Environmental Entomology, XX(XX), 2021, 1–7
https://doi.org/10.1093/ee/nvab092
Research

ENTOMOLOGICAL SOCIETY OF AMERICA
SHARING INSECT SCIENCE GLOBALLY

OXFORD

Chemical Ecology

Some Effects of *endo*-Brevicomin Background on Southern Pine Beetle (Coleoptera: Curculionidae: Scolytinae) Aggregation Behavior

Brian T. Sullivan,[1,3] and Cavell Brownie[2]

[1]USDA Forest Service, Southern Research Station, 2500 Shreveport Highway, Pineville LA 71360, USA, [2]Department of Statistics, North Carolina State University, Raleigh, NC 27695, USA, and [3]Corresponding author, e-mail: brian.sullivan2@usda.gov

Subject Editor: Matthew Ginzel

Received 30 June 2021; Editorial decision 13 August 2021

Abstract

Semiochemical background in the environment can influence insect orientation to release points of the same or different semiochemicals. *endo*-Brevicomin is a pheromone component of the tree-killing bark beetle *Dendroctonus frontalis* Zimmermann (Coleoptera: Curculionidae: Scolytinae) that has a biphasic dose–response curve, enhancing attraction at low release rates but reducing attraction at high rates. We investigated the effect of artificial manipulation of background levels of *endo*-brevicomin on *D. frontalis* responses to sources of aggregation attractant in the field. Traps baited with the aggregation pheromone component frontalin and the host odor *alpha*-pinene were deployed either with or without a background of *endo*-brevicomin produced by three surrounding dispensers of this semiochemical each located 20 m away. Two tested levels of *endo*-brevicomin background caused catches to increase by an order of magnitude above those in the absence of background. Presence of background also altered the beetles' biphasic dose–response when *endo*-brevicomin dispensers were added to traps. Background reduced or concealed attraction-enhancement otherwise observed for low-release dispensers added to traps, and it decreased the release rate necessary to produce reductions in catches. We propose that spatial variability in abundance of natural, background sources of *endo*-brevicomin in the environment (i.e., infested trees) is a cause of the observed variability in effects of *endo*-brevicomin dispensers on southern pine beetle behavior in the field. Furthermore, our results illustrate the potential complexity of the density-dependent effects of biphasic pheromone components on bark beetle mass attack and colonization behavior.

Key words: biphasic, multifunctional, semiochemical, dose–response, aggregation

Insect orientation with respect to individual sources of semiochemicals can be influenced by background semiochemicals in the environment (Miller et al. 2006, Schröder and Hilker 2008, Party et al. 2013, Conchou et al. 2019). This effect has been demonstrated in tree-killing bark beetles (Coleoptera: Curculionidae: Scolytinae) through distribution of synthetic semiochemical releasers in areas where attractant-releasing traps have been deployed (Vité et al. 1976, Payne et al. 1977, Ross and Wallin 2008). Additionally, stands and trees can be protected from bark beetle infestation through deployment of regularly-distributed dispensers of attraction inhibitors (Tilden et al. 1981, Tilden et al. 1987, Ross and Daterman 1995, Gillette et al. 2009, Andersson et al. 2011). The resulting semiochemical background within a stand possibly interferes with beetle orientation to aggregation pheromone released from beetle attacks. Natural, spatially-dispersed sources of semiochemical in the environment presumably can also influence bark beetle orientation to individual sources of pheromone, but the topic has received little attention (Zhang and Schlyter 2003, Zhang and Schlyter 2004). Mass-attacked trees distributed in active infestations should generate a pheromone background within and adjacent to these infestations, and infestations dispersed across the landscape (Coulson et al. 1999, Dodds et al. 2006, Kautz et al. 2011) may produce pheromone background at larger spatial scales. Since levels of semiochemical background should be influenced by local beetle abundance, effects on beetle behavior should be density-dependent.

A combination of beetle- and host-produced compounds mediate mass-aggregation on individual hosts by the aggressive, tree-killing bark beetle *Dendroctonus frontalis* Zimmermann (Coleoptera: Curculionidae: Scolytinae) (Gara et al. 1965, Tisdale et al. 2003). Aggregation attractant stimulates attacks on individual trees in sufficient numbers to overwhelm constitutive resin defenses of vigorous hosts (Sullivan 2016). Females initiate attacks on trees by releasing the pheromone component frontalin which attracts both sexes (Kinzer et al. 1969, Renwick and Vité 1969), and frontalin is strongly synergized by volatile constituents of defensive resin released by the damaged host tissue (Billings 1985, Pureswaran and Sullivan 2012). Males join females and release *endo*-brevicomin which can further enhance attraction, and the combination mediates mass-aggregation (Vité et al. 1985, Sullivan et al. 2007). Presumably, *endo*-brevicomin (when present with frontalin) can signal the presence of successfully establishing pairs and thus susceptible hosts. *endo*-Brevicomin may also play a role in regulating attack densities and mediating switching of attack focus to adjacent trees (Vité and Renwick 1971, Salom et al. 1992, Sullivan and Mori 2009, Sullivan et al. 2011). It can reduce responses to frontalin and host odor combinations as its concentrations increase, and in this context it may signal that the abundance of attacking pairs has reached the carrying capacity of the host (Sullivan et al. 2011, Sullivan 2016). Individual sources of *endo*-brevicomin can influence beetle behavior across a wide area, and single releasers can synergize beetle response to sources of the female-associated components of the aggregation attractant located tens of meters away (Sullivan and Mori 2009, Sullivan et al. 2016, Shepherd and Sullivan 2017). Bark beetle semiochemicals like *endo*-brevicomin that either increase or decrease response to an attractant when released at either low or high rates, respectively (i.e., have a biphasic dose–response, Calabrese 2013), have been termed 'multifunctional' because they presumably mediate both mass aggregation on a host and attack termination and switching depending on their concentration (Rudinsky et al. 1974, Rudinsky and Ryker 1980, Borden et al. 1987).

In the present study, we investigated the effect of an artificial *endo*-brevicomin background on the dose–response of *D. frontalis* to *endo*-brevicomin devices associated with a source of attractant. Previously, we observed that releasers of *endo*-brevicomin reverse from inhibitory to synergistic when either inside or outside of active infestations, respectively, and we hypothesized that pheromone background within infestations could be a sufficient cause for such a difference (Sullivan et al. 2011). Unknown influences of natural semiochemical background have the potential to interfere with the desired effects of synthetic semiochemical releasers deployed for bark beetle management.

Materials and Methods

Three lines of eight 12-unit multiple funnel traps were established within a mixed pine and hardwood forest within the Homochitto National Forest, Mississippi (within 5 km of 31° 25.2′ N, 91° 12′ W). The forest was experiencing a *D. frontalis* outbreak at the time; however, no infestations were occurring within the stands used for the tests. Traps were spaced >250 m apart both within and between lines, were suspended from metal standards with collection cups 1–1.5 m above ground, and were >15 m from the nearest pine. Trap cups contained dilute propylene glycol to preserve captured insects. All traps were baited with lures releasing frontalin (two capped polyethylene microcentrifuge tubes with 250 µl racemic frontalin; BASF, Florham Park, NJ; >99% purity; total release rate 7 mg/d at 26 ± 1°C; devices attached at trap center), and *alpha*-pinene [plastic pouch with 3:1 (−):(+) *alpha*-pinene; 2 g/d at 27 ± 2°C; Synergy Semiochemicals, Delta, British Columbia, CA; devices attached to trap top]. Four randomly-selected traps in each line were provided an artificial *endo*-brevicomin 'background' by deploying three release devices positioned ~1.5 m above ground (on plastic gardening stakes) and 20 m from the trap; these were arranged in an equilateral triangle centered on the trap (Fig. 1). The remaining four traps had no satellite release devices and were 'background free'. Within each line and background category, traps were randomly assigned either no additional device or an *endo*-brevicomin device releasing one of three rates differing by an order of magnitude (variable 'lure'; Table 1). These devices were attached at trap center.

With each collection of catches (2–7 d intervals), lure treatments were rerandomized without replacement among traps within each line and background category until every treatment had been at each trap once. After this complete rotation (four collections), the satellite *endo*-brevicomin releasers were moved to traps which lacked them in the first rotation, and a second identical rotation (with different randomization scheme) was completed. Two such complete trials were performed sequentially using the same sites. In trial 1

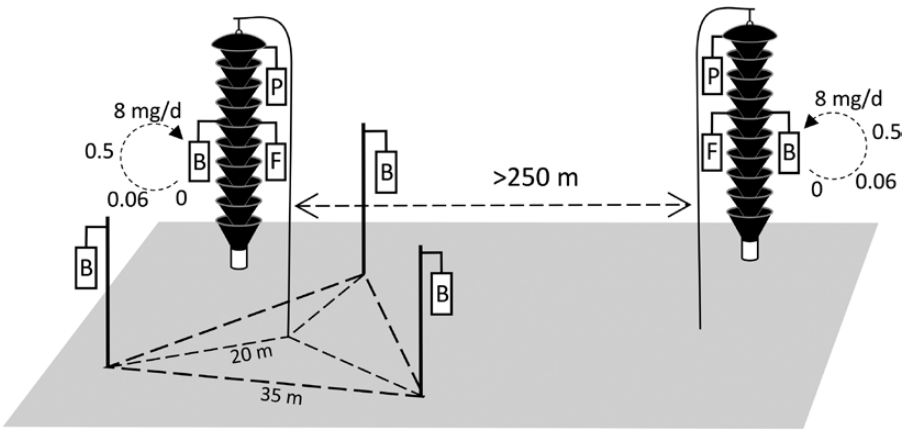

Fig. 1. Arrangement of traps and lures for experiments. Half of the traps had a background of *endo*-brevicomin ('B') produced by a trio of releasers on poles arranged in an equilateral triangle around the trap. Traps both with and without background were assigned devices with one of four release rates of *endo*-brevicomin (0, 0.06, 0.5, and 8 mg/d approximately). All traps had devices releasing components of the *D. frontalis* aggregation attractant frontalin (F) and *alpha*-pinene (P).

Table 1. *endo*-Brevicomin release devices used in experiments

Device type	Release	Rate[a]	Device construction[b]
Background	Low (trial 2)	0.16 mg/d	Single microcapillary (1.17 mm id × 32 mm)
	High (trial 1)	3.1 mg/d	Single, capped low-density polyethylene microcentrifuge tube (400-µl capacity)
Trap	Low	0.06 mg/d	Single microcapillary (0.63 mm id × 32 mm)
	Mid	0.5 mg/d	Three microcapillaries (1.17 mm id × 32 mm)
	High	8 mg/d	Single 15 ml vial with 7 mm diameter hole through phenolic cap

[a]Measured either gravimetrically or by volume loss in a fume hood at mean 23–25°C.
[b]Capillaries were secured open-end up inside an inverted, uncapped, 4-ml capacity brown glass vial.

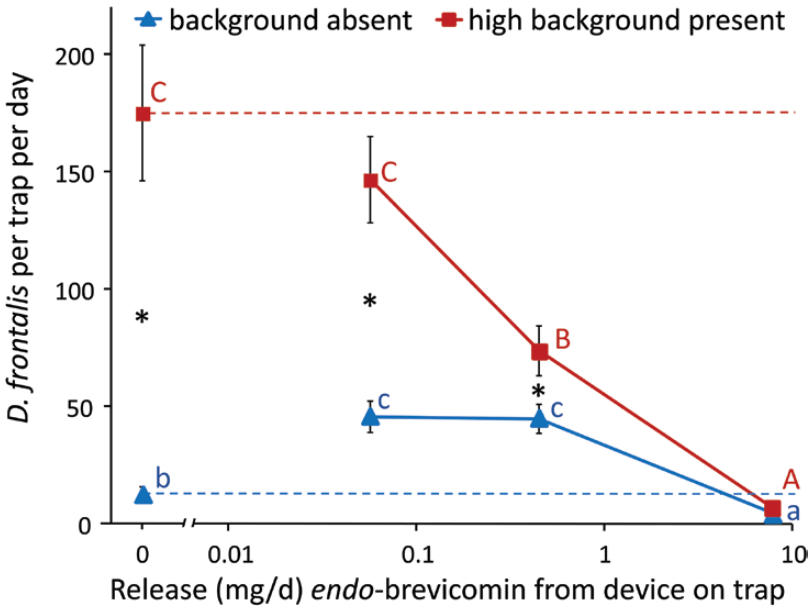

Fig. 2. Trial 1. Responses of *D. frontalis* to funnel traps baited with frontalin and *alpha*-pinene and (1) with an attached releaser of *endo*-brevicomin of one of three release rates (or none) and (2) either surrounded by three releasers of *endo*-brevicomin at 20 m distance (red) or alone (blue). Dashed lines display the mean catches that occurred in the absence of *endo*-brevicomin devices on the trap. Satellite devices each released 3.1 mg/d. Means with the same lower-case letter (background absent) or upper-case letter (background present) did not differ significantly. Asterisks indicate that catches were significantly different with or without background at the indicated release of *endo*-brevicomin from the trap. Pairwise contrasts received a Bonferroni correction ($\alpha = 0.05$). Data received a log transformation for analyses, but untransformed data are shown.

(18 February–29 March 2016) the satellite *endo*-brevicomin devices released at a 'high' rate (3.1 mg/d); in trial 2 (30 March–7 May 2016) they released a 'low' rate (0.16 mg/d; Table 1). Trees within 100 m of the traps were inspected at the start and during the trials to ensure absence of *D. frontalis* attacks that might be a source of pheromone. Captured male and female *D. frontalis* were counted.

Statistical analyses were performed with SAS 9.4 (SAS Institute, Cary, NC). Catches were log-transformed to meet test assumptions, and suitability of the transformation was based on examination of residuals plots. Interactions between sex and treatment were tested with a mixed-model ANOVA with fixed effects background, lure, sex, and all interactions; for trial 1, random effects were line, trap in line, background by trap in line, date, lure by line, and lure by background by date by trap in line; for trial 2, random effect lure by line was removed as it was not significant. No significant sex interactions were detected, and therefore sexes were pooled for further analyses. Pairwise comparisons were performed with an Estimate statement. For each trial, contrasts were made between background present and absent for each trap lure release rate (with Bonferroni adjustment for four contrasts), and we performed all-pairwise comparisons among trap lure release rates within both background categories (with Bonferroni adjustment for 12 contrasts). For all tests $\alpha = 0.05$.

Results

In trial 1 (with high background of *endo*-brevicomin;), there was not an interaction between sex and the presence of background ($F = 1.84$; df = 1, 182; $P = 0.18$), between sex and lure release rate ($F = 1.99$; df = 3, 182; $P = 0.12$), or an interaction among all three factors ($F = 0.85$; df = 3, 182; $P = 0.47$). With sexes totaled (Fig. 2), there was a strong effect due to the presence of background ($F = 154$; df = 1, 22; $P < 0.001$), lure release rate ($F = 126$; df = 3, 6; $P < 0.001$), and the interaction of these factors ($F = 64.0$; df = 3, 124; $P < 0.001$). Catches were significantly increased by presence of a high level of *endo*-brevicomin in the background when *endo*-brevicomin devices on traps were absent or released at the low or intermediate rates; presence of background had no effect with high release trap lures present. With *endo*-brevicomin absent in the background, *endo*-brevicomin devices on traps with low and intermediate release rates significantly increased catches relative to the zero rate, but high-rate trap devices significantly reduced catches. With high levels of *endo*-brevicomin present in the background, catches decreased with increasing release rates from traps.

In trial 2 (low background of *endo*-brevicomin), there was not an interaction between sex and the presence of background ($F = 3.16$;

df = 1, 183; $P = 0.077$), between sex and lure release rate ($F = 1.65$; df = 3, 183; $P = 0.18$), or an interaction among all three factors ($F = 0.94$; df = 3, 183; $P = 0.42$). With sexes totaled (Fig. 3), there was a significant effect due to the presence of background ($F = 5.50$; df = 1, 33.4; $P = 0.025$), lure release rate ($F = 28.4$; df = 3, 121; $P < 0.001$), and the interaction of these factors ($F = 7.72$; df = 3, 121; $P < 0.001$). Catches were significantly increased by presence of a low *endo*-brevicomin background when *endo*-brevicomin devices were absent from the traps or released at the low rate; background presence had no significant effect when higher release devices were on the traps. In the absence of an *endo*-brevicomin background, catches were increased by all release rates of *endo*-brevicomin from the traps, peaking at the intermediate rate. With low background present, catches likewise increased from the zero rate and peaked at the intermediate trap release rate; however, with high rate devices on the traps, catches declined to less than those with no *endo*-brevicomin device on the traps.

Discussion

The presence of synthetic *endo*-brevicomin background altered the dose–response of *D. frontalis* to single releasers of this pheromone placed on attractant-baited traps. In the absence of background, *endo*-brevicomin devices on the traps produced a peaked dose–response as observed in other studies (Sullivan 2016, B. T. Sullivan unpublished data). However, a fully biphasic effect was not observed in trial 2 (i.e., catches did not drop below the level of the zero dose on the trap), perhaps due to a change in responsiveness of *D. frontalis* to *endo*-brevicomin that occurs as spring progresses (Sullivan et al. 2016). Termination of the spring flight of *D. frontalis* likely explains the much lower, overall catches in trial 2 relative to trial 1. Background either diminished (low background) or eliminated (high background) the relative catch increase associated with low release rate devices on the trap, and it caused appearance of catch-reducing effects for devices on the traps (low background) or made these effects evident at a lower release from the trap (high background). This observed change in the dose–response is largely consistent with an additive effect of the background *endo*-brevicomin and the *endo*-brevicomin device on the trap. That is, the effect of the background largely resembled that expected for a preexisting *endo*-brevicomin device on the trap (Fig. 4). However, a genuinely additive effect would imply that catches at the peak of the dose–response curve would be the same with background either present or absent, and our data plots are not consistent with this (Figs. 2 and 3). In the high background trial in particular (trial 1), the maximum catches observed with background present (zero and low release from trap) were significantly higher than the maximum catches observed with background absent (low or middle release from trap; $t \leq -6.02$, df = 124, $P < 0.004$).

The effect of the artificial pheromone background in our experiments likely reflects what might be produced by the natural pheromone background within an active *D. frontalis* infestation. In Sullivan et al. (2009), it was estimated that total release of *endo*-brevicomin by beetles on mass-attacked pines 20–40 cm diameter (typical diameter range in a mature, managed forest of host species for *D. frontalis*) is 0.1- to 0.5-mg *endo*-brevicomin per day. Hence the total release from the background devices in our study (0.5–6 mg/d) approximately represented the production of one to 60 mass attacked trees. This suggests that the *endo*-brevicomin background inside or near such infestations could reduce, eliminate, or reverse the attraction-enhancing influence otherwise observed for low release *endo*-brevicomin sources (Sullivan et al. 2007, 2011, 2016). Hence, the presence of *endo*-brevicomin background within *D. frontalis* infestations could explain the contrast between the attraction-reducing effects of *endo*-brevicomin sources typically observed inside infestations (Payne et al. 1977, Payne et al. 1978, Richerson and Payne

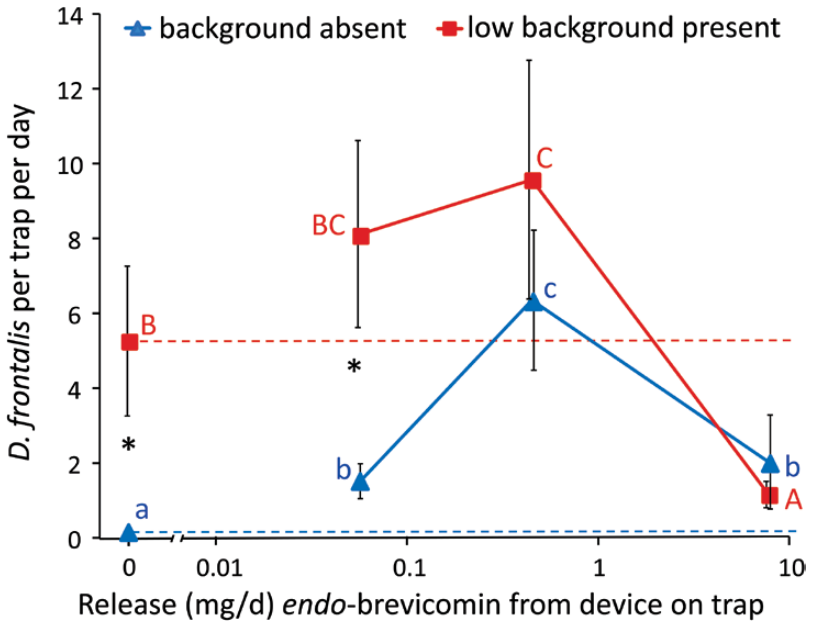

Fig. 3. Trial 2. Responses of *D. frontalis* to funnel traps baited with frontalin and *alpha*-pinene and (1) with an attached releaser of *endo*-brevicomin of one of three release rates (or none) and (2) either surrounded by three releasers of *endo*-brevicomin at 20 m distance (red) or alone (blue). Dashed lines display the mean catches that occurred in the absence of *endo*-brevicomin devices on the trap. Satellite devices each released 0.16 mg/d. Means with the same lower-case letter (background absent) or upper-case letter (background present) did not differ significantly. Asterisks indicate that catches were significantly different with or without background at the indicated release of *endo*-brevicomin from the trap. Pairwise contrasts received a Bonferroni correction ($\alpha = 0.05$). Data received a log transformation for analyses, but untransformed data are shown.

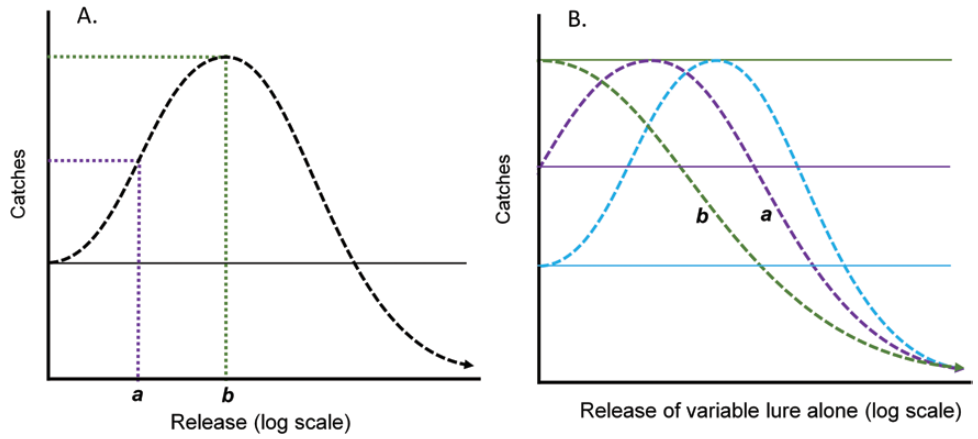

Fig. 4. Additive effects of release devices on dose–response curves for a semiochemical with a biphasic dose–response. Plot A displays a biphasic dose–response curve with the response level indicated for a lower (*a*) or higher (*b*) release rate device attached to a trap. Plot B displays the expected effect of preexistence of device *a* or *b* on the trap with respect to the dose–response curve for further increase in release of the biphasic semiochemical from the trap (dashed cyan line is the curve with no preexisting lure). Solid colored lines indicate level of catches with no further addition of semiochemical. Plots are drawn with x-axis in logarithmic scale.

1979, Vité et al. 1985, Salom et al. 1992, Sullivan et al. 2011, however, see Vité et al. 1985) and the attraction-enhancing effects typically observed outside (Billings 1985; Sullivan et al. 2007; Sullivan and Mori 2009; Sullivan et al. 2011, 2016).

endo-Brevicomin has been shown to have both a biphasic dose–response (Sullivan 2016) and the capacity to enhance *D. frontalis* attraction to sources of the female-associated components of the aggregation attractant located dozens of meters away (Sullivan and Mori 2009). Both qualities were ostensibly necessary for the observed effects of *endo*-brevicomin on *D. frontalis* behavior in this study. Although attraction-reducing effects of displaced or dispersed releasers of bark beetle semiochemicals are common (Tilden et al. 1981, Tilden et al. 1987, Ross and Daterman 1995, Gillette et al. 2009, Andersson et al. 2011, Sullivan and Clarke 2021), the few studies where the release points of synergistic semiochemicals have been separated indicated a nearly complete loss of activity with displacement of just a few meters (Byers 1987, Andersson et al. 2011). Hence, there is as yet little evidence to support the hypothesis that the response of *D. frontalis* to *endo*-brevicomin in this study has parallels with semiochemicals in other species of bark beetle. Our observations thus may not reflect a general phenomenon in the semiochemistry of bark beetles. *endo*-Brevicomin is currently used as a component of the population monitoring and forecasting lure for *D. frontalis* (Sullivan et al. 2021), and our results suggest that background of *endo*-brevicomin from infested trees in the surroundings could influence the shape of functions relating catches and local beetle abundances. However, nearby infested trees should also influence catches by being a copious source of beetles and providing competing sources of attractant.

The three discrete, widely spaced *endo*-brevicomin releasers around our traps were undoubtedly producing a very nonhomogenous atmosphere of this semiochemical. The isolated release points would have caused the ratios of the attractant (frontalin and *alpha*-pinene) and the attraction-modifying semiochemical (*endo*-brevicomin) encountered by orienting beetles to vary widely since the plumes would overlap irregularly (Byers 1987, Andersson et al. 2011). A more homogenous atmosphere of *endo*-brevicomin (which might be a better representation of natural airborne concentrations in the environment, particularly within infestations) may have produced different results.

Our results suggest that *endo*-brevicomin background, whether artificial or natural, may give pioneer females greater probability of success since it should enhance responses to their attacks. This is inferred from the very large increase in beetle response to frontalin and *alpha*-pinene, components released by pioneer female attacks, caused by *endo*-brevicomin background. It should be noted, however, that quantities of frontalin and host odors released from our trap lures were thousands of times greater than those from a single female attack, suggesting this inference should be treated cautiously. Local effects of *endo*-brevicomin might influence the spatial dimensions of infestations. Successful pioneer female attacks would presumably be more likely to occur within an area close enough to mass-attacked trees that the *endo*-brevicomin released into the environment would have a synergistic effect. Similarly, our results here and those of previous studies (Sullivan and Mori 2009) suggest that artificial releasers of *endo*-brevicomin, although not attractive in themselves (Sullivan et al. 2007), might increase infestation risk in uninfested forest by enhancing responses to pioneer female attacks.

Depending on background levels of *endo*-brevicomin, host-seeking *D. frontalis* should respond differently to individual trees having similar numbers of fresh attacks, levels of pheromone release, and phloem availability. Where local beetle densities are low and *endo*-brevicomin background is likewise low (such as at locations away from trees being mass attacked), background *endo*-brevicomin would increase the likelihood of successful mass-attack of individual trees by enhancing attraction. High concentrations of *endo*-brevicomin background occurring in or near infestations would preempt the synergism of *endo*-brevicomin from any single tree coming under mass attack and cause rejection of such trees by host-seeking beetles to begin at an earlier stage of colonization (Payne et al. 1977). We suggest that beetle response to *endo*-brevicomin background may be a feedback mechanism that promotes more dispersed attacks as local beetle densities become greater. Enhanced attraction to attacked trees around an infestation combined with reduced attraction to those within would create a 'push–pull' effect that should stimulate infestations to spread outward. Hence the beetles' tendency to aggregate within stands would be regulated by beetle densities, with infestations becoming less focused when beetle abundances are higher.

Variation in background concentrations of other *D. frontalis* semiochemicals likely influence spot growth dynamics as well.

Acknowledgments

We thank JoAnne Barrett and Matt Cloud for technical assistance in the field and the staff of the Homochitto National Forest for assistance in locating suitable field sites. Dan Miller and Darrell Ross provided helpful comments on an early draft of this manuscript.

Author Contributions

C.B. performed statistical analyses, and B.T.S. executed all other aspects of the work aided by the aforementioned technical assistance.

References Cited

Andersson, M. N., M. Binyameen, M. M. Sadek, and F. Schlyter. 2011. Attraction modulated by spacing of pheromone components and anti-attractants in a bark beetle and a moth. J. Chem. Ecol. 37: 899–911.

Billings, R. F. 1985. Southern pine bark beetles and associated insects: effects of rapidly-released host volatiles on response to aggregation pheromones. J. Appl. Entomol. 99: 483–491.

Borden, J. H., L. C. Ryker, L. J. Chong, H. D. Pierce, Jr., B. D. Johnston, and A. C. Oehlschlager. 1987. Response of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae), to five semiochemicals in British Columbia lodgepole pine forests. Can. J. For. Res. 17: 118–128.

Byers, J. A. 1987. Interactions of pheromone component odor plumes of western pine beetle. J. Chem. Ecol. 13: 2143–2157.

Calabrese, E. J. 2013. Biphasic dose responses in biology, toxicology and medicine: accounting for their generalizability and quantitative features. Environ. Pollut. 182: 452–460.

Conchou, L., P. Lucas, C. Meslin, M. Proffit, M. Staudt, and M. Renou. 2019. Insect odorscapes: from plant volatiles to natural olfactory scenes. Front. Physiol. 10: 972.

Coulson, R. N., B. A. McFadden, P. E. Pulley, C. N. Lovelady, J. W. Fitzgerald, and S. B. Jack. 1999. Heterogeneity of forest landscapes and the distribution and abundance of the southern pine beetle. Forest Ecol. Manag. 114: 471–485.

Dodds, K. J., S. L. Garman, and D. W. Ross. 2006. Landscape analyses of Douglas-fir beetle populations in northern Idaho. For. Ecol. Mgmt. 231: 119–130.

Gara, R. I., J. P. Vité, and H. H. Cramer. 1965. Manipulation of *Dendroctonus frontalis* by use of a population aggregation pheromone. Contrib. Boyce Thompson Inst. 23: 55–66.

Gillette, N., C. Mehmel, J. Webster, S. Mori, N. Erbilgin, D. Wood, and J. Stein. 2009. Aerially applied methylcyclohexenone-releasing flakes protect Pseudotsuga menziesii stands from attack by Dendroctonus pseudotsugae. For. Ecol. Manag. 257: 1231–1236.

Kautz, M., K. Dworschak, A. Gruppe, and R. Schopf. 2011. Quantifying spatio-temporal dispersion of bark beetle infestations in epidemic and non-epidemic conditions. For. Ecol. Manag. 262: 598–608.

Kinzer, G. W., A. F. Fentiman, Jr, T. F. Page, Jr, R. L. Foltz, and J. P. Vité. 1969. Bark beetle attractants: identification, synthesis and field bioassay of a new compound isolated from Dendroctonus. Nature. 221: 477–478.

Miller, J., L. Gut, F. De Lame, and L. Stelinski. 2006. Differentiation of competitive vs. non-competitive mechanisms mediating disruption of moth sexual communication by point sources of sex pheromone (part I): theory 1. J. Chem. Ecol. 32: 2089–2114.

Party, V., C. Hanot, D. S. Büsser, D. Rochat, and M. Renou. 2013. Changes in odor background affect the locomotory response to pheromone in moths. PLoS One 8: e52897.

Payne, T. L., J. E. Coster, and P. C. Johnson. 1977. Effects of slow-release formulation of synthetic *endo*- and *exo*-brevicomin on southern pine beetle flight and landing behavior. J. Chem. Ecol. 3: 133–141.

Payne, T. L., J. E. Coster, J. V. Richerson, L. J. Edson, and E. R. Hart. 1978. Field response of the southern pine beetle to behavioral chemicals. Environ. Entomol. 7: 578–582.

Pureswaran, D. S., and B. T. Sullivan. 2012. Semiochemical emission from individual galleries of the southern pine beetle, (Coleoptera: Curculionidae: Scolytinae), attacking standing trees. J. Econ. Entomol. 105: 140–148.

Renwick, J. A. A., and J. P. Vité. 1969. Bark beetle attractants: mechanism of colonization by *Dendroctonus frontalis*. Nature 224: 1222–1223.

Richerson, J. V., and T. L. Payne. 1979. Effects of bark beetle inhibitors on landing and attack behavior of the southern pine beetle and beetle associates. Environ. Entomol. 8: 360–364.

Ross, D. W., and G. E. Daterman. 1995. Efficacy of an antiaggregation pheromone for reducing Douglas-fir beetle, *Dendroctonus pseutotsugae* Hopkings (Coleoptera: Scolytidae), infestation in high risk stands. Can. Entomol. 127: 805–811.

Ross, D. W., and K. F. Wallin. 2008. High release rate 3-methylcyclohex-2-en-1-one dispensers prevent Douglas-fir beetle (Coleoptera: Curculionidae) infestation of live Douglas-fir. J. Econ. Entomol. 101: 1826–1830.

Rudinsky, J. A., and L. C. Ryker. 1980. Multifunctionality of Douglas-fir beetle pheromone 3,2-MCH confirmed with solvent dibutyl phthalate. J. Chem. Ecol. 6: 193–201.

Rudinsky, J. A., M. E. Morgan, L. M. Libbey, and T. B. Putnam. 1974. Antiaggregative-rivalry pheromone of the mountain pine beetle, and a new arrestant of the southern pine beetle. Environ. Entomol. 3: 90–97.

Salom, S. M., R. F. Billings, W. W. Upton, M. J. Dalusky, D. M. Grosman, T. L. Payne, C. W. Berisford, and T. N. Shaver. 1992. Effect of verbenone enantiomers and racemic endo-brevicomin on response of *Dendroctonus frontalis* (Coleoptera, Scolytidae) to attractant-baited traps. Can. J. For. Res. 22: 925–931.

Schröder, R., and M. Hilker. 2008. The relevance of background odor in resource location by insects: a behavioral approach. Bioscience 58: 308–316.

Shepherd, W. P., and B. T. Sullivan. 2017. Spatial displacement of a lure component can reduce catches of two nontarget species during spring monitoring of southern pine beetle. J. Insect. Sci. 18: 1–4.

Sullivan, B. T. 2016. Chapter four - semiochemicals in the natural history of southern pine beetle *Dendroctonus frontalis* Zimmermann and their role in pest management. Adv. Insect Physiol. 50: 129–193.

Sullivan, B. T., and S. R. Clarke. 2021. Semiochemicals for management of the southern pine beetle (Coleoptera: Curculionidae: Scolytinae): successes, failures, and obstacles to progress. Can. Entomol. 153: 36–61.

Sullivan, B. T., and K. Mori. 2009. Spatial displacement of release point can enhance activity of an attractant pheromone synergist of a bark beetle. J. Chem. Ecol. 35: 1222–1233.

Sullivan, B. T., W. P. Shepherd, D. S. Pureswaran, T. Tashiro, and K. Mori. 2007. Evidence that (+)-endo-brevicomin is a male-produced component of the Southern pine beetle aggregation pheromone. J. Chem. Ecol. 33: 1510–1527.

Sullivan, B. T., M. J. Dalusky, K. Mori, and C. Brownie. 2011. Variable responses by southern pine beetle, *Dendroctonus frontalis* Zimmermann, to the pheromone component endo-brevicomin: influence of enantiomeric composition, release rate, and proximity to infestations. J. Chem. Ecol. 37: 403–411.

Sullivan, B. T., C. Brownie, and J. P. Barrett. 2016. Intra-annual variation in responses by flying southern pine beetles (Coleoptera: Curculionidae: Scolytinae) to pheromone component *endo*-brevicomin. J. Econ. Entomol. 109: 1720–1728.

Sullivan, B. T., W. P. Shepherd, J. T. Nowak, S. R. Clarke, P. R. Merten, R. F. Billings, W. W. Upton, J. J. Riggins, and C. Brownie. 2021. Alternative formulations of trap lures for operational detection, population monitoring, and outbreak forecasting of southern pine beetle in the United States. J. Econ. Entomol. 114: 1189–1200.

Tilden, P. E., W. D. Bedard, D. L. Wood, and H. A. Stubbs. 1981. Interruption of response of *Dendroctonus brevicomi*s to its attractive pheromone by components of the pheromone. J. Chem. Ecol. 7: 183–196.

Tilden, P. E., W. D. Bedard, D. L. Wood, and L. E. Browne. 1987. Interruption of response of *Dendroctonus brevicomis* to attractive pheromone by release of pheromone at several rates and spacings. J. Chem. Ecol. 13: 85–97.

Tisdale, R. A., T. E. Nebeker, and J. D. Hodges. 2003. Role of oleoresin flow in initial colonization of loblolly pine by southern pine beetle (Coleoptera: Scolytidae). J. Entomol. Sci. 38: 576–582.

Vité, J. P., and J. A. A. Renwick. 1971. Inhibition of *Dendroctonus frontalis* response to frontalin by isomers of brevicomin. Naturwissenschaften 58: 418–419.

Vité, J. P., P. R. Hughes, and J. A. A. Renwick. 1976. Southern pine beetle: effect of aerial pheromone saturation on orientation. Naturwissenschaften 63: 44.

Vité, J. P., R. F. Billings, C. W. Ware, and K. Mori. 1985. Southern pine beetle: enhancement or inhibition of aggregation response mediated by enantiomers of *endo*-brevicomin. Naturwissenschaften 72: 99–100.

Zhang, Q. H., and F. Schlyter. 2003. Redundancy, synergism, and active inhibitory range of non-host volatiles in reducing pheromone attraction in European spruce bark beetle *Ips typographus*. Oikos 101: 299–310.

Zhang, Q. H., and F. Schlyter. 2004. Olfactory recognition and behavioural avoidance of angiosperm nonhost volatiles by conifer-inhabiting bark beetles. Agric. For. Entomol. 6: 1–19.