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FIELD RESPONSE OF *Ips paraconfusus*, *Dendroctonus brevicomis*, AND THEIR PREDATORS TO 2-METHYL-3-BUTEN-2-OL, A NOVEL ALCOHOL EMITTED BY PONDEROSA PINE

DENNIS W. GRAY*

Department of Ecology and Evolution
State University of New York
Stony Brook, New York 11794–5245, USA

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Abstract—Methylbutenol (MBO) is a major component of the aggregation pheromone of the European spruce beetle *Ips typographus* and also has been found to be emitted in large amounts by several species of pine native to western North America. This study investigates the influence this signal may have on the behavior of North American bark beetles and examines whether MBO functions as a defensive compound for emitting pines. The response of two North American bark beetles (*Ips paraconfusus* and *Dendroctonus brevicomis*) and their predaceous beetles (Trogositidae and Cleridae) to MBO, pheromone, and monoterpenes in varying release rates was investigated in the field using Lindgren funnel traps. MBO exhibited no repellent properties when tested alone, nor did MBO appear to have any effect on the aggregation response of these bark beetles and their predators to their pheromones. These results provide no support for a defensive function of MBO.

Key Words—Bark beetle, methylbutenol, MBO, 2-methyl-3-buten-2-ol, pheromone, *Ips paraconfusus*, *Dendroctonus brevicomis*, Cleridae, Trogositidae, Scolytidae, monoterpene, predator, plant defense, Ponderosa pine, *Pinus ponderosa*.

INTRODUCTION

Among the insect pests of conifers, the bark beetles of the family Scolytidae are by far the most important and destructive. During outbreaks, bark beetles may kill large numbers of trees within a given stand, and timber losses caused by bark

* E-mail: denwgray@life.bio.sunysb.edu

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beetles during single outbreaks can range into the billions of board feet (Miller and Keen, 1960; Furniss and Carolin, 1977). The destructive potential of bark beetles stems largely from their use of chemical cues and signals that allow them to choose weakened hosts and to coordinate mass attacks. Understanding the ecological chemistry of bark beetle behavior and the role of volatile compounds in modulating this behavior is crucial to both basic questions in plant–insect interactions and to developing protocols for minimizing the economic impacts of these insects.

The chemical mediation of bark beetle behavior has received extensive study for more than 30 years; and researchers have described several distinct phases of these attacks (Stark, 1981; Wood, 1982). The initial attack on a tree is made by a small number of pioneer beetles that alight upon the bark and begin burrowing tunnels into the bole. Host choice at the initial selection phase has been ascribed to attraction to host volatiles (Rudinsky et al., 1971; Miller and Borden, 1990), visual cues (Henson, 1962), or random landing behavior (Burnell, 1977; Moeck et al., 1981). These pioneer beetles then begin emitting aggregation pheromones that attract conspecific beetles to the source (Byers, 1988). Some species such as *D. pseudostugae* and *D. frontalis* are capable of producing pheromones immediately upon landing (Renwick and Vité, 1968; Vité and Renwick, 1968; Ryker et al., 1979), whereas others such as *Trypodendron lineatum* and *I. paraconfusus* appear to produce pheromones after tunneling and feeding on the host (Wood and Bushing, 1963; Pitman et al., 1965; Chapman, 1966; Borden and Slater, 1969). Emission of these aggregation pheromones results in a mass attack that can overwhelm the tree's resin defenses and even lead to its death. The pheromones are sometimes synthesized by the bark beetle by using host monoterpenes as precursors (Hughes, 1974, 1975; Hendry et al., 1980; Byers, 1981) or are synthesized *de novo* by the bark beetle (Ivarsson et al., 1993; Seybold et al., 1995). Following the successful mass attack, some species enter a third phase in which the bark beetles begin emitting different pheromones that repel additional beetles from the attacked host. Schlyter et al. (1989) showed that the production of ipsenol by *Ips typographus* inhibited the aggregation response of this insect. Emission of the antiaggregation pheromones has been interpreted as a mechanism for preventing overcrowding and competition for larval food resources.

Although the role of insect-derived pheromones in mediating bark beetle behavior has received extensive study (Borden, 1985), the role of host volatiles in mediating bark beetle behavior is less clear. Host monoterpenes have been shown to both attract (Rudinsky et al., 1971; Miller and Borden, 1990; Hobson et al., 1993) and inhibit the attraction (Hayes et al., 1994) of bark beetles. Green leaf volatiles have also been shown to inhibit the attraction (Wilson et al., 1996), and volatiles present in non-hosts have been shown to disrupt the response of bark beetles to attractant-baited traps (Huber and Borden, 2001).

Recently 2-methyl-3-buten-2-ol (MBO) was discovered to be a major component of the volatiles emitted by several species of pine native to western North

America (Harley et al., 1998). For example, in ponderosa pine, *Pinus ponderosa* Laws, MBO emissions exceeded the emission of monoterpenes by a factor of 2–10, and represented an energetic investment of 0.5% of the tree's net photosynthetic carbon assimilation (Lerdau and Gershenzon, 1997; Schade et al., 2000). However, unlike monoterpenes, MBO is not stored in plant tissues and is instead emitted immediately upon production (Harley et al., 1998). Such a large investment of energy and carbon into MBO production, relative to monoterpene production, by MBO-emitting pines suggests that this compound may serve a biological function to the emitting plant and that insect pests (and/or their predators) may use MBO for host (prey) detection.

In addition to its synthesis by some North American pines, MBO production also occurs in the European spruce bark beetle, *Ips typographus*, and is used by this insect as part of its aggregation pheromone (Bakke, 1977). The MBO produced by *I. typographus* is synthesized *de novo* by the insect (Lanne et al., 1989) and not sequestered from its host plant, Norway spruce (*Picea abies*), which does not manufacture MBO. In fact, no MBO emitting plants have yet been discovered in Europe where two bark beetles (*Ips typographus* and *Orthotomicus erosus*) use MBO as parts of their pheromone systems (Bakke, 1976; Giesen et al., 1984; Harley et al., 1998). A complete survey of the pines native to Europe has shown that none manufacture MBO (Harley et al., 1998; Gray unpublished data). In contrast, in North America, where several pines produce MBO, MBO has not been reported as a major component of the pheromone system of any North American bark beetle. It has, however, been reported as a minor pheromone component for *Polygraphus rufipennis* and may possess anti-attractant properties for *Dendroctonus rufipennis* (Werner and Holsten, 1995).

The large energetic investment in MBO production made by MBO producing pines, the appearance of MBO as a bark beetle pheromone, and some indications that MBO possesses anti-attractant properties, led to the hypothesis that in North America MBO may function as a defensive compound protecting emitting trees against bark beetle attack. MBO might serve as a defensive compound in two fashions: directly by influencing bark beetle behavior or indirectly by attracting predators and parasitoids to the emitting tree. Since it is not stored in plant tissues or manufactured in the wood, any direct defensive properties exhibited by MBO probably influence host location and acceptance behavior rather than larval survival.

MBO may have repellent properties similar to those found for 4-allylanisole (Hayes et al., 1994; Hobson, 1995), or it may inhibit landing behavior similar to the landing inhibition that Schlyter et al. (1987b) observed for *I. typographus* in response to high MBO concentrations. MBO might also inhibit the aggregation response of bark beetles. Such a response was shown by Birch and Wood (1975) when they observed that the pheromones of *I. pini* inhibited the aggregation response of *I. paraconfusus* and vice versa. In addition to these potential direct influences, MBO may benefit an emitting tree indirectly by attracting predators

and parasitoids. In Europe, bark beetle predators have been shown to be attracted to MBO (Bakke and Kvamme, 1981), and in North America the pheromones of several bark beetles have been shown to attract the predators of bark beetles (Kohnle and Vité, 1984; Mizell et al., 1984; Herms et al., 1991).

To help elucidate the function of MBO emissions, we examined the response of two North American scolytid bark beetles (*Ips paraconfusus* and *Dendroctonus brevicomis*) and predatory beetles in the families Cleridae and Trogositidae that feed on bark beetles to differing MBO release rates alone or in the presence of attractive monoterpenes or bark beetle pheromone. *I. paraconfusu*s is a marginally aggressive *Ips* found in North America that feeds on a broad range of pines (including *P. ponderosa*) and occasionally attacks and kills live trees. *D. brevicomis* is one of the most aggressive tree-killing bark beetles in North America (Furniss and Carolin, 1977), and feeds predominantly on *P. ponderosa*. The impact of MBO on bark beetle and predatory beetle behavior was examined by using field trapping experiments; insect capture rates were then used to determine whether MBO aids either plant defense against herbivores or insect location of suitable trees.

METHODS AND MATERIALS

Field-trapping experiments were conducted in the central Sierra Nevada mountains of California at the UC Berkeley Blodgett Forest Research station (38°53′, 42.9″N, 120°37′, 57.9″W). Lindgren funnel traps (Lindgren, 1983) were placed in small clearcuts located in compartments 260 (1999), and 400 (2000). These sites were logged the previous year and the slash was piled and burned the previous winter in compartment 260 or treated with a rotary masticator the previous fall in compartment 400 prior to conducting the trapping studies. The trapping sites were surrounded by second-growth mixed-conifer forest (approximately 80 years old) containing Douglas fir (*Pseudotsuga menziesii*), Ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus lambertiana*), incense cedar (*Calocedrus decurrens*), and white fir (*Abies concolor*) in roughly equal proportions, and scattered individuals of California black oak (*Quercus kellogii*). In both years and at both sites, trees within 1 km of the trapping sites were observed to be attacked and killed by bark beetles.

The experiments conducted were fully factorial designs with two levels of attractant bait (presence or absence) and four levels of MBO release. Each attractant bait by MBO release rate combination was replicated once within the trapping array ($N = 2$) and additional replication was achieved by sampling repeatedly through time. Sampling durations ranged from one to seven days depending on bark beetle flight intensity. Longer sampling durations were used during periods of low bark beetle activity to avoid having to analyze sampling periods with no captures in any treatment. MBO and monoterpenes were released from 2 ml microcentrifuge tubes suspended from the middle of the Lindgren funnel trap. Release rates were

TABLE 1. DESCRIPTION OF TREATMENTS, METHYLBUTENOL RELEASE RATES, AND MBO-EMITTING DEVICES USED IN EXPERIMENTS

Treatment	Nominal release rate (mg/day)[a]	Design
None	0	NA
Low	2.5	2-ml polypropylene Eppendorf tube fitted with a 5-ul capillary tube inserted through the cap
Medium	5	Two 2.5 mg/day releasers
High	50	2-ml polypropylene Eppendorf tube with a 1.59-mm hole drilled in cap
Very high	1000	2-ml polypropylene Eppendorf tube without cap

[a] Nominal release rates were determined by measuring weight lost from emitting devices held at 25°C in the laboratory.

varied by drilling holes of various sizes in the cap of the microcentrifuge tube, fitting a glass microcapillary tube in the cap, or leaving the tube uncapped. MBO releasing devices were constructed to achieve release rates corresponding to the MBO release rates shown to influence the behavior of *Ips typographus* by Schlyter et al. (1987a). Nominal release rates of these devices were determined by measuring volatilization gravimetrically from devices held at 25°C. Release rates and device descriptions are shown in Table 1. These release rates fall within the range of MBO levels that bark beetles are likely to encounter from phytogenic sources in the field. Leaf level MBO emission rates have been measured as high as 3.44 mg MBO/g needle tissue/day in Ponderosa pine (Gray, unpublished data), thus allowing a single fascicle to equal the release rate of the lowest MBO-emitting device. At the other end of the scale, canopy-level MBO emission rates have been measured between 172 and 344 mg MBO/m^2/s (Baker et al., 1999, 2001; Schade et al., 2000).

Sixteen eight-unit funnel traps were arrayed in four groups of four traps (Figure 1), with a spacing of 6 m between traps within a trap group and 12 m between traps in adjacent trap groups. Each trap within a group contained the same level of attractant bait, but contained a device releasing MBO at a different rate (Table 1). The collecting cups were filled with soapy water in which the captured insects drowned. This prevented captured predatory beetles from consuming the captured bark beetles. At the end of each sampling period, the traps within each group and the groups within the array were rotated clockwise to minimize the effect of trap position on the results. Captured insects were frozen or preserved in ethanol until identified and counted.

Three experiments tested whether MBO affected the behavior of bark beetles or their predators and whether MBO mediated the response of bark beetles or their predators to pheromone signals. In experiment 1, a multicomponent *Ips paraconfusus* lure (Phero Tech Inc., Delta, British Columbia) containing ipsenol, ipsdienol, and *cis*-verbenol was used as the attractant bait, and the MBO release

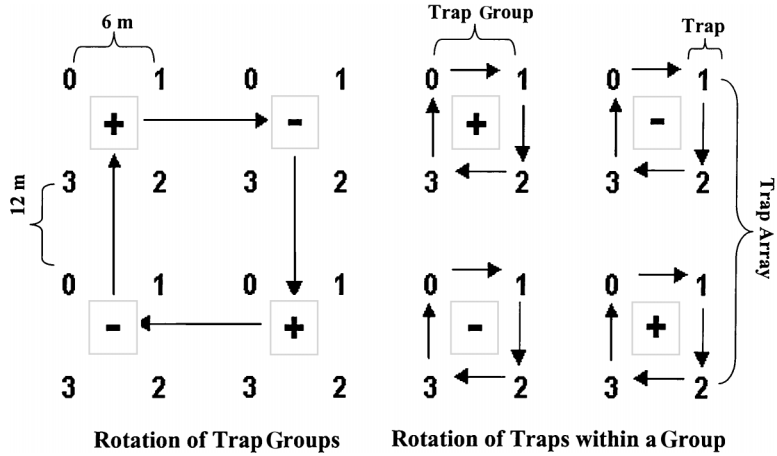

FIG. 1. Funnel trap layout and rotation scheme. Numbers 0–3 represent increasing MBO release rates as specified for each experiment. The +/− symbols denote the presence or absence of attractant bait (pheromone or monoterpenes) in traps within a trap group. Traps were spaced 6 m apart within a trap group and 12 m between traps in adjacent groups.

rates used were none, low, medium, or high (Table 1). Experiment 2 also used the *Ips paraconfusus* lure, but replaced the low MBO release rate with the very high treatment. Experiment 3 used a multicomponent *Dendroctonus brevicomis* lure (Phero Tech Inc., Delta, British Columbia) containing *exo*-brevicomin, frontalin, and myrcene as the attractant bait; and the MBO release rates were none, medium, high, and very high (Table 1).

A fourth experiment tested whether MBO affected the behavior of bark beetles or their predators to attractive host monoterpenes in the absence of a pheromone signal. In this experiment, host monoterpenes previously shown to be attractive to bark beetles (Rudinsky et al., 1971; Borden, 1985; Miller and Borden, 1990) were used instead of pheromones as the attractive bait. The MBO release rates were none, medium, high, and very high (Table 1). Monoterpenes were released from open-top 2 ml polypropylene microcentrifuge tubes at the following nominal rates: α-pinene = 0.47 g/day, β-pinene = 0.49 g/day, myrcene = 0.24 g/day.

Insects captured in the funnel-trap collection cups were collected at the end of each sampling period and frozen or preserved in ethanol until they were identified and counted. Scolytid bark beetles were identified to species, and all other captured insects were identified to family. The effects of attractant bait and MBO release rate on captures per sampling period were analyzed by three-way ANOVA using the GLM procedure of SAS (1990). The sampling period was included in the model as a covariate to take into account differences in sampling period duration (one to seven days) and differences in climatic conditions across samplings periods

such as temperature, cloud cover, and wind that may alter bark beetle activity levels (Bennett and Borden, 1971; Coster et al., 1978; Borden, 1981). Data were $\log_{10}(X + 1)$ transformed to meet the ANOVA assumptions of normality and homoscedasticity (Sokal and Rohlf, 1995).

RESULTS

In experiment 1, the addition of pheromone bait to traps increased the capture rate of *Ips paraconfusus* by a factor of more than 100. However, the addition of MBO did not alter the magnitude or pattern of captures across traps (Table 2, Figure 2). Predatory beetles in the families Cleridae and Trogositidae were not influenced by either *Ips paraconfusus* pheromone or MBO release rate (Table 2).

Similar results were observed in experiment 2 despite the addition of a much larger MBO release rate treatment. Pheromone bait increased bark beetle captures by a factor of more than 100; however, no effect of MBO release rate on captures of *Ips paraconfusus* could be detected (Table 3, Figure 3). No influence of either

TABLE 2. ANOVA ON EFFECTS OF SAMPLING DATE, PHEROMONE PRESENCE/ABSENCE, AND MBO RELEASE RATE ON CAPTURES OF *Ips paraconfusus*, CLERIDAE, AND TROGOSITIDAE AT LINDGREN FUNNEL TRAPS IN EXPERIMENT 1

Taxa	Source	*df*	MS	*F*	*P*
Ips paraconfusus					
	Main effects				
	Day	2	0.03836	0.4800	<0.6208
	Pheromone	1	256.856	3232.73	<0.0001
	MBO[a]	3	0.07976	1.0000	<0.4017
	Interactions				
	Pheromone × MBO	3	0.08548	1.0800	<0.3709
Cleridae					
	Main effects				
	Day	2	0.0100094	1.00	<0.3774
	Pheromone	1	0.0100094	1.00	<0.3236
	MBO[a]	3	0.0100094	1.00	<0.4034
	Interactions				
	Pheromone × MBO	3	0.0100094	1.00	<0.4034
Trogositidae					
	Main effects				
	Day	2	0.070066	1.14	<0.3315
	Pheromone	1	0.090085	1.46	<0.2342
	MBO[a]	3	0.063393	1.03	<0.3909
	Interactions				
	Pheromone × MBO	3	0.036701	0.60	<0.0622

[a] MBO release rates as in Table 1 with "very high" treatment omitted.

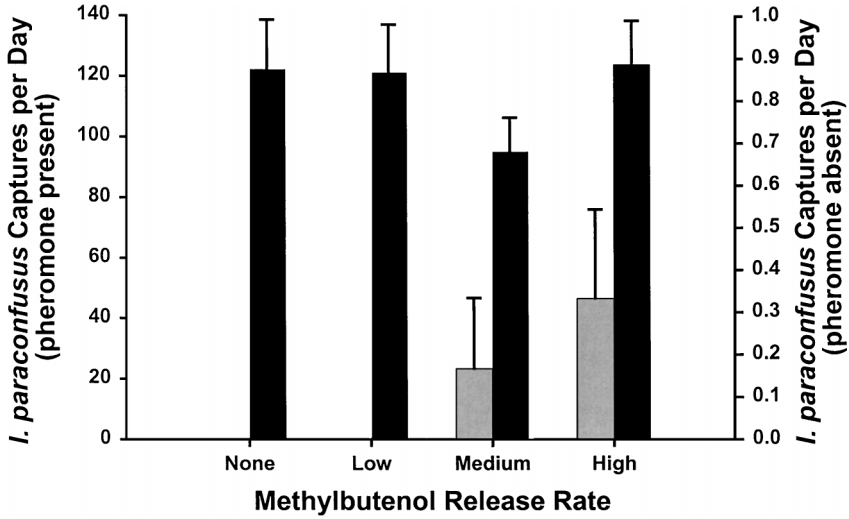

FIG. 2. Catches of *Ips paraconfusus* in eight-unit Lindgren funnel traps baited with varying release rates of MBO and with (black bars) or without (gray bars) *I. paraconfusus* pheromone in experiment 1. Error bars represent ±1 standard error.

pheromone or MBO release could be detected on the capture rates of predatory clerids or trogositids (Table 3).

In experiment 3, the addition of *D. brevicomis* pheromone caused a significant increase in *D. brevicomis* and trogositid captures. On the other hand, MBO release rate did not change *D. brevicomis* or trogositid capture rates in either the presence or absence of pheromone (Table 4, Figure 4). Neither pheromone nor MBO release rate changed the capture rates of predacious clerid beetles (Table 4).

In experiment 4, where host monoterpenes were used as the attractant bait, the number of bark beetles captured during the trapping period was quite low, and no differences were seen among treatments. Analysis of the predatory beetles captured showed that neither monoterpenes nor MBO release rate affected clerid or trogotidid captures (Table 5, Figure 5).

DISCUSSION

The results of the trapping experiments did not support the hypothesis that MBO emissions from Ponderosa pine provide protection against bark beetle attack. The data showed no indication that *I. paraconfusus* or *D. brevicomis* were repelled by MBO alone, or by MBO in combination with host monoterpenes or bark beetle pheromone. Similarly, the major insect predators of these bark beetles were not attracted by MBO, suggesting that MBO does not provide an indirect defense.

TABLE 3. ANOVA ON EFFECTS OF SAMPLING DATE, PHEROMONE PRESENCE/ABSENCE, AND MBO RELEASE RATE ON CAPTURES OF *Ips paraconfusus*, CLERIDAE, AND TROGOSITIDAE AT LINDGREN FUNNEL TRAPS IN EXPERMENT 2

Taxa	Source	*df*	MS	*F*	*P*
Ips paraconfusus					
	Main effects				
	Day	3	5.6594	17.54	<0.0001
	Pheromone	1	166.47	515.83	<0.0001
	MBO[a]	3	0.2065	0.64	<0.5927
	Interactions				
	Pheromone × MBO	3	0.2271	0.70	<0.5539
Cleridae					
	Main effects				
	Day	3	0.00751	1.00	<0.4001
	Pheromone	1	0.00751	1.00	<0.3219
	MBO[a]	3	0.00751	1.00	<0.4001
	Interactions				
	Pheromone × MBO	3	0.00751	1.00	<0.4001
Trogositidae					
	Main effects				
	Day	3	0.0100	0.65	<0.5838
	Pheromone	1	0.0000	0.00	<1.0000
	MBO[a]	3	0.0100	0.65	<0.5838
	Interactions				
	Pheromone × MBO	3	0.0200	1.31	<0.2813

[a] MBO release rates as in Table 1 with "low" treatment omitted.

Despite the lack of evidence that MBO possesses defensive properties, it should be noted that this study examined only two of the many species of bark beetle found in North American pine forests. While *I. paraconfusus* is one of the most aggressive *Ips* in North America and attacks a wide range of pines, it is much less aggressive than its European congeners (especially *I. typographus*). Nonetheless, *I. paraconfusus* is an aggressive killer of pole-size trees and the tops of mature trees, especially *P. ponderosa* in the central Sierra Nevada mountains where this study was conducted (Furniss and Carolin, 1977). *D. brevicomis*, on the other hand, is one of the most destructive bark beetles present in North America and frequently attacks healthy trees. However, since both species of pine (*P. ponderosa* and *P. coulteri*) attacked by *D. brevicomis* produce MBO (Harley et al., 1998), its failure to respond to MBO may indicate an adaptation to feeding on these hosts. If, in fact, MBO has a defensive function, it likely has its effect on those bark beetle species that do not feed on MBO-producing trees, and this may help account for host specificity among bark beetle species. Perhaps MBO production excludes *P. ponderosa* from the host range of Scolytids that feed on non-MBO-producing

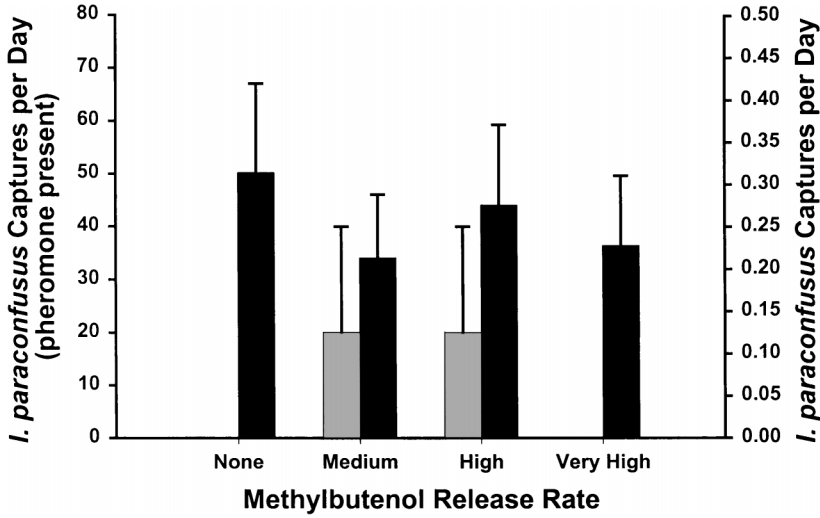

FIG. 3. Catches of *Ips paraconfusus* in eight-unit Lindgren funnel traps baited with varying release rates of MBO and with (black bars) or without (gray bars) *I. paraconfusus* pheromone in experiment 2. Error bars represent ±1 standard error.

TABLE 4. ANOVA ON EFFECTS OF SAMPLING DATE, PHEROMONE PRESENCE/ABSENCE, AND MBO RELEASE RATE ON CAPTURES OF *Dendroctonus brevicomis*, CLERIDAE, AND TROGOSITIDAE AT LINDGREN FUNNEL TRAPS IN EXPERMENT 3

Taxa	Source	*df*	MS	*F*	*P*
Dendroctonus brevicomis					
	Main effects				
	Day	9	2.39077	7.91	<0.0001
	Pheromone	1	116.73	386.39	<0.0001
	MBO[a]	3	0.15709	0.52	<0.6692
	Interactions				
	Pheromone × MBO	3	0.04864	0.16	<0.9224
Cleridae					
	Main effects				
	Day	9	0.04671	1.00	<0.4442
	Pheromone	1	0.04804	1.03	<0.3126
	MBO[a]	3	0.05205	1.11	<0.3462
	Interactions				
	Pheromone × MBO	3	0.02402	0.51	<0.6736
Trogositidae					
	Main effects				
	Day	9	1.10599	5.61	<0.0001
	Pheromone	1	11.8484	60.07	<0.0001
	MBO[a]	3	0.25450	1.29	<0.2801
	Interactions				
	Pheromone × MBO	3	0.33673	1.71	<0.1682

[a] MBO release rates as in Table 1 with "low" treatment omitted.

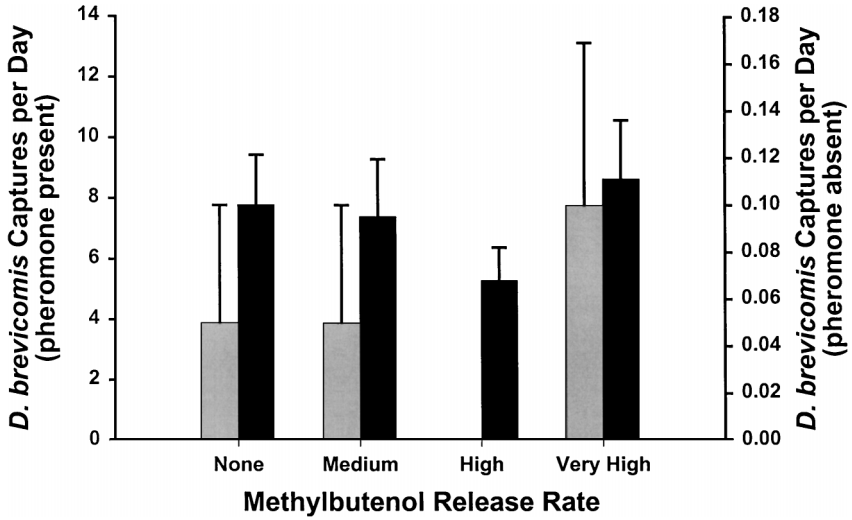

FIG. 4. Catches of *Dendroctonus brevicomis* in eight-unit Lindgren funnel traps baited with varying release rates of MBO and with (black bars) or without (gray bars) *D. brevicomis* pheromone in experiment 3. Error bars represent ±1 standard error.

TABLE 5. ANOVA ON EFFECTS OF SAMPLING DATE, MONOTERPENE PRESENCE/ABSENCE, AND MBO RELEASE RATE ON CAPTURES OF PREDACEOUS CLERIDAE AND TROGOSITIDAE AT LINDGREN FUNNEL TRAPS IN EXPERMENT 4

Taxa	Source	*df*	MS	*F*	*P*
Cleridae					
	Main effects				
	Day	1	0.6851	2.88	<0.1032
	Monoterpene	1	0.0086	0.04	<0.8512
	MBO[a]	3	0.1269	0.53	<0.6647
	Interactions				
	Monoterpene × MBO	3	0.1481	0.62	<0.6075
Trogositidae					
	Main effects				
	Day	1	0.1059	0.26	<0.6168
	Monoterpene	1	0.3693	0.90	<0.3532
	MBO[a]	3	0.1264	0.31	<0.8199
	Interactions				
	Monoterpene × MBO	3	0.1533	0.37	<0.7735

[a] MBO release rates as in Table 1 with "low" treatment omitted.

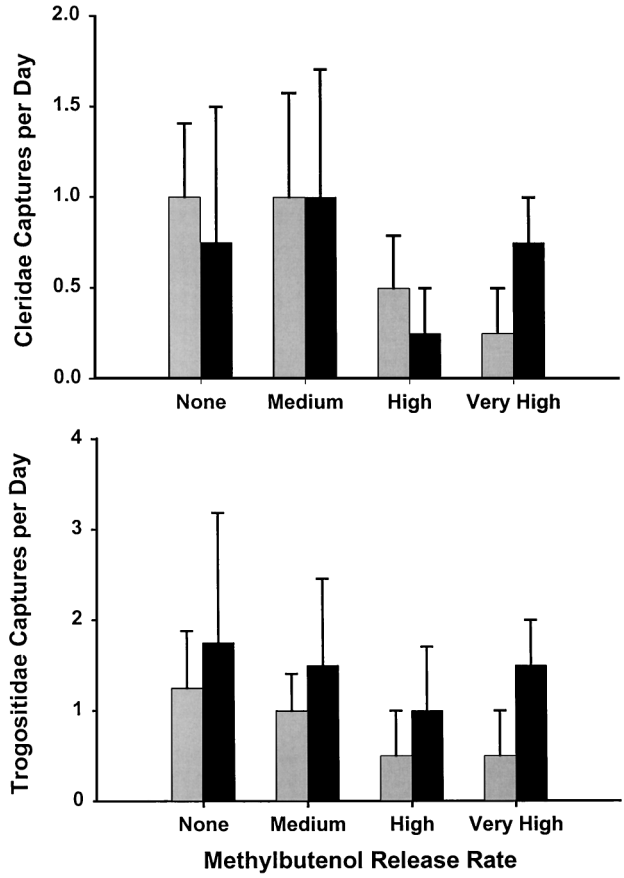

FIG. 5. Catches of predacious beetles in the families Cleridae and Trogositidae in eight-unit Lindgren funnel traps baited with varying release rates of MBO and with (black bars) or without (gray bars) monoterpenes in experiment 4. Monoterpenes were released at nominal rates of: α-pinene = 0.47 g/day, β-pinene = 0.49 g/day, myrcene = 0.24 g/day. Error bars represent ± 1 standard error.

conifers (*A. concolor*, *P. menziezii*, *C. decurrens*, and *P. lambertiana*). However, scolytid species that feed exclusively on non-MBO-producing conifers have not been screened for their response to MBO.

A spatial discontinuity also exists between the site of MBO production and bark beetle attack. MBO production only occurs in the photosynthetic tissues, whereas bark beetles attack the non-photosynthetic trunks. For this reason, it is possible that bark beetles never encounter strong MBO plumes emanating from potential host trees. However, insects feeding on the foliage or reproductive structures

of MBO-emitting pines would certainly encounter MBO. No such insect has yet been tested for its response to MBO.

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