, T.D. & Miller, J.C. (1980) Influence of chemically mediated behavior on host tree colonization by four cohabiting species of bark beetles. *Journal of Chemical Ecology*, **6**, 395–414.

Borden, J.H. (1989) Semiochemicals and bark beetle populations: exploitation of natural phenomena by pest management strategists. *Holarctic Ecology*, **12**, 501–510.

Bousquet, Y. & LaPlante, S. (1999) *Les Coleopteres Histerides Du Quebec*. Fabreries Supplement 8. Association Des Entomologistes Amateurs Du Quebec, Canada.

Bright, D.E. Jr (1976) *The Insects and Arachnids of Canada. Part 2. The Bark Beetles of Canada and Alaska (Coleoptera: Scolytidae)*. Agriculture Canada, Publication 1573. Canadian Department of Agriculture, Canada.

Carmer, S.G. & Swanson, M.R. (1973) Evaluation of ten pairwise multiple comparison procedures by Monte Carlo methods. *Journal of the American Statistical Association*, **68**, 66–74.

Chatelain, M.P. & Schenk, J.A. (1984) Evaluation of frontalin and *exo*-brevicomin as kairomones to control mountain pine beetles (Coleoptera: Scolytidae) in lodgepole pine. *Environmental Entomology*, **13**, 1666–1674.

Clarke, S.R., Evans, R.E. & Billings, R.F. (2000) Influence of pine bark beetles on the west gulf coastal plain. *Texas Journal of Science*, **52**, 105–126.

Clemens, W.A. (1916) The pine bark beetle. *Cornell University Agricultural Experiment Station Bulletin*, **383**, 287–298.

Cognato, A.I., Seybold, S.J. & Sperling, F.A.H. (1999) Incomplete barriers to mitochondrial gene flow between pheromone races of the North American pine engraver, *Ips pini* (Say) (Coleoptera: Scolytidae). *Proceedings of the Royal Society of London − Series B: Biological Sciences*, **266**, 1843–1850.

Conner, M.D. & Wilkinson, R.C. (1983) *Ips Bark Beetles in the South*. Forest Insect and Disease Leaflet 129. USDA Forest Service, Washington, DC.

Cronin, J.T., Reeve, J.D., Wilkens, R. & Turchin, P. (2000) The pattern and range of movement of a checkered beetle predator relative to its bark beetle prey. *Oikos*, **90**, 127–138.

Delcourt, H.R. (1979) Late quaternary vegetation history of the Eastern Highland Rim and adjacent Cumberland Plateau of Tennessee. *Ecological Monographs*, **49**, 255–280.

Delcourt, H.R. & Delcourt, P.A. (1985) Quaternary palynology and vegetational history of the southeastern United States. *Pollen Records of Late-Quaternary North American Sediments* (ed. by V. M. Vryant Jr and R. G. Holloway), pp. 440. American Association of Stratigraphic Palynologists Foundation, http://www.palynology.org/.

DeMars, C.J. Jr, Dahlsten, D.L., Sharpnack, N.X. & Rowney, D.L. (1986) Tree utilization and density of attacking and emerging populations of the western pine beetle (Coleoptera: Scolytidae) and its natural enemies, Bass Lake, California, 1970–71. *Canadian Entomologist*, **118**, 881–900.

Dixon, W.N. & Payne, T.L. (1979) Aggregation of *Thanasimus dubius* on trees under mass-attack by the southern pine beetle. *Environmental Entomology*, **8**, 178–181.

Downie, N.M. & Arnett, R.H. Jr (1996) *The Beetles of Northeastern North America*. Sandhill Crane Press, Gainesville, Florida.

Drooz, A.T. (1985) *Insects of Eastern Forests*. USDA Forest Service Miscellaneous Publication No. 1426. US Government Printing Office, Washington, DC.

Erbilgin, N. & Raffa, K.F. (2001a) Kairomonal range of generalist predators in specialized habitats: responses to multiple phloeophagous species emitting pheromones vs. host odors. *Entomologia Experimentalis et Applicata*, **99**, 205–210.

Erbilgin, N. & Raffa, K.F. (2001b) Modulation of predator attraction to pheromones of two prey species by stereochemistry of plant volatiles. *Oecologia*, **127**, 444–453.

Erbilgin, N. & Raffa, K.F. (2002) Association of declining red pine stands with reduced populations of bark beetle predators, seasonal increases in root colonizing insects, and incidence of root pathogens. *Forest Ecology and Management*, **164**, 221–236.

Erbilgin, N. & Raffa, K.F. (2003) Spatial analysis of forest gaps resulting from bark beetle colonization of red pines experiencing belowground herbivory and infection. *Forest Ecology and Management*, **177**, 145–153.

Erbilgin, N., Nordheim, E.V., Aukema, B.H. & Raffa, K.F. (2002) Population dynamics of *Ips pini* and *Ips grandicollis* in red pine plantations in Wisconsin: within- and between-year associations with predators, competitors, and habitat quality. *Environmental Entomology*, **31**, 1043–1051.

Erbilgin, N., Powell, J.S. & Raffa, K.F. (2003) Effect of varying monoterpene concentrations on the response of *Ips pini* (Coleoptera: Scolytidae) to its aggregation pheromone: implications for pest management and ecology of bark beetles. *Agricultural and Forest Entomology*, **5**, 269–274.

Flamm, R.O., Pulley, P.E. & Coulson, R.N. (1993) Colonization of disturbed trees by the southern pine bark beetle guild (Coleoptera: Scolytidae). *Environmental Entomology*, **22**, 62–70.

Furniss, R.L. & Carolin, V.M. (1977) *Western Forest Insects*. USDA Forest Service Miscellaneous Publication No. 1339. US Government Printing Office, Washington, DC.

Furniss, M.M., Baker, B.H. & Hostetler, B.B. (1976) Aggregation of spruce beetles (Coleoptera: Scolytidae) to seudenol and repression of attraction by methylcyclohexenone in Alaska. *Canadian Entomologist*, **108**, 1297–1302.

Furniss, M.M., Holsten, E.H. & Schultz, M.E. (2002) Species of Alaska Scolytidae: distribution, hosts, and historical review. *Journal of the Entomological Society of British Columbia*, **99**, 83–92.

Gandhi, K.J.K. & Seybold, S.J. (2002) Tamarack (Pinaceae): previously unrecorded developmental host for pine engraver and southern pine engraver (Coleoptera: Scolytidae). *Canadian Entomologist*, **134**, 299–302.

Gara, R.I., Werner, R.A., Whitmore, M.C. & Holsten, E.H. (1995) Arthropod associates of the spruce beetle *Dendroctonus rufipennis* (Kirby) (Col., Scolytidae) in spruce stands of south-central and interior Alaska. *Journal of Applied Entomology*, **119**, 585–590.

Gray, D.W. (2002) Field response of *Ips paraconfusus*, *Dendroctonus brevicomis*, and their predators to 2-methyl-3-buten-2-ol, a novel alcohol emitted by ponderosa pine. *Journal of Chemical Ecology*, **28**, 1583–1597.

Gries, G., Pierce, H.D., Lindgren, B.S. & Borden, J.H. (1988) New techniques for capturing and analyzing semiochemicals for scolytid beetles (Coleoptera: Scolytidae). *Journal of Economic Entomology*, **81**, 1715–1720.

Grosman, D.M., Salom, S.M., Ravlin, F.W. & Young, R.W. (1997) Geographic and gender differences in semiochemicals in emerging adult southern pine beetle (Coleoptera: Scolytidae). *Annals of the Entomological Society of America*, **90**, 438–446.

Haack, R.A. & Paizschwartz, G. (1997) Bark beetle (Coleoptera, Scolytidae) outbreak in pine forests of the Sierra de las Minas biosphere reserve, Guatemala. *Entomological News*, **108**, 67–76.

Haberkern, K.E. & Raffa, K.F. (2003) Phloeophagous and predaceous insects responding to synthetic pheromones of bark beetles inhabiting white spruce stands in the Great Lakes region. *Journal of Chemical Ecology*, **29**, 1651–1663.

Haberkern, K.E., Illman, B.L. & Raffa, K.F. (2002) Bark beetles and fungal associates colonizing white spruce in the Great

Lakes region. *Canadian Journal of Forest Research*, **32**, 1137–1150.

Haynes, K.F. & Yeargan, K.V. (1999) Exploitation of intraspecific communication systems: illicit signalers and receivers. *Annals of the Entomological Society of America*, **92**, 960–970.

Kennedy, A.A. & McCullough, D.G. (2002) Phenology of the larger European pine shoot beetle *Tomicus piniperda* (L.) (Coleoptera: Scolytidae) in relation to native bark beetles and natural enemies in pine stands. *Environmental Entomology*, **31**, 261–272.

Klepzig, K.D., Raffa, K.F. & Smalley, E.B. (1991) Association of insect-fungal complexes with Red Pine Decline in Wisconsin. *Forest Science*, **41**, 1119–1139.

Langor, D.W. (1991) Arthropods and nematodes co-occurring with the eastern larch beetle, *Dendroctonus simplex* (Col. Scolytidae), in Newfoundland. *Entomophaga*, **36**, 303–313.

Lindgren, B.S. (1983) A multiple-funnel trap for scolytid beetles. *Canadian Entomologist*, **115**, 299–302.

Littrell, R.C., Milliken, G.A., Stroup, W.W. & Wolfinger, R.D. (1996) *SAS System for Mixed Models*. SAS Institute, Cary, North Carolina.

Mazur, S. (1999) Preliminary studies upon the *Platysoma* complex (Col., Histeridae). *Annals of Warsaw Agricultural University – SGGW: Forestry and Wood Technology*, **49**, 3–29.

Miller, M.C., Moser, J.C., McGregor, M., Grégoire, J.C., Baisier, M., Dahlsten, D.L. & Werner, R.A. (1987) Potential for biological control of native North American *Dendroctonus* beetles (Coleoptera: Scolytidae). *Annals of the Entomological Society of America*, **80**, 417–428.

Mizell, R.F., Frazier, J.L. & Nebeker, T.E. (1984) Response of the clerid predator *Thanasimus dubius* (F.) to bark beetle pheromones and tree volatiles in a wind tunnel. *Journal of Chemical Ecology*, **10**, 177–187.

Moore, G.E. (1972) Southern pine beetle mortality in North Carolina caused by parasites and predators. *Environmental Entomology*, **1**, 58–65.

Moser, J.C., Thatcher, R.C. & Pickard, L.S. (1971) Relative abundance of southern pine beetle associates in east Texas. *Annals of the Entomological Society of America*, **64**, 72–77.

O'Brien, C.W. & Wibmer, G.J. (1982) Annotated checklist of the weevils (Curculionidae *sensu lato*) of North America, Central America, and the West Indies (Coloptera: Cuculionoidea). *Memoirs of the American Entomological Institute*, **34**, 1–382.

Payne, T.L., Coster, J.E., Richardson, J.V., Edson, L.J. & Hart, E.R. (1978) Field response of the southern pine beetle to behavioral chemicals. *Environmental Entomology*, **7**, 578–582.

Poland, T.M. & Borden, J.H. (1997) Attraction of a bark beetle predator, *Thanasimus undatulus* (Coleoptera: Cleridae), to pheromones of the spruce beetle and two secondary bark beetles (Coleoptera: Scolytidae). *Journal of the Entomological Society of British Columbia*, **94**, 35–41.

Poland, T.M. & Borden, J.H. (1998) Semiochemical-induced competition between *Dendroctonus rufipennis* and two secondary species, *Ips tridens* and *Dryocoetes affaber* (Coleoptera, Scolytidae). *Journal of Economic Entomology*, **91**, 1142–1149.

Rabaglia, R.J. (2003) Annotated list of the bark and ambrosia beetles (Coleoptera: Scolytidae) of Maryland, with new distributional records. *Proceedings of the Entomological Society of Washington*, **105**, 373–379.

Rabaglia, R.J. & Valenti, M.A. (2003) Annotated list of the bark and ambrosia beetles (Coleoptera: Scolytidae) of Delaware, with new distributional records. *Proceedings of the Entomological Society of Washington*, **105**, 312–319.

Raffa, K.F. (1991) Temporal and spatial disparities among bark beetles, predators, and associates responding to synthetic bark beetle pheromones: *Ips pini* (Coleoptera: Scolytidae) in Wisconsin. *Environmental Entomology*, **20**, 1665–1679.

Raffa, K.F. & Klepzig, K.D. (1989) Chiral escape of bark beetles from predators responding to a bark beetle pheromone. *Oecologia*, **80**, 566–569.

Reeve, J.D. (1997) Predation and bark beetle dynamics. *Oecologia*, **112**, 48–54.

Reeve, R.J., Coster, J.E. & Johnson, P.C. (1980) Spatial distribution of flying southern pine beetle (Coleoptera: Scolytidae) and the predator *Thanasimus dubius* (Coleoptera: Cleridae). *Environmental Entomology*, **9**, 113–118.

Richerson, J.V., McCarty, F.A. & Payne, T.L. (1980) Disruption of the southern pine beetle, *Dendroctonus frontalis*, with frontalure. *Environmental Entomology*, **9**, 90–93.

Sanchez-Martinez, G. & Wagner, M.R. (2002) Bark beetle community structure under four ponderosa pine forest stand conditions in northern Arizona. *Forest Ecology and Management*, **170**, 145–160.

Santoro, A.E., Lombardero, M.J., Ayres, M.P. & Ruel, J.J. (2001) Interactions between fire and bark beetles in an old growth pine forest. *Forest Ecology and Management*, **144**, 245–254.

Savely, H.E. Jr (1939) Ecological relations of certain animals in dead pine and oak logs. *Ecological Monographs*, **9**, 321–385.

Schenk, J.A. & Benjamin, D.M. (1969) Notes on the biology of *Ips pini*. Central Wisconsin jack pine forests. *Annals of the Entomological Society of America*, **62**, 480–485.

Seybold, S.J., Albers, M.A. & Katovich, S.A. (2002) *Eastern Larch Beetle*. Forest Insect and Disease Leaflet 175. USDA Forest Service, Washingon, DC.

Smith, M.T., Payne, T.L. & Birch, M.C. (1990) Olfactory–based behavioral interactions among 5 species in the southern pine bark beetle group. *Journal of Chemical Ecology*, **16**, 3317–3331.

Svihra, P., Paine, T.D. & Birch, M.C. (1980) Interspecific olfactory communications in southern pine beetles. *Naturwissenschaften*, **67**, 518–520.

Thatcher, R.C. & Pickard, L.S. (1966) The clerid beetle, *Thanasimus dubius*, as a predator of the southern pine beetle. *Journal of Economic Entomology*, **59**, 955–957.

Thomas, J.B. (1955) Notes on insects and other arthropods in red and white pine logging slash. *Canadian Entomologist*, **87**, 338–344.

Turchin, P., Lorio, P.L. Jr, Taylor, A.D. & Billings, R.F. (1991) Why do populations of southern pine beetles (Coleoptera: Scolytidae) fluctuate? *Environmental Entomology*, **20**, 401–409.

Turnbow, R.H. & Franklin, R.T. (1981) *Platysoma cylindrica* response to ipsenol. *Journal of the Entomological Society of Georgia*, **16**, 171–175.

Vité, J.P. & Williamson, D.L. (1970) *Thanasimus dubius*: prey perception. *Journal of Insect Physiology*, **16**, 233–239.

Weslien, J. (1994) Interactions within and between species at different densities of the bark beetle *Ips typographus* and its predator *Thanasimus formicarius*. *Entomologia Experimentalis et Applicata*, **71**, 133–143.

Wood, D.L. (1982a) The role of pheromones, kairomones, and allomones in the host selection and colonization behavior of bark beetles. *Annual Review of Entomology*, **27**, 411–446.

Wood, S.L. (1982b) *The Bark and Ambrosia Beetles of North and Central America (Coleoptera: Scolytidae). A Taxonomic Monograph*. Great Basin Naturalist Memoirs, Vol. 6. Brigham Young University, Provo, Utah.

Wright, H.E. Jr (1964) Aspects of the early postglacial forest succession in the Great Lakes region. *Ecology*, **45**, 439–448.

Wright, H.E. Jr (1968) The roles of pine and spruce in the forest history of Minnesota and adjacent areas. *Ecology*, **49**, 937–955.