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ARTICLE

Semiochemicals for management of the southern pine beetle (Coleoptera: Curculionidae: Scolytinae): successes, failures, and obstacles to progress

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Abstract

The southern pine beetle, *Dendroctonus frontalis* Zimmermann (Coleoptera: Curculionidae: Scolytinae), is among the most destructive bark beetle pests of pines (Pinaceae) of the southeast and mid-Atlantic United States of America, Mexico, and Central America. Numerous volatile compounds can stimulate or reduce attraction of the beetle, but efforts to incorporate these into effective, practical technologies for pest management have yielded mixed results. Attractants have been incorporated into lures used in monitoring traps that are employed operationally to forecast outbreaks and detect emerging populations. The attraction inhibitor, verbenone, shows efficacy for suppressing southern pine beetle infestations but has not yet been adopted operationally. No effective semiochemical tree protectant has been developed for the beetle. We discuss complexities in the chemical ecology of the beetle that likely have impeded research and development of semiochemical management tools, and we describe basic science gaps that may hinder further progress if not addressed. We also report some supporting, original experimental data indicating (1) that a verbenone device can inhibit the beetle's response to sources of attractant in a radius of at least several metres, (2) similar olfactory responses by the beetle to both enantiomers of verbenone, and (3) that pheromone background can cause conflicting results in semiochemical field tests.

Introduction

The southern pine beetle, *Dendroctonus frontalis* Zimmermann (Coleoptera: Curculionidae: Scolytinae), remains one of the most economically significant insect pests of forestry in the pine-growing portions of the southeastern United States of America, Mexico, and Central America, and its impact is expanding northwards along the eastern coast of North America due to climate change (Lesk *et al.* 2017; Dodds *et al.* 2018). Intensive research on the beetle's semiochemistry from the 1960s through the 1980s was stimulated by the possibility that release of small amounts of benign chemicals could reduce beetle-caused losses (Vité 1970). However, scientists quickly became aware of issues that would limit the efficacy and applicability of such technology (Vité 1970; Coulson *et al.* 1973a; Vité and Francke 1976). The topic has received far less attention from researchers in the past two decades. Two anti-attractant semiochemicals (verbenone and 4-allylanisole) were developed operationally and received EPA registrations (United States Environmental Protection Agency 1999, 2001) as bioinsecticides for southern pine beetle management. However, neither has been adopted in practice. In contrast, significant technological

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successes have been achieved with southern pine beetle attractants. These are used for monitoring the beetle's populations and range expansion (Dodds *et al.* 2018) and for forecasting outbreaks and their intensity (Billings 2011b).

This article is not a comprehensive review of the literature on basic science and application of semiochemicals in southern pine beetle management, and the reader is directed to other recent publications (Strom and Clarke 2011; Sullivan 2011, 2016). Instead, we critically review past efforts at development of semiochemical tools for the beetle's management, assess the present state of this technology, and discuss impediments to future technology development. Although our discussion is limited to southern pine beetle, many issues raised are applicable to the development of semiochemical management tools for other bark beetle pests. The review is divided into sections that provide general background to southern pine beetle management and chemical ecology, describe and discuss successes and failures in application of semiochemicals for the beetle's management, and evaluate where knowledge gaps and practical impediments challenge progress.

Southern pine beetle infestation dynamics, management, and chemical ecology

In the southern United States of America, landscape disturbances caused by southern pine beetle normally occur as spatially discrete infestations, or "spots," consisting of continuous zones of killed, dying, and newly infested trees, that often are surrounded by broad areas of uninfested forest (Schowalter *et al.* 1981; Ayres *et al.* 2011). If not controlled, spots may grow to encompass new trees at rates of a few to dozens – in extreme cases, hundreds – per week (Hedden and Billings 1979; Clarke and Billings 2003). Southern pine beetle spot infestations typically are initiated in the spring (Coulson *et al.* 1985; Ayres *et al.* 2011; Martinson *et al.* 2013) and often start in single trees or small groups of trees weakened by lightning strike (Hodges and Pickard 1971; Coulson *et al.* 1983). They may continue to accumulate infested trees along their margin throughout the summer and early fall (Thatcher and Pickard 1964; Franklin 1970). Multiple small spots may coalesce. This pattern of mortality accumulation, in which all trees along a growing front or "head" are killed and mortality builds continuously during the growing season, is generally not observed in other aggressive *Dendroctonus* sp., and mortality from those species is typically more evenly dispersed and accumulates in an area over successive years rather than months (Roe and Amman 1970; Safranyik *et al.* 1974; Wood 1982; Mitchell and Preisler 1991; Borden 1993; Shore *et al.* 2006). In the northeastern United States of America, southern pine beetle infestations may not form distinct boundaries between attacked and unattacked trees; rather, they may be more diffuse with dispersed mortality occurring around the periphery of the infestations (Dodds *et al.* 2018).

Because southern pine beetle spot growth may persist for months, there is a large window of opportunity for reducing further growth (Billings 2011a). Within growing spots, trees at immediate risk to beetle attack are those located closest to trees that are being mass-attacked and thus are identified easily (Gara and Coster 1968; Johnson and Coster 1978). Spots typically expand in a single direction (generally downwind) at any one time (Coster *et al.* 1978), and tree-protection efforts can be targeted at trees in the anticipated direction of spot movement. Hence, direct control of southern pine beetle has focussed on suppression of growth of individual spots (Billings 2011a) or protection of individual, high-value trees threatened by a growing spot head.

Two recommended and widely used strategies for suppressing the beetle's infestations currently exist. They are the cut-and-remove strategy, in which infested trees and a buffer of apparently uninfested trees in the direction of spot growth are felled and salvaged, and the cut-and-leave strategy, where timber is felled similarly but is left on site in the opening created by the cut (Billings 2011b). Cut-and-remove is the preferred suppression method because beetles in the infested trees are eliminated from the forest, the value of the felled timber can be recovered, and the cleared opening facilitates regeneration while also reducing wildfire risk. However, in recent years, cut-and-leave applications in the southern United States of America have increased due to the loss of outlets for the timber. Cut-and-leave treatments have been successful in the areas of southern pine beetle–range expansion that lack commercial infrastructure for harvesting and processing trees (Dodds *et al.* 2018).

The efficacy of these two strategies is substantially derived from the semiochemical-driven dynamics of spot growth. Beetle spots expand through a process called "switching," in which the aggregation pheromone plume associated with mass-attacked trees triggers attack initiation on – and switching of attack focus to – immediately adjacent, healthy trees (Renwick and Vité 1970). As a consequence, elimination of trees with pheromone-producing beetles can be sufficient to stop infestation growth even if trees with developing and emerging brood are left in place (Gara 1967; Clarke *et al.* 1999). Without nearby sources of aggregation pheromone, brood emerging from infested trees typically disperse rather than mass-attack uninfested trees next to the spot (Billings and Pase 1979; Cronin *et al.* 1999). Although trees being mass-attacked are left onsite in cut-and-leave treatments, felling can cause rapid reductions in production of aggregation attractant by the attacking beetles (Vité and Crozier 1968), and felling of both mass-attacked and buffer trees disrupts normal pheromone plume movement due to the forest canopy being opened (Thistle *et al.* 2005).

Semiochemicals for manipulating southern pine beetle

Development of semiochemical management tools for bark beetles has focussed on compounds that either attract or inhibit attraction of the flying insects. A third class of semiochemicals (termed "multifunctional") acts as either attractants or attraction inhibitors at either low or high concentrations, respectively (Rudinsky 1973a; Borden 1995), and the desired effect is obtained by adjusting the release rate. However, because airborne concentrations decrease with distance from the point of release, high rates of multifunctional-type semiochemicals can enhance attraction within the wider area while reducing attraction at or near the point of release (Sullivan and Mori 2009).

Dozens of semiochemicals have been discovered that can influence the behaviour of southern pine beetle and thus have potential as management tools.

Attractants. As with other aggressive bark beetles, southern pine beetle must attack *en masse* in order to overcome host defences and reproduce in otherwise healthy trees (Christiansen *et al.* 1987; Raffa *et al.* 1993), and semiochemicals from both the beetles themselves and the host trees mediate mass attacks. These compounds cause beetles to concentrate their attacks on individual trees and, as attack numbers and semiochemical levels increase, initiate attacks on nearby trees (Borden 1974; Geiszler *et al.* 1980; Sullivan 2016). The aggregation pheromone for southern pine beetle consists of the female-released attractant frontalin and the male-released synergist *endo*-brevicomin (Renwick and Vité 1969; Sullivan *et al.* 2007b). The frontalin–*endo*-brevicomin combination is synergised by volatile compounds within the host's defensive resin, which is expelled copiously in vigorous pines at the beetles' entrances (Kinzer *et al.* 1969; Pureswaran and Sullivan 2012). Although they are strong attractant synergists, resin odours alone are unattractive to the beetle (Billings 1985), and little evidence exists of a primary attractant for pioneer southern pine beetle (Payne 1986). Female beetles also produce large quantities of the attractive synergist *trans*-verbenol; however, its effect is redundant with host odours (Payne *et al.* 1978a; Shepherd and Sullivan 2018). *endo*-Brevicomin is a potent attractant synergist (Vité *et al.* 1985; Sullivan *et al.* 2007b) but is classified as a multifunctional pheromone for southern pine beetle because it can strongly reduce beetle attraction at high release rates (Salom *et al.* 1992).

Anti-attractants. Southern pine beetles also produce attraction inhibitors that may function as antiaggregation pheromones that signal that attack densities have rendered the host substrate unsuitable for further colonisation (Byers 1989; Borden 1997; Ross and Niwa 1997; Seybold *et al.*

2018). Anti-attractants released by southern pine beetle include numerous oxygenated monoterpenes, with verbenone and myrtenol occurring in greatest abundance (Renwick *et al.* 1973; Sullivan 2005; Pureswaran *et al.* 2006). Oxygenated monoterpenes associated with the beetle's host colonisation also have nonbeetle origins, including both spontaneous and microbial oxidation of monoterpenes in host resin (Brand *et al.* 1975, 1976; Hunt *et al.* 1989; Sullivan *et al.* 2000). In this context, they may signal decrepitude and unsuitability of colonised or decaying hosts (Byers *et al.* 1989). Southern pine beetles also produce nonmonoterpene attraction inhibitors acetophenone and 2-phenylethanol (Sullivan 2005; Sullivan *et al.* 2007a). Other sources of anti-attractant semiochemicals for the beetle include host tree species (*e.g.*, resin constituents 4-allylanisole and myrcene; Hayes *et al.* 1994; Munro *et al.* 2020) and nonhost tree species (Dickens *et al.* 1992; Sullivan *et al.* 2007a; Shepherd and Sullivan 2013).

Successes and failures in semiochemical technology development for southern pine beetle

Attractants for monitoring

The most successful and widespread use of semiochemicals in management of southern pine beetle has been their deployment in traps for detecting cryptic populations and forecasting damage.

Operational lures and traps. The three-component combination of frontalin, *endo*-brevicomin, and host resin monoterpenes is the current, recommended operational lure for southern pine beetle trapping in the United States of America (Dodds *et al.* 2018; Mooneyham 2019). This lure has seen two significant improvements since its original development in the late 1960s, namely, the inclusion of devices with an elevated release rate (grams per day) of host odours in the mid-1980s and of devices with a low release rate of *endo*-brevicomin in the 2000s (Billings 1985; Sullivan *et al.* 2007b). The beetle produces almost solely the (+)-enantiomer of *endo*-brevicomin and predominantly (–)-frontalin (Payne *et al.* 1982; Sullivan *et al.* 2007b); however, for both compounds, the much less costly racemic blend has activity similar to the predominant enantiomer (Payne *et al.* 1982; Sullivan and Mori 2009; Sullivan *et al.* 2011) and is used in the operational lure. It is recommended that the *endo*-brevicomin device be placed several metres from the trap to maximise the synergistic effect of the *endo*-brevicomin on the attractant in the trap (Sullivan and Mori 2009; B.T.S., unpublished data) while reducing unwanted bycatches of *endo*-brevicomin–attracted species whose presence complicates sample handling (Shepherd and Sullivan 2017). Until recently, the recommended host odour component for the operational lure had been turpentine, a resin distillate, from the host species *Pinus taeda* Linnaeus (Pinaceae). However, due to difficulty in obtaining this material, this component has changed to a 2:1 combination of host monoterpenes *alpha*-pinene and *beta*-pinene, which typically are the two dominant resin monoterpenes of the southern pine beetle's preferred hosts (Mirov 1961). *alpha*-Pinene and *beta*-pinene individually are synergists of the aggregation pheromone (Staeben *et al.* 2015; Munro *et al.* 2020); however, the superiority of this particular compound pairing and ratio has not to our knowledge been demonstrated. Inclusion of additional host odour components (*e.g.*, 4-allylanisole; Munro *et al.* 2020) and adjustment of their enantiomeric composition (*e.g.*, favouring the (+)-enantiomer of *alpha*-pinene (Staeben et al. 2015)) might further increase lure potency. Due to the risk of the operational beetle lure producing spillover attacks on adjacent pines (Vité 1970), it is recommended that monitoring traps be placed approximately 23 m from the nearest susceptible pine and at even greater distances when the beetles are abundant.

The most common trap design used operationally for southern pine beetle detection and monitoring is the 12- or 16-unit black multiple-funnel trap (Lindgren 1983). However, a range of trap designs (*e.g.*, funnel, slot traps, and cross-vane traps) have all proven effective for trapping the beetle (Moser and Browne 1978; McCravy *et al.* 2000; Munro *et al.* 2020). McCravy *et al.* (2000) found Theyson slot traps (Niemeyer *et al.* 1983) to be similar in effectiveness to 12-unit funnel traps for trapping southern pine beetle; however, to our knowledge, multiple-funnel traps have not been directly compared to other designs. Traps with low reflectance (dark in shade) are superior to lighter ones, but the beetles show no preference among dark colours (Strom *et al.* 1999; Strom and Goyer 2001).

Operational use of monitoring traps. Baited funnel traps currently are used in the southeastern United States of America as part of a region-wide survey being conducted cooperatively by federal and state agencies each spring to estimate the likelihood of southern pine beetle outbreaks during the following summer (Billings and Upton 2010; Billings 2011b). The resulting county-scale forecasts allow forest managers to make advance preparations, including earlier execution and greater frequency of aerial spot detection surveys, for handling coming outbreaks. Traps are distributed widely, with one to three traps allotted per county (1 500 km^2 average area) for a 6-week interval coinciding with the beetle's annual dispersal flight (Sullivan *et al.* 2016). Counts are made of both southern pine beetle and the predator *Thanasimus dubius* (Fabricius) (Coleoptera: Cleridae), which also responds to the lure (Vité and Williamson 1970). These counts and the numbers of infestations during the previous year have been used to estimate beetle population trends, as well as the abundance of infestations (ranked as low, medium, or high) for the coming summer (Billings and Upton 2010). Comprehensive analyses of forecast accuracy for the first two decades of the survey verified the programme's utility but indicated shortcomings. For example, state-level forecasts were 85% correct when they were for low spot abundances but only 32% correct when they were for high spot abundances for the years 1987–2005 (Billings and Upton 2010). An updated model and revised sampling procedures are being implemented to increase accuracy and precision in predicting spot abundances. Additional data types may be derived from the trap catches and prove useful for forecasting outbreaks; this possibility is currently being explored. For example, during the years 2016 and 2017, traps in outbreak areas had a significantly higher proportion of male beetles in their catches than did traps in non-outbreak areas (McNichol 2018). The trapping interval was recently extended from four to six weeks to better capture the spring flight; however, this period can last several months (Sullivan *et al.* 2016). Because of this, the catches cannot provide phenological data. Baited traps have also been essential tools in delineating the extent of this insect's recent range expansion into the northeastern United States of America in response to climate change (Lesk *et al.* 2017; Dodds *et al.* 2018).

Attractants for direct control

Several different strategies have been explored experimentally for using attractant semiochemicals for reducing pine mortality, but none has shown promise as an operational management tool.

Aggregation disruption. Southern pine beetle attacks must be concentrated on a limited number of trees within a spot; otherwise, attack densities may be insufficient to overcome host defences. The aggregation attractant allows the beetles to maintain the required focus. Releasing synthetic aggregation attractant over a broad area would presumably disrupt this semiochemical targeting of single trees. Vité *et al.* (1976) attempted this in a single southern pine beetle spot: rice soaked with frontalin and *alpha*-pinene was dispersed aerially within the spot head and among surrounding trees to saturate the atmosphere with aggregation attractant. The treatment, surprisingly, caused attacks to intensify, and tree mortality was not reduced. A modification of this approach aims to attract beetles away from the spot head into portions of the spot with previously colonised trees. In experiments where aggregation attractant–releasing devices were attached only to killed trees and nonhost species in the zone behind the growing infestation head, flying beetles were successfully redistributed away from the spot head and into an area where they were presumably harmless (Richerson *et al.* 1980). The technique appeared efficacious in slowing or stopping spot growth when local spot densities were low, but it was unable to control spots during severe outbreaks (Payne *et al.* 1985a,b). It is possible that, when local beetle population levels are high, recruitment of dispersing beetles into the spot by the synthetic attractant negates its value in redistributing beetles within the spot.

In a third approach, attractants are used to redirect beetle spot growth towards stands of hardwoods, forest openings, or other host-free areas adjacent to the spot head and thereby cause spot collapse. This tactic was used in federal wilderness areas in Texas, United States of America, to protect neighbouring private lands (S.R.C., unpublished data). However, this strategy would be applicable only to spots with compact heads and in close proximity to pre-existing barriers to spot growth. Urban forests, where distributions of susceptible pines are patchy and surrounded by host-free areas, may be ideal for this technique. Spot redirection also has potential for turning spot growth away from high-value areas such as endangered species habitat or other landowner's pine stands. Caution is advised, however, because of the potential for increased recruitment of beetles from outside the spot.

Trap trees and trap-out. Semiochemical baits may be used to reduce local insect pest populations and damage by luring pests to traps or insecticides or by concentrating them in host material that is either treated with insecticide or subsequently destroyed (Borden *et al.* 1983; El-Sayed *et al.* 2006, 2009; McCullough *et al.* 2016; Negron *et al.* 2019). In experimental trials, healthy pines adjacent to those being mass-attacked in a southern pine beetle infestation were baited with aggregation attractant and simultaneously treated with the herbicide cacodylic acid (Coulson *et al.* 1973b). The goal was to concentrate attacks on trees where reproduction would fail (Copony and Morris 1972; Coulson *et al.* 1973b, 1975). However, these trees were not sufficiently effective sinks for attacking beetles, and spot growth was not reduced (Coulson *et al.* 1973a).

One of the authors (B.T.S.) recently performed a pilot trial for using mass trapping within a spot to suppress spot growth. Funnel traps (3 m length) were suspended from 4–5 m height among trees with larval-through-adult–brood stages and were baited repeatedly along their length with frontalin- and host odour–release devices. Two low release *endo*-brevicomin devices were positioned among vacated trees and 8–10 m from the traps. We believed that we might address shortcomings of previous attempted, attractant-based redirection methods by (1) removing attractant-redirected beetles from the spot entirely, (2) using a more potent – and thus more competitive – lure (*i.e.*, one that included a high release rate of host odours and displaced *endo*-brevicomin devices; Billings 1985; Sullivan and Mori 2009), and (3) releasing attractant across more of the range of heights preferred by southern pine beetle for flight and attack (Gara *et al.* 1965; Coster *et al.* 1977b). In addition, a sieve was placed over the traps' collection cups, thereby allowing the beetles to pass through but stopping predators from being captured (Ross and Daterman 1998). Although these traps removed tens of thousands of southern pine beetles, the spot growth rate increased rather than decreased. A severe outbreak was occurring at the time, with many spots having received cut-and-leave treatment; we suspect that the high quantities of attractant from the traps recruited beetles dispersing from these controlled spots (Cronin *et al.* 1999).

Anti-attractants for direct control

Successful mass attack requires response to the aggregation attractant; therefore, semiochemicals that inhibit this response have been explored for suppressing southern pine beetle spot growth and for protecting individual trees from colonisation. Among identified anti-attractants for southern pine beetle, only brevicomin, 4-allylanisole, and verbenone have been the focus of extensive efforts towards developing a control technology.

Brevicomin. Both the *endo*- and *exo*-isomers of brevicomin can reduce southern pine beetle response to attractant-baited traps (Vité and Renwick 1971; Payne *et al.* 1978a). In an attempt to disrupt spot growth, devices releasing *endo*- and *exo*-brevicomin were distributed regularly through the head of a growing spot and on adjacent, uninfested trees (Payne *et al.* 1977). This reduced beetle landings on trees but failed to redistribute beetles away from the spot head. Attachment of *endo*- and *exo*-brevicomin devices at 2-m intervals vertically along the boles of uninfested trees adjacent to the spot head reduced southern pine beetle landings, but the treatment did not protect the trees from attack (Payne and Richerson 1979; Richerson and Payne 1979). Moreover, landings, attacks, and reproduction by the competing bark beetle species *Ips avulsus* (Eichoff) (Coleoptera: Curculionidae) were increased by these brevicomin treatments (Richerson and Payne 1979; Payne and Richerson 1985), suggesting that competitive displacement of southern pine beetle by the less aggressive species could cause spot collapse. This potential technology was never developed, possibly due to the unappealing prospect of significant tree mortality due to *Ips* attacks occurring before spot collapse.

4-Allylanisole. This phenylpropanoid is a common secondary plant compound and a minor component (typically 1–10%) of the resin volatiles of southern pine beetle host pines (Mirov 1961; Bookwalter *et al.* 2019). Walking beetles are repelled by 4-allylanisole applied to the substrate, and devices releasing 4-allylanisole can reduce the beetle's responses to attractant-baited traps (Hayes *et al.* 1994; Strom *et al.* 1999). In initial studies, trees at immediate risk of southern pine beetle attack due to lightning strike or proximity to beetle activity appeared to be protected by releasers of 4-allylanisole attached along the bole (Strom *et al.* 1995; Hayes *et al.* 1996), and 4-allylanisole was patented as a biorational insecticide (Hayes *et al.* 1995). However, in a subsequent study, no reduction of beetle-caused mortality was observed when the bole was treated with microencapsulated 4-allylanisole (either sprayed or applied within projectiles) or 4-allylanisole release devices (Strom *et al.* 2004). In this test, trees were rendered susceptible to southern pine beetle attack by treatment with either aggregation attractant or a biocide. There has been no further development of 4-allylanisole for control of the beetle.

Both brevicomin and 4-allylanisole, which were investigated as tree protectants because of their anti-attractant effects in traps, were subsequently found to be attractant synergists for the southern pine beetle at least under certain conditions (Vité *et al.* 1985; Sullivan *et al.* 2007b; Pureswaran *et al.* 2008; Sullivan and Mori 2009; Munro *et al.* 2020). Presumably, unknown or unappreciated attractant effects in compounds applied for tree protection could undermine some of their benefits; however, there is no evidence that brevicomin and 4-allylanisole failed as tree protectants for this reason.

Verbenone – basic knowledge. The oxygenated monoterpene verbenone has received more attention than any other semiochemical for control of southern pine beetle. It is present in large quantities in newly emerged males (Renwick 1967), and they release it when they join a female in her gallery (Pureswaran and Sullivan 2012). It reduces response to synthetic attractants both in field (Renwick and Vité 1969; Payne *et al.* 1978a) and laboratory (Rudinsky 1973b; McCarty *et al.* 1980) assays, and it is thought to function as an antiaggregation pheromone (Smith *et al.* 1993). Some laboratory bioassays indicated that verbenone is a multifunctional semiochemical because it increased arrestment responses by walking beetles to frontalin at low concentrations but reduced responses at high concentrations (Rudinsky 1973b; McCarty *et al.* 1980). Additionally, southern pine beetle attacks have commonly been noticed around points of application of verbenone treatments on trees that were otherwise unattacked (S.R.C., personal observation). However, limited evidence from controlled

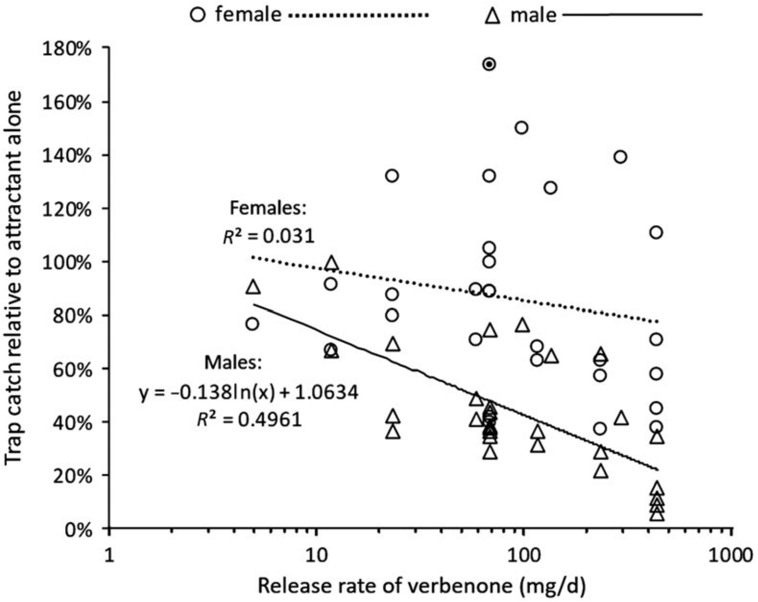

Fig. 1. Effects of release rate of verbenone devices on southern pine beetle response to attractant-baited traps. Plotted data are from multiple experiments reported in three sources (Payne *et al.* 1978a, Salom *et al.* 1992; Sullivan *et al.* 2007a). Points represent mean response to a single treatment within a multi-treatment experimental trial that also included an attractant-only control. The y-axis variable is response to the treatment divided by response to the control. Tests were performed at different times during summer and fall, in different locations, and with attractant lures that differed substantially in release rate and composition of the host component (*i.e.*, *alpha*-pinene or turpentine) of the attractant lure. The enantiomeric composition of the verbenone ranged approximately from 17 to 69% (+). Regression lines are drawn for a log-linear dose-response relationship, which is common for bark beetle responses to semiochemicals. A significant correlation between verbenone dose and change in response to attractant was detected only for males (hence the female function is not shown). The filled circle is the only instance where beetle attraction was reported as significantly increased by verbenone.

field studies exists for the multifunctionality of verbenone. Of 29 experimental treatments – varying in release rate and enantiomeric ratio of verbenone and in composition of the attractant – that have been reported in challenge tests of verbenone (Fig. 1; full explanation in the next paragraph), significant enhancement of attraction was detected only once (Salom *et al.* 1992). In a study by one of the authors (B.T.S.), reduction of the beetle's responses to attractant-baited traps was similar whether a verbenone-releasing device (a BeetleBlock$^{\mathrm{TM}}$ pouch; Synergy Semiochemicals, Delta, British Columbia, Canada) was co-located with the attractant releaser or was located 4 m away (Fig. 2; procedure described in Supplementary Materials 1). This result shows that the operational verbenone device does not act as an attractive synergist when located several metres from a source of southern pine beetle attractant, as occurs with high-rate release devices of the multifunctional-type pheromone component *endo*-brevicomin (Sullivan and Mori 2009; Sullivan 2016; B.T.S., unpublished data). Another encouraging inference from these data is that the anti-attractant effects of a verbenone release device can occur over a sufficient radius (*i.e.*, at least several metres) to influence responses to potentially many adjacent trees.

To summarise all findings from published attractant-challenge trapping experiments with verbenone (Payne *et al.* 1978a; Salom *et al.* 1992; Sullivan *et al.* 2007a), we analysed across studies the relationship between change in catches caused by a verbenone device and the release rate of the device. Data were included only if verbenone was the sole agent used to challenge the attractant, and verbenone enantiomers (whose ratios varied among trials) were summed to obtain the release rate. We thereby obtained 29 data points. This analysis indicated that inhibition of male attraction

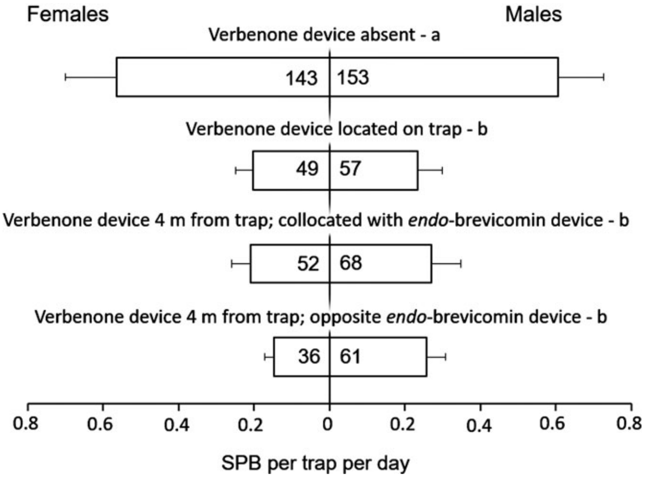

Fig. 2. Effects of displacement of a verbenone device on southern pine beetle catches in attractant-baited funnel traps. Traps were placed into uninfested, mixed pine and hardwood stands and baited invariably with frontalin and turpentine devices that were placed directly on the trap, as well as with an *endo*-brevicomin device located 4 m horizontally from the trap. A verbenone-releasing polyethylene pouch device was either absent, on the trap itself, at the same location as the *endo*-brevicomin device, or 4 m from the trap but opposite the *endo*-brevicomin device. Integers are the total catches by each treatment. Treatments associated with the same lowercase letter did not differ significantly in catches of the sexes summed (Tukey test; $\alpha = 0.05$). See Supplementary Materials 1 for details.

increases with increasing release rates of verbenone (from 5 to 450 mg/day; Spearman rank order correlation; $r = -0.655$, $P < 0.001$, $n = 29$; Fig. 1). Mean reduction in catches across all studies was significantly greater for males than for females (56% (94% maximum) *versus* 14% (62% maximum); paired *t*-test, $t = -6.599$, $df = 28$, $P < 0.001$), and female response was not significantly correlated with the concentration of verbenone (Spearman correlation; $r = -0.27$, $P = 0.156$, $n = 29$). These results indicate that, across the broad range of conditions for the different trials, verbenone has very limited ability to reduce attraction of the sex that first invades the host (*i.e.*, females) and initiates the mass attack. Also, an 80% or greater reduction in male response to a strong attractive source may require verbenone release that is greater than 400 mg/day.

This analysis did not account for the enantiomeric composition of verbenone used in the trials, which varied considerably. Enantiomeric composition can strongly influence bark beetle responses to semiochemicals (Vité *et al.* 1985; Seybold 1993), and variability exists in southern pine beetle production of and response to the enantiomers of verbenone. Newly emerged male beetles contain an average ratio of 36% (+)-verbenone to 64% (–)-verbenone, with some geographic variation (Grosman *et al.* 1997); however, paired males may produce mostly the (+)-enantiomer (unpublished data from Sullivan 2005). Some published trapping trials indicate that (+)-verbenone is a stronger attraction inhibitor than its antipode, but others do not (Salom *et al.* 1992). Our experiments with a coupled gas chromatograph–electroantennographic detector, which was fitted with an enantiomer-discriminating gas chromatograph column, indicate similar olfactory sensitivities to both enantiomers of verbenone by both males and females (methods are described in Supplementary Materials 2; Fig. 3). The effect of the enantiomeric composition of verbenone on tree protection and spot suppression has not been examined in a controlled study; however, devices releasing 34%, 66%, or 89% of the (–)-enantiomer all demonstrated ability to reduce spot growth (Payne *et al.* 1992; Clarke *et al.* 1999). Therefore, existing data do not strongly indicate either verbenone enantiomer as having greater biological importance or likelihood of efficacy in southern pine beetle management.

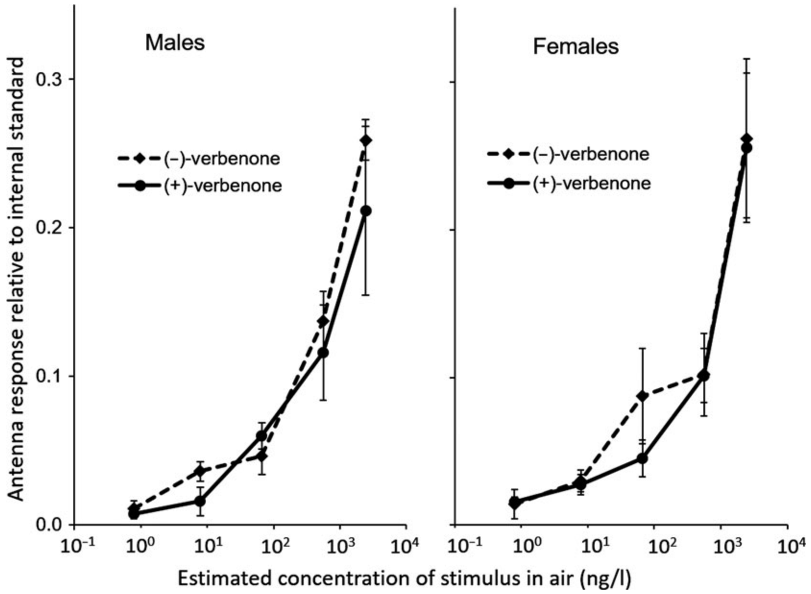

Fig. 3. Gas chromatography–electroantennographic detection analyses of southern pine beetle olfactory responses to a dilution series of the enantiomers of verbenone. Analyses were performed on a chiral gas chromatography column that provided wide separation of retention times and an expected purity of the enantiomers that was greater than 99% during exposure. Pairwise *t*-tests between responses to enantiomers at each dose failed to find a statistically significant difference in either sex ($P \geq 0.13$). See Supplementary Materials 2 for details.

Verbenone for spot suppression. Verbenone has been the primary semiochemical investigated for suppression of southern pine beetle infestations. Rather than replacing the two main methods of spot suppression (cut-and-remove and cut-and-leave), verbenone was intended for use in areas where tree felling was restricted. Two applications were developed: verbenone-only and verbenone-plus-felling (Payne *et al.* 1992; Clarke *et al.* 1999). For the verbenone-only treatment, all trees currently under attack and a buffer of uninfested trees around the spot head were treated with verbenone. In the verbenone-plus-felling treatment, all currently infested trees were felled towards the infestation centre, and a buffer of uninfested trees around the spot head was treated with verbenone. Pilot investigations of these techniques (1986–1987, in eastern Texas) indicated mean reductions in spot growth of 87% for verbenone-plus-felling (six spots) and 62% for verbenone alone (eight spots) (Payne *et al.* 1992). In a more extensive study conducted in Texas, Georgia, and Virginia, United States of America, in 1995–1997, treatment methodology was standardised for operational use. A table providing the number of releasers to be deployed was developed for both treatments, based on the number of currently infested pines and the average diameter (Clarke *et al.* 1999). The buffer for verbenone-only treatments was a minimum of 12 m or three rows of trees past the last infested tree, and 8 m or two rows of trees for the verbenone-plus-felling treatments. When using these guidelines, mortality did not expand beyond the treated buffer in 86% of spots treated with verbenone and felling and in 69% of spots treated with verbenone alone (21 and 45 treated infestations, respectively; Clarke *et al.* 1999). All untreated infestations continued to expand, with 22 of 28 spots adding one or more new trees per day. However, these methods of using verbenone for spot suppression presume that the spot head has clear boundaries and direction of growth, as these conditions are needed for assigning trees to either cutting or verbenone treatment. Infestations in the northeast United States of America may not develop an identifiable area of expansion (Dodds *et al.* 2018), thereby limiting the utility of this treatment.

The techniques developed for operational use involved deployment of a verbenone pouch – a sealed polyethylene bag containing an absorbent pad – loaded with 5 mL of a 34% (+)-verbenone: 66% (–)-verbenone mixture. This enantiomeric ratio was selected in order to reproduce that present in newly emerged male southern pine beetles (Grosman *et al.* 1997). The devices had a target verbenone release rate of approximately 100 mg/day, which is a higher rate than that released from an average pine under southern pine beetle attack (Salom *et al.* 1992), and lasted 40–50 days in the field. Pouches were affixed to pines at 4–5 m height to keep the devices out of human reach and to maximise verbenone concentrations at the height at which the beetles' flight and initial attack principally occurs (Gara *et al.* 1965; Coster *et al.* 1977a,b). A specially developed hammer, called the "Hundle hammer", with an extended handle allowed personnel to secure pouches with nails at these heights.

However, implementation of verbenone as an operational beetle treatment was stymied by several developments. The verbenone pouch registered with the United States Environmental Protection Agency for use in bark beetle control had labelling that was tailored for use against western bark beetle species and contained a lower percentage of (+)-verbenone than had been used during development of the operational protocol for southern pine beetle. Additionally, the product label limited deployment of pouches to 60 per acre per year, a number which would be adequate only for small southern pine beetle infestations, according to application rates provided in Clarke *et al.* (1999).

The partial success of spot-growth reduction with attractants suggests that the effectiveness of verbenone treatments might be improved by implementing a push–pull tactic (Lindgren and Borden 1993; Borden *et al.* 2006; Cook *et al.* 2006; Eigenbrode *et al.* 2016). This tactic would redirect beetle aggregation away from the spot head into less favourable areas in the spot through a combination of attractants deployed among colonised or abandoned trees and inhibitors deployed at the infestation head. An initial pilot study of three infestations indicated that inclusion of the pull element did not improve the effectiveness of verbenone-only treatment (Payne and Billings 1989). Billings *et al.* (1995) tested this tactic successfully, but further field trials are needed before operational use can be recommended. Inclusion of *endo*-brevicomin, which was absent in the aforementioned studies, as part of the lure for the pull component of this technique might improve results. However, use of a more powerful attractant may lead to unwanted attacks on trees in the vicinity of the lures or to recruitment of beetles from outside the spot, as discussed earlier in this paper.

An alternative technology for applying verbenone for spot suppression is Specialised Pheromone & Lure Application Technology (SPLAT; ISCA Technologies Inc., Riverside, California, United States of America). This technology consists of a semi-solid wax matrix infused with semiochemicals that can be applied with a caulk gun as dollops or lines to branches and the trunks of trees (Mafra-Neto *et al.* 2013). The semiochemicals are released from the applied material at a controlled rate. The product SPLAT-Verb, which uses (–)-verbenone, has been successfully tested for protecting lodgepole pine from attack by *Dendroctonus ponderosae* Hopkins, the mountain pine beetle (Coleoptera: Curculionidae) (Fettig *et al.* 2015). However, SPLAT-Verb treatment did not reduce southern pine beetle responses to a trap baited with attractant. A revised formulation, SPLAT-SPB, which has 95% (+)-verbenone, significantly decreased southern pine beetle catch in attractive traps (S.R.C., unpublished data). Initial field trials for infestation suppression have so far been inconclusive (S.R.C., unpublished data). The major expected benefit of SPLAT-SPB over the earlier pouch technology is greater ease of application.

Verbenone for protection of individual trees. High-value trees such as nest trees of red-cockaded woodpeckers, *Leuconotopicus borealis* (Vieillot) (Piciformes: Picidae), and urban landscape or yard pines have received particular attention as targets for single-tree protection from southern pine beetle with verbenone. Red-cockaded woodpecker is an endangered species that nests in cavities in living pines and pecks resin wells around the cavity to protect their young (Conner and Rudolph 1995; Conner *et al.* 2001). Active loblolly pine (*P. taeda*) and shortleaf pine (*P. echinata* Miller) (both Pinaceae) nest trees are apparently preferentially attacked by southern pine beetle, with 2–40% killed annually during an outbreak in Texas (Conner *et al.* 1998).

However, verbenone has not shown efficacy in protecting individual trees from mass attack by the beetle. Verbenone releasers spaced regularly lengthwise and encircling the boles of healthy pines located near the head of a growing infestation failed to reduce beetle landings, gallery densities, or beetle-caused mortality (Richerson and Payne 1979). A limited trial was conducted in Texas and Louisiana, United States of America, to determine if verbenone pouches could protect nest trees of red-cockaded woodpecker from southern pine beetle attack, but four of the six treated trees were killed (S.R.C., unpublished data). The reason for these failures is suggested by trapping studies that have shown that even very high release rates of verbenone do not deter a significant portion of the beetles (Fig. 1). Attacks by undeterred beetles may produce adequate aggregation attractant to negate the deterrent effects of verbenone, or local beetle densities may be sufficiently high that attacks by the undeterred beetles are adequate to kill the tree. Use of semiochemicals to protect urban pines is also problematic. These pines are usually widely spaced, so it is difficult to predict which trees are at greatest risk even when infestations are near. Systemic insecticides have been developed that can protect pines for multiple years (Grosman *et al.* 2009), and, as such, systemic insecticide treatments offer many advantages over semiochemical methods, which are limited by the short lifetime of release devices (generally less than two months).

Verbenone for protection of stands. In general, use of attraction inhibitors to protect entire stands from bark beetle infestation has met with mixed results, and greater efficacy has been observed for species that produce fewer generations per year (*e.g.*, mountain pine beetle) and during periods of low to moderate population levels (Amman *et al.* 1989; Shea *et al.* 1992; Borden *et al.* 2003; Progar *et al.* 2013; Perkins *et al.* 2015). Protecting stands from the western pine beetle (*Dendroctonus brevicomis* Hopkins) (Coleoptera: Curculionidae) has been difficult: this species produces up to four generations per year and has required the combination of verbenone with nonhost volatiles to achieve satisfactory levels of stand protection (Fettig *et al.* 2012). Seven or more overlapping generations of southern pine beetle can occur each year in the southern United States of America, where damage from this pest historically has been concentrated (Birt 2011). In those areas, extended periods occur during which emerging and dispersing beetles are continuously available; this impedes semiochemical-based stand protection efforts once infestations are established. The distribution of attacked trees on the landscape and the spatial and temporal aspects of tree-mortality accumulation associated with southern pine beetle differ greatly from those associated with mountain pine beetle, and semiochemical control strategies applicable to mountain pine beetle may not be relevant to southern pine beetle management. With mountain pine beetle, stands that have high probability of future mortality can be identified by the presence of mortality within the stand from the previous year. Verbenone-releasing devices can be distributed across such stands before beetle flight in order to reduce further attacks and mortality. In contrast, southern pine beetle spots are commonly initiated by a spatially unpredictable phenomenon (*i.e.*, lightning; Hodges and Pickard 1971; Flamm *et al.* 1993), and the appearance of new spots has limited relationship to locations of existing or controlled spots (Fitzgerald *et al.* 1994). Thus, the barriers to identifying and prioritising stands that would benefit from treatment generally preclude semiochemical-based stand protection in the case of southern pine beetle. In the beetle's northern range extremes, fewer generations per year occur, mortality accumulation is more dispersed, and mortality tends to continue in the same stands for multiple years (Dodds *et al.* 2018). Because of this, semiochemical-based stand protection shows greater promise for northern southern pine beetle populations. This possibility merits study.

Verbenone – prospects. As already discussed, verbenone treatment of individual trees does not reduce southern pine beetle landings, attacks, or mortality. This suggests that the behavioural mechanism underlying spot suppression by verbenone is not strictly inhibition of attraction and attack and that unknown behavioural influences likely are also at play. Due to these gaps of knowledge about verbenone, proposed improvements to verbenone-based spot suppression methods are largely based on conjecture and anecdotal field observations. Development of verbenone into a widely used management tool for southern pine beetle may require a far deeper understanding of how the compound functions in host colonisation and infestation growth.

Obstacles to progress in research, development, and application

Obstacles – attractants. One goal set forth in early research on attractants for southern pine beetle was the synthesis of an attractive target for beetles that could compete with – and preferably out-compete – natural sources of attractant (Vité 1970). Presumably, if a baited trap was a superior attractive target to an attacked tree, mass attacks on adjacent trees would not be induced accidentally and traps could be effective population sinks for beetles. However, subsequent lure improvements appear to have increased, rather than decreased, the risk of traps inducing spillover attacks on adjacent trees (authors' observations). This shortcoming is a barrier to the development of attractant-based technology for southern pine beetle control and limits the stand compositions and host densities where monitoring traps can be deployed safely. The inability of synthetic lures and traps to compete with natural attractive semiochemical sources may have several causes.

Attractant composition. Synthetic lures, including the recommended operational lure for southern pine beetle, may lack important, undiscovered attractive semiochemicals produced by mass-attacked trees. Since the 2000s, investigation of undiscovered semiochemicals – both attractants and attraction inhibitors – for the southern pine beetle has been aided by coupled gas chromatography–mass spectrometry and gas chromatography–electroantennographic detection, in particular (Sullivan 2005; Shepherd and Sullivan 2013; Niño-Domínguez *et al.* 2015; Niño-Domínguez *et al.* 2018; Munro *et al.* 2020). Using this latter method, compounds within odour blends isolated from natural sources are separated and assayed individually for their capacity to stimulate the antenna of the target insect (Bjostad 1998). Typically, odour blends produced by natural sources (such as a mass-attacked tree) of bark beetle attractant are highly complex and contain potentially hundreds of compounds at widely varying concentrations (Sullivan 2005; Shepherd and Sullivan 2013; Niño-Domínguez *et al.* 2015). Gas chromatography–electroantennographic detection is a rigorous means for detecting olfactory stimulants (ostensibly the only compounds capable of being semiochemicals) within such mixtures, and subsequent behavioural bioassays can be limited to just a subset of compounds. To date, the method has been used to screen for southern pine beetle olfactory stimulants produced by emerged beetles, attacking beetles, attack entrances, frass, and host resin (Sullivan 2005; Shepherd and Sullivan 2013; Niño-Domínguez *et al.* 2015, 2018; Munro *et al.* 2020). The sensitivity and thoroughness of this chemical-detection approach has enabled identification of dozens of olfactory stimulants, and thus potential semiochemicals, for the beetle. However, many southern pine beetle olfactory stimulants identified via this method have not yet been investigated behaviourally for either attractive or inhibitory effects. Additionally, there may be semiochemicals not detected using this method because their chemical properties (*e.g.*, thermal lability) make them unsuitable.

Attractant quantity. Lure release rates and proportions among the semiochemical components ostensibly influence a lure's capacity to compete with natural attractive sources. Semiochemical release has been quantified from individual southern pine beetle gallery entrances (Pureswaran and Sullivan 2012), and thus lure release rates can be estimated as numbers of "attack equivalents." Commercial devices for the operational southern pine beetle lure release 5–12 mg/day of frontalin and 0.1–0.5 mg/day of *endo*-brevicomin (B.T.S. data), which equals pheromone release from 10^3 to 10^4 newly established beetle entrances (Pureswaran and Sullivan 2012). Given that hundreds to thousands of attacks occur on southern pine beetle–colonised pines (Coulson *et al.* 1976; Fargo *et al.* 1978), the lures probably duplicate one to several mass-attacked trees in their release of pheromone. This suggests that the lack of competitiveness of these lures cannot be attributed to insufficient release of these compounds. However, the proportions of the pinene component in the operational lure (which is released at 1–5 g/day) relative to the pheromone component are an order of magnitude lower than those detected from beetle attacks; therefore, they may represent an unnatural presentation of the aggregation signal (Pureswaran and Sullivan 2012).

High rates of bark beetle aggregation pheromone components released from a target such as a trap or tree may render surrounding sources of attractive semiochemicals or uninfested trees relatively more attractive, even while increasing attraction to the target (Tilden *et al.* 1983; Schlyter *et al.* 1987). For southern pine beetle, this effect has been demonstrated both for *endo*-brevicomin and frontalin (Vité 1970; Sullivan and Mori 2009). This phenomenon no doubt helps drive host switching (as described above) and spot growth. Without field experimentation, it may not be possible to select release rates that maximise desired effects of an attractant while keeping risk to the surrounding forest at acceptable levels. Rate adjustment is further complicated because current, local beetle population densities appear to influence the risk of spillover attacks, and these densities often cannot be gauged in advance.

Non-semiochemical cues and signal presentation. Several studies show that attraction of southern pine beetles is greatly increased if semiochemical attractants are accompanied by a dark, vertical silhouette that provides a visual stimulus similar to that produced by the host tree (Gara *et al.* 1965; Strom *et al.* 1999; Strom and Goyer 2001). No thorough studies of how dimensions of the visual target (diameter, height) influence response by the beetle have been undertaken. However, the funnel traps typically used operationally differ conspicuously in dimensions from host trees, and this may make them relatively less attractive to the beetles.

Furthermore, the spatial distribution of semiochemical emission from an attacked tree differs greatly from that of commercial lures and traps. Because release devices are relatively small and are deployed singly, a baited trap releases semiochemical typically from a single point, although the resulting plume is diffused somewhat by the trap body (Lindgren 1983). This spatially concentrated semiochemical release differs greatly from that of an attacked tree, which has many discrete points, each of which releases semiochemicals at a low rate across the surface of the bole. A more dispersed release may increase attraction (Tilden *et al.* 1983). Furthermore, southern pine beetle flight and attacks on the host are concentrated at 3–5 m height (Gara *et al.* 1965; Coster *et al.* 1977a,b), whereas traps used operationally for the beetle are deployed less than 3 m above ground level.

Local environment and semiochemical background. The attractiveness of a lure may be influenced by naturally occurring semiochemicals in the environment. At a single release rate, *endo*-brevicomin enhanced responses to traps baited with attractant (frontalin and turpentine) outside of active infestations but reduced responses inside (Sullivan *et al.* 2011; Fig. 4). This effect may be due to semiochemical background – specifically, a background of beetle-produced *endo*-brevicomin – present inside infestations but absent outside, as suggested by an unpublished experiment (see Supplementary Materials 3 for a description). In trials in uninfested stands, addition of an *endo*-brevicomin device to attractant-baited traps either increased or decreased beetle catches, depending on whether a trio of 20-m-distant *endo*-brevicomin release devices (a source of *endo*-brevicomin background) was absent or present, respectively (Fig. 5). The multifunctional dose-response curve associated with *endo*-brevicomin may have caused this effect (Sullivan 2016). The *endo*-brevicomin released from the trio of devices may have produced a low, synergistic concentration at the trap,

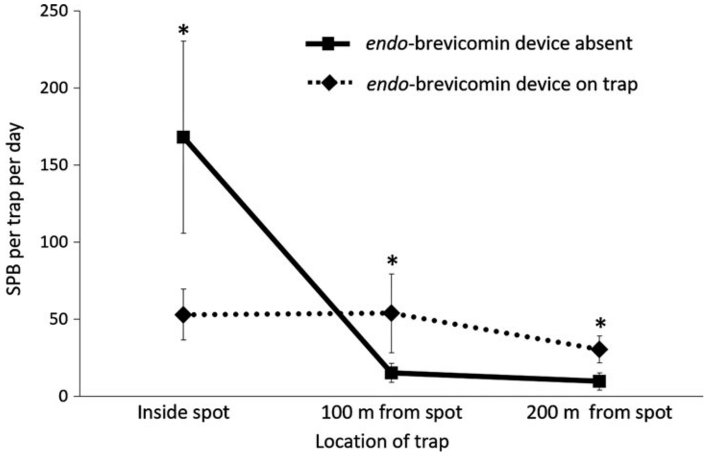

Fig. 4. Differing effects of *endo*-brevicomin devices on southern pine beetle catches in attractant-baited funnel traps located either inside or outside active beetle infestations. Individual funnel traps were baited with frontalin and turpentine and alternately had one or no *endo*-brevicomin devices attached. The data are combined from eight infestations each in Georgia and Mississippi, United States of America. An asterisk indicates that catches with or without *endo*-brevicomin differed significantly at the indicated location (α = 0.05). Data are derived from Sullivan *et al.* (2011), Table 2.

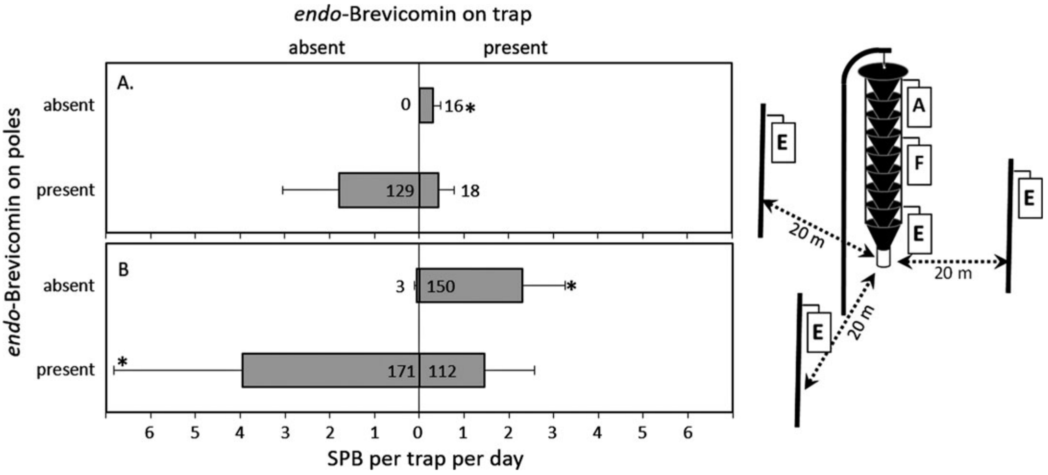

Fig. 5. Catches of southern pine beetle in funnel traps baited with frontalin and *alpha*-pinene and varying in two factors: (1) presence of an *endo*-brevicomin device attached to the trap, and (2) presence of an *endo*-brevicomin background from three *endo*-brevicomin devices surrounding the trap at 20-m distance. Trials were performed either with a relatively higher (trial A: 2–5 mg/day) or lower (trial B: 0.3–0.7 mg/day) release of *endo*-brevicomin from the devices attached to the trap itself (the release from the 20-m-distant devices was invariant, 2–5 mg/day). Trials were at the same site but at different dates for trials A (19 April to 8 May 2013) and B (8 to 28 May 2013). Release devices in the schematic diagram are frontalin (F), *alpha*-pinene (A), and *endo*-brevicomin (E). The integers adjacent to or inside bars indicate total beetles trapped by the treatment. An asterisk indicates significantly different catches due to the presence or absence of the *endo*-brevicomin device on the trap (α = 0.05). The large error bars are due to variation in catches among blocks. Experiments were in uninfested mixed pine/hardwood forests in southwestern Mississippi. See Supplementary Materials 3 for details.

whereas the additional amounts released by the device added to the trap could have increased the *endo*-brevicomin concentration above an optimally attractive level. These observations suggest that specific lure compositions may be more or less competitive in the presence of different local population densities of southern pine beetle and the ambient pheromone concentrations they may generate. Furthermore, unknown qualities of the semiochemical milieu could produce misleading results in semiochemical tests with this and other bark beetles, and semiochemical responses observed in one context may not occur in another context where application is desired.

Obstacles – anti-attractants

Extensive laboratory and field experiments over the past 50 years have identified numerous compounds that can reduce southern pine beetle response to attractants. However, extensive efforts to develop tree-protection and spot-suppression technologies with these compounds have not yielded a management tool receiving significant use. At least two major obstacles hinder development of southern pine beetle management technology with anti-attractants.

Complexities of semiochemical function. Past research has shown that semiochemicals can have complex and subtle influences on behaviour of this and other bark beetle species that may not be readily discovered or characterised. However, understanding these influences may be essential to technology development. In southern pine beetle and other bark beetles, behavioural effects of attraction-modifying semiochemicals have typically been established with "challenge"-type trapping experiments. Challenge tests contrast catches among attractant-baited traps when a subset is amended with releasers of candidate attraction modifiers (Reeve and Strom 2004; Fettig *et al.* 2006; Strom *et al.* 2013). A candidate that reduces catches is inferred to have the potential to protect trees because response to aggregation attractant is critical for beetle colonisation of healthy hosts. Trap challenge tests are appealing because they can be performed quickly, do not require that trees be killed, and produce statistically robust data sets. Fourteen anti-attractant semiochemicals for the southern pine beetle have been identified with challenge tests (Sullivan 2011).

However, challenge tests neither distinguish true repellents from attraction reducers nor show whether the candidate could deter landings occurring randomly or when not mediated by olfactory attraction. These tests may provide an overly simplified view of semiochemical activity, and reliance on them likely has delayed recognition of key properties of southern pine beetle semiochemicals. For example, challenge tests alone do not elucidate the spatial effects of a semiochemical, which may be critical information for effective application. *endo*-Brevicomin can inhibit the beetle's response to attractant at its point of release but synergise responses to sources of attractant up to tens of metres away (Sullivan and Mori 2009; B.T.S., unpublished data); therefore, a semiochemical characterised as an anti-attractant in challenge tests (as *endo*-brevicomin was; Payne *et al.* 1978a,b; Salom *et al.* 1992) could inadvertently put surrounding resources at greater risk if deployed for protecting trees. Furthermore, aspects of the environment and methodology of challenge tests can yield conflicting results. As already discussed, *endo*-brevicomin can synergise response to attractant outside of southern pine beetle infestations but inhibit attraction inside an infestation, and presence of *endo*-brevicomin background (Fig. 5) and variation in trap spacing (Sullivan and Mori 2009) can produce similar activity "reversals." Once discovered, the influence of variables such as location and spatial distribution of semiochemical sources can be determined with additional experiments. However, the above evidence indicates sufficient characterisation of the activity and biological function of a candidate control semiochemical may require substantially more sophisticated and resource-intensive experimentation than typically has been applied to this problem.

Also, it is likely that important variables governing activity of anti-attractants for southern pine beetle have yet to be discovered. In challenge tests, 4-allylanisole was shown to inhibit the beetle's response to attractant-baited traps (Hayes *et al.* 1994; Strom *et al.* 1999), whereas more recent tests indicate it acts as a potent attractant synergist (Munro *et al.* 2020). These two sets of challenge studies differed in a variety of aspects, but ongoing investigations have failed to reproduce the earlier-reported inhibitory effects of 4-allylanisole, and several hypotheses regarding causes for the contrasting results have been ruled-out (B.T.S., unpublished data). Likewise, the simultaneous success of verbenone as a spot suppressant but failure as a tree protectant defies simple explanation. The functions of semiochemicals in southern pine beetle biology may be much more complex than envisioned during the early period of semiochemical research; this complexity reduces the near-term prospect for an efficacious, reliable semiochemical technology to control the beetle.

Difficulties with tests of spot suppression. In the development of southern pine beetle spot suppression technology, the experimental unit of replication is a single spot and treatment of dozens of spots is necessary to evaluate a semiochemical treatment. Collection of data from individual spots is time-consuming and labour-intensive. Availability of spots for experiments may be limited due to annual variability in location, intensity, accessibility, and expanse of outbreaks, and permission for experiments may be difficult to obtain. Managers of the national forests where experimentation generally occurs typically prefer to aggressively control spots through cuts, particularly when they threaten private lands or high-value resources such as red-cockaded woodpecker colonies. Untreated spots for use as experimental controls are necessary but understandably disliked; however, sophisticated models for predicting spot growth can be used as a partial substitute for untreated control spots (Stephen and Lih 1985; Coulson *et al.* 1989). The high levels of replication needed for evaluating efficacy of spot-suppression techniques slows technology improvements because every proposed modification (*e.g.*, adjustments to height, densities, and tree characteristics for deployment of verbenone devices) must receive the same, copious replication before recommendations are altered.

Conclusions

Research on southern pine beetle semiochemical attractants has resulted in management technologies that are widely used and have unquestionable value (*i.e.*, trap lures for forecasting and detecting beetle populations). In contrast, extensive efforts to develop semiochemical-based spot-suppression and tree-protection technology for the beetle have, to date, failed to generate a management tool that has been adopted in practice, and achievement of this goal will require extensive additional work. A long list of anti-attractants for the species now exists, but most of these semiochemicals have received little, if any, investigation as resource protectants, due in part to their sheer number. Verbenone still shows much potential for being adopted operationally as a spot suppressant, and the barriers to this goal are surmountable despite being significant. Geographic variability in southern pine beetle population dynamics likely deserves greater attention in future research: semiochemical management technologies may be more applicable in the southern states, where past research has been focussed, compared to the northern limits of the insect's range, where relevant aspects of its population dynamics appear to differ. Independent efforts at development of semiochemical management are advisable in the northeast United States of America.

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References

Amman, G.D., Thier, R.W., McGregor, M.D., and Schmitz, R.F. 1989. Efficacy of verbenone in reducing lodgepole pine infestation by mountain pine beetles in Idaho. Canadian Journal of Forest Research, **19**: 60–64.

Ayres, M.P., Martinson, S.J., and Friedenberg, N.A. 2011. Southern pine beetle ecology: populations within stands. *In* The Southern Pine Beetle II. *Edited by* R.N. Coulson and K.D. Klepzig. General Technical Report SRS-140. United States Department of Agriculture Forest Service, Southern Research Station, Asheville, North Carolina, United States of America. Pp. 75–89.

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

Billings, R.F. 2011a. Mechanical control of southern pine beetle infestations. *In* The Southern Pine Beetle II. *Edited by* R.N. Coulson and K.D. Klepzig. General Technical Report SRS-140. United States Department of Agriculature Forest Service, Southern Research Station. Pp. 399–413.

Billings, R.F. 2011b. Aerial detection, ground evaluation, and monitoring of the southern pine beetle: states perspectives. *In* The Southern Pine Beetle II. *Edited by* R.N. Coulson and K.D. Klepzig. General Technical Report SRS-140. United States Department of Agriculture Forest Service, Southern Research Station, Asheville, North Carolina, United States of America. Pp. 245–261.

Billings, R.F., Berisford, C.W., Salom, S.M., and Payne, T.L. 1995. Applications of semiochemicals in the management of southern pine beetle infestations: current status of research. General Technical Report INT-GTR-318. United States Department of Agriculture Forest Service, Intermountain Research Station, Ogden, Utah, United States of America. Pp. 30–38.

Billings, R.F. and Pase, H.A., III. 1979. Spot proliferation patterns as a measure of the area-wide effectiveness of southern pine beetle control tactics. *In* Evaluating control tactics for the southern pine beetle. *Edited by* J.E. Coster and J.L. Searcy. Technical Bulletin 1613. United States Department of Agriculture Forest Service, Washington D.C., United States of America. Pp. 86–97.

Billings, R.F. and Upton, W.W. 2010. A methodology for assessing annual risk of southern pine beetle outbreaks across the southern region using pheromone traps. *In* Advances in Threat Assessment and Their Application to Forest and Rangeland Management. *Edited by* J.M. Pye, H.M. Rauscher, Y. Sands, D.C. Lee, and J.S. Beatty. General Technical Report PNW-GTR-802. United States Department of Agriculture Forest Service, Pacific Northwest and Southern Research Stations, Portland, Oregon, United States of America. Pp. 73–85.

Birt, A. 2011. Regional population dynamics. *In* Southern Pine Beetle II. *Edited by* R. N. Coulson and K. D. Klepzig. General Technical Report SRS-140. United States Department of Agriculture Forest Service, Southern Research Station, Asheville, North Carolina, United States of America. Pp. 109–128.

Bjostad, L.B. 1998. Electrophysiological methods. *In* Methods in Chemical Ecology, Volume **1**: Chemical Methods. *Edited by* J.G. Millar and K.F. Haynes. Kluwer Academic Publishers, Boston, Massachusetts. United States of America. Pp. 339–375.

Bookwalter, J., Riggins, J., Dean, J., Mastro, V., Schimleck, L., Sullivan, B., and Gandhi, K. 2019. Colonization and development of *Sirex noctilio* (Hymenoptera: Siricidae) in bolts of a native pine host and six species of pine grown in the southeastern United States. Journal of Entomological Science, **54**: 1–18.

Borden, J.H. 1974. Aggregation pheromones in the Scolytidae. *In* Frontiers of Biology. *Edited by* A. Neuberger and E.L. Tatum. North Holland Publishing Company, Amsterdam, The Netherlands. Pp. 135–160.

Borden, J.H. 1993. Uncertain fate of spot infestations of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins. The Canadian Entomologist, **125**: 167–169.

Borden, J.H. 1995. From identifying semiochemicals to developing a suppression tactic: a historical review. *In* Application of semiochemicals for management of bark beetle infestations – proceedings of an informal conference. *Edited by* S.M. Salom and K.R. Hobson. General

Technical Report INT-GTR-318. United States Department of Agriculture Forest Service, Indianapolis, Indiana, United States of America. Pp. 3–10.

Borden, J.H. 1997. Disruption of semiochemical-mediated aggregation in bark beetles. *In* Insect Pheromone Research: New Directions. *Edited by* R.T. Cardé and A.K. Minks. Chapman and Hall, New York, United States of America. Pp. 421–438.

Borden, J.H., Birmingham, A.L., and Burleigh, J.S. 2006. Evaluation of the push–pull tactic against the mountain pine beetle using verbenone and non-host volatiles in combination with pheromone-baited trees. The Forestry Chronicle, **82**: 579–590.

Borden, J.H., Chong, L.J., Earle, T.J., and Huber, D.P.W. 2003. Protection of lodgepole pine from attack by the mountain pine beetle, *Dendroctonus ponderosae* (Coleoptera: Scolytidae) using high doses of verbenone in combination with nonhost bark volatiles. The Forestry Chronicle, **79**: 685–691.

Borden, J.H., Chong, L.J., and Fuchs, M.C. 1983. Application of semiochemicals in post-logging manipulation of the mountain pine beetle, *Dendroctonus ponderosae* (Coleoptera: Scolytidae). Journal of Economic Entomology, **76**: 1428–1432.

Brand, J.M., Bracke, J.W., Britton, L.N., Markovetz, A.J., and Barras, S.J. 1976. Bark beetle pheromones: production of verbenone by a mycangial fungus of *Dendroctonus frontalis*. Journal of Chemical Ecology, **2**: 195–199.

Brand, J.M., Bracke, J.W., Markovetz, A.J., Wood, D.L., and Browne, L.L. 1975. Production of verbenol pheromone by a bacterium isolated from bark beetles. Nature, **254**: 136–137.

Byers, J.A. 1989. Behavioral mechanisms involved in reducing competition in bark beetles. Holarctic Ecology, **12**: 466–476.

Byers, J.A., Lanne, B.S., and Lofqvist, J. 1989. Host tree unsuitability recognized by pine shoot beetles in flight. Experientia, **45**: 489–492.

Christiansen, E., Waring, R.H., and Berryman, A.A. 1987. Resistance of conifers to bark beetle attack: searching for general relationships. Forest Ecology and Management, **22**: 89–106.

Clarke, S.R. and Billings, R.F. 2003. Analysis of the southern pine beetle suppression program on the national forests in Texas in the 1990s. Southern Journal of Applied Forestry, **27**: 122–129.

Clarke, S.R., Salom, S.M., Billings, R.F., Berisford, C.W., Upton, W.W., McClellan, Q.C., and Dalusky, M.J. 1999. A *Scents*ible approach to controlling southern pine beetles. Journal of Forestry, **97**: 26–31.

Cook, S.M., Khan, Z.R., and Pickett, J.A. 2006. The use of push–pull strategies in integrated pest management. Annual Review of Entomology, **52**: 375–400.

Conner, R.N. and Rudolph, D.C. 1995. Losses of red-cockaded woodpecker cavity trees to southern pine beetles. The Wilson Bulletin, **107**: 81–92.

Conner, R.N., Saenz, D., Rudolph, D.C., and Coulson, R.N. 1998. Southern pine beetle-induced mortality of pines with natural and artificial red-cockaded woodpecker cavities in Texas. The Wilson Bulletin, **110**: 100–109.

Conner, R.N., Saenz, D., Rudolph, D.C., Ross, W.G., Kulhavy, D.L., and Coulson, R.N. 2001. Does red-cockaded woodpecker excavation of resin wells increase risk of bark beetle infestation of cavity trees? The Auk, **118**: 21–224.

Copony, J.A. and Morris, C.L. 1972. Southern pine beetle suppression with frontalure and cacodylic acid treatments. Journal of Economic Entomology, **65**: 754–747.

Coster, J.E., Hicks, R.R., Jr., and Watterston, K.G. 1978. Directional spread of southern pine beetle (Coleoptera: Scolytidae) infestations in East Texas. Journal of the Georgia Entomological Society, **13**: 315–321.

Coster, J.E., Payne, T.L., Hart, E.R., and Edson, L.J. 1977a. Seasonal variations in mass attack behavior of southern pine beetle. Journal of the Georgia Entomological Society, **12**: 204–211.

Coster, J.E., Payne, T.L., Hart, E.R., and Edson, L.J. 1977b. Aggregation of the southern pine beetle in response to attractive host trees. Environmental Entomology, **6**: 725–731.

Coulson, R.N., Feldman, R.M., Sharpe, P.J.H., Pulley, P.E., Wagner, T.L., and Payne, T.L. 1989. An overview of the Tambeetle model of *Dendroctonus frontalis* population dynamics. Holarctic Ecology, **12**: 445–450.

Coulson, R.N., Flamm, R.O., Wagner, T.L., Rykiel, E.J., Sharpe, P.J.H., Payne, T.L., and Lin, S.K. 1985. Population dynamics of initiation and growth of southern pine beetle infestations. *In* Proceedings of the Integrated Pest Management Symposium. *Edited by* S.J. Branham and R.C. Thatcher. General Technical Report SO-56. United States Department of Agriculture Forest Service, New Orleans, Louisiana, United States of America. Pp. 136–151.

Coulson, R.N., Foltz, J.L., Mayyasi, A.M., and Hain, F.P. 1975. Quantitative evaluation of frontalure and cacodylic acid treatment effects on within-tree populations of the southern pine beetle. Journal of Economic Entomology, **68**: 671–678.

Coulson, R.N., Hennier, P.B., Flamm, R.O., Rykiel, E.J., Hum, L.C., and Pa, T.L. 1983. The role of lightning in the epidemiology of the southern pine beetle. Zeitschrift für Angewandte Entomologie, **96**: 182–193.

Coulson, R.N., Oliveria, F.L., Payne, T.L., and Houseweart, M.W. 1973a. Variables associated with use of frontalure and cacodylic acid in supression of the southern pine beetle. 1. Factors influencing manipulation to prescribed trap trees. Journal of Economic Entomology, **66**: 893–896.

Coulson, R.N., Oliveria, F.L., Payne, T.L., and Houseweart, M.W. 1973b. Variables associated with use of frontalure and cacodylic acid in suppression of the southern pine beetle. 2. Brood reduction in trees treated with cacodylic acid. Journal of Economic Entomology, **66**: 897–899.

Coulson, R.N., Pulley, P.E., Foltz, J.L., and Martin, W.C. 1976. Procedural guide for quantitatively sampling within-tree populations of *Dendroctonus frontalis*. Miscellaneous Publication MP-1267. Texas Agricultural Experiment Station, United States of America. Pp. 1–26.

Cronin, J.T., Turchin, P., Hayes, J.L., and Steiner, C.A. 1999. Area-wide efficacy of a localized forest pest management practice. Environmental Entomology, **28**: 496–504.

Dickens, J.C., Billings, R.F., and Payne, T.L. 1992. Green leaf volatiles interrupt aggregation pheromone response in bark beetles infesting southern pines. Experientia, **48**: 523–524.

Dodds, K.J., Aoki, C.F., Arango-Velez, A., Cancelliere, J., D'Amato, A.W., DiGirolomo, M.F., and Rabaglia, R.J. 2018. Expansion of southern pine beetle into northeastern forests: management and impact of a primary bark beetle in a new region. Journal of Forestry, **116**: 178–191.

Eigenbrode, S.D., Birch, A.N.E., Lindzey, S., Meadow, R., and Snyder, W.E. 2016. A mechanistic framework to improve understanding and applications of push–pull systems in pest management. Journal of Applied Ecology, **53**: 202–212.

El-Sayed, A., Suckling, D., Byers, J., Jang, E., and Wearing, C. 2009. Potential of "lure and kill" in long-term pest management and eradication of invasive species. Journal of Economic Entomology, **102**: 815–835.

El-Sayed, A.M., Suckling, D.M., Wearing, C.H., and Byers, J.A. 2006. Potential of mass trapping for long-term pest management and eradication of invasive species. Journal of Economic Entomology, **99**: 1550–1564.

Fargo, W.S., Coulson, R.M., Pulley, P.E., Pope, D.N., and Kelley, C.L. 1978. Spatial and temporal patterns of within-tree colonization by *Dendroctonus frontalis* (Coleoptera: Scolytidae). The Canadian Entomologist, **110**: 1213–1232.

Fettig, C.J., Dabney, C.P., McKelvey, S.R., and Borys, R.R. 2006. An assessment of re-randomization methods in bark beetle (Scolytidae) trapping bioassays. Agricultural and Forest Entomology, **8**: 267–271.

Fettig, C.J., McKelvey, S.R., Dabney, C.P., and Huber, D.P. 2012. Responses of *Dendroctonus brevicomis* (Coleoptera: Curculionidae) in behavioral assays: implications to development of a semiochemical-based tool for tree protection. Journal of Economic Entomology, **105**: 149–160.

Fettig, C.J., Munson, A.S., Reinke, M., and Mafra-Neto, A. 2015. A novel semiochemical tool for protecting *Pinus contorta* from mortality attributed to *Dendroctonus ponderosae* (Coleoptera: Curculionidae). Journal of Economic Entomology, **108**: 173–182.

Fitzgerald, J.W., Coulson, R.N., Pulley, P.E., Flamm, R.O., Oliveria, F.L., Swain, K.M., and Drummond, D.B. 1994. Suppression tactics for *Dendroctonus frontalis* Zimmerman (Coleoptera: Scolytidae): an examination of the occurrence of infestations adjacent to treatment sites. Journal of Economic Entomology, **87**: 417–425.

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

Franklin, R.T. 1970. Southern pine beetle population behavior. Journal of the Georgia Entomological Society, **5**: 175–182.

Gara, R.I. 1967. Studies on the attack behavior of the southern pine beetle. I. The spreading and collapse of outbreaks. Contributions to the Boyce Thompson Institute, **23**: 349–354.

Gara, R.I. and Coster, J.E. 1968. Studies on the attack behavior of the southern pine beetle. III. Sequence of tree infestation within stands. Contributions to the Boyce Thompson Institute, **24**: 77–85.

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

Geiszler, D.R., Gallucci, V.F., and Gara, R.I. 1980. Modeling the dynamics of mountain pine beetle aggregation in a lodgepole pine stand. Oecologia, **46**: 244–253.

Grosman, D.M., Clarke, S.R., and Upton, W.W. 2009. Efficacy of two systemic insecticides injected into loblolly pine for protection against southern pine bark beetles (Coleoptera: Curculionidae). Journal of Economic Entomology, **102**: 1062–1069.

Grosman, D.M., Salom, S.M., Ravlin, F.W., and 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.

Hayes, J.L., Meeker, J.R., Foltz, J.L., and Strom, B.L. 1996. Suppression of bark beetles and protection of pines in the urban environment: a case study. Journal of Arboriculture, **22**: 67–74.

Hayes, J.L., Strom, B.L., Roton, L.M., and Ingram, L.L. 1994. Repellent properties of the host compound 4-allylanisole to the southern pine beetle. Journal of Chemical Ecology, **20**: 1595–1615.

Hayes, J.L., Strom, B.L., Roton, L., and Ingram Jr, L. 1995. Scolytid repellant. United States Patent US 5,403,863.

Hedden, R.L. and Billings, R.F. 1979. Southern pine beetle: factors influencing the growth and decline of summer infestations in East Texas. Forest Science, **25**: 547–556.

Hodges, J.D. and Pickard, L.S. 1971. Lightning in the ecology of the southern pine beetle, *Dendroctonus frontalis* (Coleoptera: Scolytidae). The Canadian Entomologist, **103**: 44–51.

Hunt, D.W.A., Borden, J.H., Lindgren, B.S., and Gries, G. 1989. The role of autoxidation of *alpha*-pinene in the production of pheromones of *Dendroctonus ponderosae* (Coleoptera: Scolytidae). Canadian Journal of Forest Research, **19**: 1275–1282.

Johnson, P.C. and Coster, J.E. 1978. Probability of attack by southern pine beetle in relation to distance from an attractive host tree. Forest Science, **24**: 574–580.

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

Lesk, C., Coffel, E., D'Amato, A.W., Dodds, K., and Horton, R. 2017. Threats to North American forests from southern pine beetle with warming winters. Nature Climate Change, **7**: 7–13.

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

Lindgren, B. and Borden, J. 1993. Displacement and aggregation of mountain pine beetles, *Dendroctonus ponderosae* (Coleoptera: Scolytidae), in response to their antiaggregation and aggregation pheromones. Canadian Journal of Forest Research, **23**: 286–290.

Mafra-Neto, A., de Lame, F.M., Fettig, C.J., Munson, A.S., Perring, T.M., Stelinski, L.L., *et al.* 2013. Manipulation of insect behavior with specialized pheromone and lure application technology

(SPLAT®). *In* Pest Management with natural products. ACS Publications, Washington D.C., United States of America. Pp. 31–58.

Martinson, S.J., Ylioja, T., Sullivan, B.T., Billings, R.F., and Ayres, M.P. 2013. Alternate attractors in the population dynamics of a tree-killing bark beetle. Population Ecology, **55**: 95–106.

McCarty, F.A., Billings, P.M., Richerson, J.V., Payne, T.L., and Edson, L.J. 1980. Response of the southern pine beetle to behavioral chemicals in the laboratory. Journal of the Georgia Entomological Society, **15**: 307–317.

McCullough, D.G., Poland, T.M., and Lewis, P.A. 2016. Lethal trap trees: a potential option for emerald ash borer (*Agrilus planipennis* Fairmaire) management. Pest Management Science, **72**: 1023–1030.

McCravy, K.W., Nowak, J.T., Douce, G.K., and Berisford, C.W. 2000. Evaluation of multiple-funnel and slot traps for collection of southern pine bark beetles and predators. Journal of Entomological Science, **35**: 77–82.

McNichol, B.H. 2018. Population dynamics of four bark beetle species (Coleoptera: Curculionidae: Scolytidae) on southern pines. Masters' thesis. University of Georgia, Athens, Georgia, United States of America.

Mirov, N.T. 1961. Composition of gum turpentines of pines. Technical Bulletin No. 1239. United States Department of Agriculture Forest Service, Pacific Southwest Forest and Range Experiment Station. Pp. 158.

Mitchell, R.G. and Preisler, H.K. 1991. Analysis of spatial patterns of lodgepole pine attacked by outbreak populations of the mountain pine beetle. Forest Science, **37**: 1390–1408.

Mooneyham K. 2019. Forest Health Pest Update [online]. Virginia Department of Forestry, Charlottesville, Virginia, United States of America. Available from https://www.vaforestry.org/assets/ForestHealthUpdates19.pdf [accessed 5 September 2020].

Moser, J.C. and Browne, L.E. 1978. A nondestructive trap for *Dendroctonus frontalis* Zimmerman (Coleoptera: Scolytidae). Journal of Chemical Ecology, **4**: 1–7.

Munro, H.L., Gandhi, K.J.K., Barnes, B.F., Montes, C.R., Nowak, J., Shepherd, W.P., *et al.* 2020. Electrophysiological and behavioral responses of two bark beetles, *Dendroctonus frontalis* and *D. terebrans* (Coleoptera: Curculionidae), to resin odors of host pines (*Pinus* spp.) [online]. Chemoecology, 2020. https://doi.org/10.1007/s00049–020–00311–7.

Negron, J.F., Cain, R., Cadenhead, A., and Waugh, B. 2019. A test of lethal trap trees for control of spruce beetles. Research Note RMRS-RN-83. United States Department of Agriculture Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, United States of America. P. 83.

Niemeyer, H., Schröder, T., and Watzek G. 1983. Eine neue Lockstoff-Falle zur Bekämpfung von rinden-und holzbrütenden Borkenkäfern. Der Forst- und Holzwirt, **38**: 105–112.

Niño-Domínguez, A., Sullivan, B.T., López-Urbina, J.H., and Macías-Sámano, J.E. 2015. Pheromone-mediated mate location and discrimination by two syntopic sibling species of *Dendroctonus* bark beetles in Chiapas, Mexico. Journal of Chemical Ecology, **41**: 746–756.

Niño-Domínguez, A., Sullivan, B.T., Lopez-Urbina, J.H., and Macías-Sámano, J.E. 2018. Discrimination of odors associated with conspecific and heterospecific frass by sibling species *Dendroctonus frontalis* (Coleoptera: Curculionidae: Scolytinae) and *Dendroctonus mesoamericanus*. Environmental Entomology, **47**: 1532–1540.

Payne, T.L. 1986. Olfaction and vision in host finding by a bark beetle. *In* Mechanisms in Insect Olfaction. *Edited by* T.L. Payne, M.C. Birch, and C.E. Kennedy. Clarendon Press, Oxford, United Kingdom. Pp. 111–116.

Payne, T.L. and Billings, R.F. 1989. Evaluation of (S)-verbenone applications for suppressing southern pine beetle (Coleoptera: Scolytidae) infestations. Journal of Economic Entomology, **82**: 1702–1708.

Payne, T.L., Billings, R.F., Berisford, C.W., Salom, S.M., Grosman, D.M., Dalusky, M.J., and Upton, W.W. 1992. Disruption of *Dendroctonus frontalis* (Col., Scolytidae) infestations with an inhibitor pheromone. Journal of Applied Entomology, **114**: 341–347.

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

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

Payne, T.L., Coster, J.E., Richerson, J.V., Hart, E.R., Hedden, R.L., and Edson, L.J. 1978b. Reducing variation in field tests of behavioral chemicals for the southern pine beetle. Journal of the Georgia Entomological Society, **13**: 85–90.

Payne, T.L., Kudon, L.H., Walsh, K.D., and Berisford, C.W. 1985a. Influence of infestation density on suppression of *D. frontalis* infestations with attractant. Zeitschrift für Angewandte Entomologie, **99**: 39–43.

Payne, T.L., Kudon, L.H., Berisford, C.W., O'Donnel, B.P., and Walsh, D.K. 1985b. Effects of frontalure in suppressing southern pine beetle spot growth under endemic and epidemic population levels. *In* Integrated Pest Management Research Symposium: The Proceedings. *Edited by* S.J. Branham and R.C. Thatcher. General Technical Report SO-56. United States Department of Agriculture Forest Service, New Orleans, Louisiana, United States of America. Pp. 28–287.

Payne, T.L. and Richerson, J.V. 1979. Management implications of inhibitors for *Dendroctonus frontalis* (Col. Scolytidae). Bulletin de la Société Entomologique Suisse, **52**: 323–331.

Payne, T.L. and Richerson, J.V. 1985. Pheromone-mediated competitive replacement between two bark beetle populations: influence on infestation suppression. Zeitschrift für Angewandte Entomologie, **99**: 131–138.

Payne, T.L., Richerson, J.V., Dickens, J.C., West, J.R., Mori, K., Berisford, C.W., *et al.* 1982. Southern pine beetle: olfactory receptor and behavior discrimination of enantiomers of the attractant pheromone frontalin. Journal of Chemical Ecology, **8**: 873–881.

Perkins, D.L., Jorgensen, C.L., and Rinella, M.J. 2015. Verbenone decreases whitebark pine mortality throughout a mountain pine beetle outbreak. Forest Science, **61**: 747–752.

Progar, R., Blackford, D., Cluck, D., Costello, S., Dunning, L., Eager, T., *et al.* 2013. Population densities and tree diameter effects associated with verbenone treatments to reduce mountain pine beetle-caused mortality of lodgepole pine. Journal of Economic Entomology, **106**: 221–228.

Pureswaran, D.S., Hofstetter, R.W., and Sullivan, B.T. 2008. Attraction of the southern pine beetle, *Dendroctonus frontalis*, to pheromone components of the western pine beetle, *Dendroctonus brevicomis* (Coleoptera: Curculionidae: Scolytinae), in an allopatric zone. Environmental Entomology, **37**: 70–78.

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

Pureswaran, D.S., Sullivan, B.T., and Ayres, M.P. 2006. Fitness consequences of pheromone production and host selection strategies in a tree-killing bark beetle (Coleoptera: Curculionidae: Scolytinae). Oecologia, **148**: 720–728.

Raffa, K.F., Phillips, T.W., and Salom, S.M. 1993. Strategies and mechanisms of host colonization by bark beetles. *In* Beetle-pathogen interactions in conifer forests. *Edited by* R.D. Schowalter and G.M. Filip. Academic Press, London, United Kingdom. Pp. 103–128.

Reeve, J.D. and Strom, B.L. 2004. Statistical problems encountered in trapping studies of scolytids and associated insects. Journal of Chemical Ecology, **30**: 1575–1590.

Renwick, J.A.A. 1967. Identification of two oxygenated terpenes from the bark beetles *Dendroctonus frontalis* and *Dendroctonus brevicomis*. Contributions to the Boyce Thompson Institute, **23**: 355–360.

Renwick, J.A.A., Hughes, P.R., and Ty, T.D. 1973. Oxidation products of pinene in the bark beetle *Dendroctonus frontalis*. Journal of Insect Physiology, **19**: 1735–1740.

Richerson, J.V., McCarthy, F.A., and Payne, T.L. 1980. Disruption of southern pine beetle infestations with frontalure. Environmental Entomology, **9**: 90–93.

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

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

Renwick, J.A.A. and Vité, J.P. 1970. Systems of chemical communication in *Dendroctonus*. Contributions to the Boyce Thompson Institute, **24**: 283–292.

Roe, A.L. and Amman, G.D. 1970. The mountain pine beetle in lodgepole pine forests. Research Paper INT-71. United States Department of Agriculture Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah, United States of America. Pp. 1–23.

Ross, D.W. and Daterman, G.E. 1998. Pheromone-baited traps for *Dendroctonus pseudotsugae* (Coleoptera: Scolytidae): influence of selected release rates and trap designs. Journal of Economic Entomology, **91**: 500–506.

Ross, D.W. and Niwa, C.G. 1997. Using aggregation and antiaggregation pheromones of the Douglas-fir beetle to produce snags for wildlife habitat. Western Journal of Applied Forestry, **12**: 52–54.

Rudinsky, J.A. 1973a. Multiple functions of the Douglas fir beetle pheromone 3-methyl-2-cyclohexen-1-one. Environmental Entomology, **2**: 579–585.

Rudinsky, J.A. 1973b. Multiple functions of the southern pine beetle pheromone verbenone. Environmental Entomology, **2**: 511–514.

Safranyik, L., Shrimpton, D.M., and Whitney, H.S. 1974. Management of lodgepole pine to reduce losses from the mountain pine beetle. Canadian Forest Service Technical Report 1. Canadian Forest Service, Victoria, British Columbia, Canada. Pp. 1–25.

Salom, S.M., Billings, R.F., Upton, W.W., Dalusky, M.J., Grosman, D.M., Payne, T.L., *et al.* 1992. Effect of verbenone enantiomers and racemic *endo*-brevicomin on response of *Dendroctonus frontalis* (Coleoptera, Scolytidae) to attractant-baited traps. Canadian Journal of Forest Research, **22**: 925–931.

Schlyter, F., Byers, J.A., and Löfqvist, J. 1987. Attraction to pheromone sources of different quantity, quality, and spacing: density-regulation mechanisms in bark beetle *Ips typographus*. Journal of Chemical Ecology, **13**: 1503–1523.

Schowalter, T.D., Pope, D.N., Coulson, R.N., and Fargo, W.S. 1981. Patterns of southern pine beetle (*Dendroctonus frontalis* Zimm.) infestation enlargement. Forest Science, **27**: 837–849.

Seybold, S.J. 1993. Role of chirality in olfactory-directed behaviour: aggregation of pine engraver beetles in the genus *Ips* (Coleoptera, Scolytidae). Journal of Chemical Ecology, **19**: 1809–1831.

Seybold, S.J., Bentz, B.J., Fettig, C.J., Lundquist, J.E., Progar, R.A., and Gillette, N.E. 2018. Management of western North American bark beetles with semiochemicals. Annual Review of Entomology, **63**: 407–432.

Shea, P.J., McGregor, M.D., and Daterman, G.E. 1992. Aerial application of verbenone reduces attack of lodgepole pine by mountain pine beetle. Canadian Journal of Forest Research, **22**: 436–441.

Shepherd, W.P. and Sullivan, B.T. 2013. Southern pine beetle, *Dendroctonus frontalis*, antennal and behavioral responses to nonhost leaf and bark volatiles. Journal of Chemical Ecology, **39**: 481–493.

Shepherd, W.P. and Sullivan, B.T. 2017. Spatial displacement of a lure component can reduce catches of two nontarget species during spring monitoring of southern pine beetle. Journal of Insect Science, **18**: 1–4. Available from https://www.fs.usda.gov/treesearch/pubs/55622 [accessed 5 September 2020].

Shepherd, W.P. and Sullivan, B.T. 2018. Southern pine beetle (Coleoptera: Curculionidae: Scolytinae) pheromone component *trans*-verbenol: enantiomeric specificity and potential as a lure adjuvant. Environmental Entomology, **48**: 193–201.

Shore, T.L., Safranyik, L., Hawkes, B.C., and Taylor, S.W. 2006. Effects of the mountain pine beetle on lodgepole pine stand structure and dynamics. *In* The mountain pine beetle: A synthesis of biology, management and impacts on lodgepole pine. *Edited by* L. Safranyik and B. Wilson. Canadian Forest Service, Victoria, British Columbia, Canada. Pp. 94–114.

Smith, M.T., Salom, S.M., and Payne, T.L. 1993. The southern pine bark beetle guild: a historical review of the research on the semiochemical-based communication system of the five principal species. Virginia Agricultural Experiment Station Bulletin, **93–94**: 1–106.

Staeben, J.C., Sullivan, B.T., Nowak, J.T., and Gandhi, K.J. 2015. Enantiospecific responses of southern pine beetle (*Dendroctonus frontalis*) and its clerid predator, *Thanasimus dubius*, to α-pinene. Chemoecology, **25**: 73–83.

Stephen, F.M. and Lih, M.P. 1985. A *Dendroctonus frontalis* infestation growth model: organization, refinement, and utilization. *In* Proceedings, integrated pest management research symposium. *Edited by* S.J. Branham and R.C. Thatcher. General Technical Report SO-56. United States Department of Agriculture Forest Service, Southern Forest Experiment Station, New Orleans, Louisiana, United States of America. Pp. 186–194.

Strom, B.L. and Clarke, S.R. 2011. Use of semiochemicals for southern pine beetle infestation management and resource protection. *In* Southern Pine Beetle II. *Edited by* R.N. Coulson and K.D. Klepzig. General Technical Report SRS-140. United States Department of Agriculture Forest Service, Southern Research Station, Asheville, North Carolina, United States of America. Pp. 381–397.

Strom, B.L., Clarke, S.R., and Shea, P.J. 2004. Efficacy of 4-allylanisole-based products for protecting individual loblolly pines from *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae). Canadian Journal of Forest Research, **34**: 659–665.

Strom, B.L. and Goyer, R.A. 2001. Effect of silhouette color on trap catches of *Dendroctonus frontalis* (Coleoptera: Scolytidae). Annals of the Entomological Society of America, **94**: 948–953.

Strom, B.L., Goyer, R.A., and Hayes, J.L. 1995. Naturally occuring compound can protect pines from the southern pine beetle. Louisiana Agriculture, **38**: 5–7.

Strom, B.L., Roton, L.M., Goyer, R.A., and Meeker, J.R. 1999. Visual and semiochemical disruption of host finding in the southern pine beetle. Ecological Applications, **9**: 1028–1038.

Strom, B., Smith, S., and Brownie, C. 2013. Attractant and disruptant semiochemicals for *Dendroctonus jeffreyi* (Coleoptera: Curculionidae: Scolytinae). Environmental Entomology, **42**: 323–332.

Sullivan, B.T. 2005. Electrophysiological and behavioral responses of *Dendroctonus frontalis* (Coleoptera: Curculionidae) to volatiles isolated from conspecifics. Journal of Economic Entomology, **98**: 2067–2078.

Sullivan, B.T. 2011. Southern pine beetle behavior and semiochemistry. *In* Southern Pine Beetle II. *Edited by* R.N. Coulson and K.D. Klepzig. General Technical Report SRS-140. United States Department of Agriculture Forest Service, Southern Research Station, Asheville, North Carolina, United States of America. Pp. 25–50.

Sullivan, B.T. 2016. Chapter Four. Semiochemicals in the natural history of southern pine beetle *Dendroctonus frontalis* Zimmermann and their role in pest management. Advances in Insect Physiology, **50**: 129–193.

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

Sullivan, B.T., Dalusky, M.J., Mori, K., and Brownie, C. 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. Journal of Chemical Ecology, **37**: 403–411.

Sullivan, B.T., Dalusky, M.J., Wakarchuk, D., and Berisford, C.W. 2007a. Field evaluations of potential aggregation inhibitors for the southern pine beetle, *Dendroctonus frontalis* (Coleoptera: Curculionidae). Journal of Entomological Science, **42**: 139–149.

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

Sullivan, B.T., Pettersson, E.M., Seltmann, K.C., and Berisford, C.W. 2000. Attraction of the bark beetle parasitoid *Roptrocerus xylophagorum* (Hymenoptera: Pteromalidae) to host-associated olfactory cues. Environmental Entomology, **29**: 1138–1151.

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

Thatcher, R.C. and Pickard, L.S. 1964. Seasonal variations in activity of the southern pine beetle in east Texas. Journal of Economic Entomology, **57**: 840–842.

Thistle, H.W., Peterson, H., Allwine, G., Lamb, B., Edburg, S., and Strom, B. 2005. The influence of stand thinning on surrogate pheromone plumes. *In* Proceedings, 16th US Department of Agriculture interagency research forum on gypsy moth and other invasive species 2005. *Edited by* K.W. Gottschalk. General Technical Report NE-337. United States Department of Agriculture Forest Service, Newtown Square, Pennyslvania, United States of America. Pp. 83–85.

Tilden, P.E., Bedard, W.D., Lindahl, K.Q., Jr., and Wood, D.L. 1983. Trapping *Dendroctonus brevicomis*: changes in attractant release rate, dispersion of attractant, and silhouette. Journal of Chemical Ecology, **9**: 311–321.

United States Environmental Protection Agency. 1999. Notice of pesticide registration, Verbenone, Reg. No. 56261–3, 6 December 1999. Available from https://www3.epa.gov/pesticides/chem_search/ppls/056261–00003–19991206.pdf [accessed 10 October 2020].

United States Environmental Protection Agency. 2001. Notice of pesticide registration, 4-allyl anisole, Reg. No. 72098–4, 28 September 2001. Available from https://www3.epa.gov/pesticides/chem_search/ppls/072098–00004–20010928.pdf [accessed 10 October 2020].

Vité, J.P. 1970. Pest management systems using synthetic pheromones. Contributions to the Boyce Thompson Institute, **24**: 343–350.

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

Vité, J.P. and Crozier, R.G. 1968. Studies on the attack behavior of the southern pine beetle. IV. Influence of host condition on aggregation pattern. Contributions to the Boyce Thompson Institute, **24**: 87–93.

Vité J.P. and Francke W. 1976. The aggregation pheromones of bark beetles: progress and problems. Naturwissenschaften, **63**: 550–555

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

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

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

Wood, S.L. 1982. The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. Great Basin Naturalist Memoirs, **6**: 1–1359.

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