

Repellent semiochemical solutions to mitigate the impacts of global climate change on arthropod pests

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15.1 Introduction

In the millennia-long rivalry for resources between humanity and pestiferous arthropods, the arthropods appear to have gained a significant advantage in present times from the same phenomenon at the heart of so many of today's greatest challenges: the effects of global climate change. Populations of arthropods harmful to human interests, such as pests that feed on food and fiber crops and vectors that transmit disease, have responded to increasing average temperatures in a variety of ways, many of which exacerbate negative impacts. The mosquitoes responsible for the transmission of blood-borne pathogens such as malaria and dengue—the world's deadliest and most common mosquito-transmitted diseases—are steadily expanding their ranges into regions that were once ecologically unsuitable for them (Ellis, 2019; Ryan et al., 2019). In the United States, *Ae. aegypti* (L.), the yellow fever mosquito (which also transmits a variety of other pathogens, including the causal agents of dengue, chikungunya, and Zika) has spread north at an annual rate of approximately 240 km over the last half-decade, while the Asian tiger mosquito, *Ae. albopictus* (Skuse), has expanded its range northward in Europe by around 150 km per year (Kraemer et al., 2019; Yale School of the Environment, 2019). Should these trends continue, by 2050, populations of *Ae. aegypti* could be found in such northerly cities as Shanghai and Chicago, placing nearly half (49%) of the global human population at risk from the diseases carried by these vectors (Kraemer et al., 2019; Yale School of the Environment, 2019). Mosquitoes are also likely to move into higher altitudes as average temperatures rise, opening opportunities for mosquito-borne diseases like malaria to reemerge in urban environments such as Mexico City, where malaria was eradicated decades ago (Reiter, 2001). In addition to these expansions in range, warmer temperatures and higher levels of carbon dioxide in the atmosphere contribute to increased health

threats from mosquitoes by increasing rates of evolution, and thus speciation, as well as changes to seasonal dynamics such as extending breeding seasons, creating more robust and diverse populations with higher density (Tang et al., 2018; Pope, 2019). According to Ryan et al. (2019), the net increase in people threatened by exposure to *Aedes*-transmitted pathogens over the next century could be as high as 1 billion, with most new cases likely to occur in Europe and tropical and subtropical high-elevation regions.

Productivity and sustainability of agriculture and forestry resources also face increasing threats from arthropod pests as the world grows warmer. North American forests, already threatened by more frequent, severe, and larger wildfires, such as those consuming the state of California at the time of this writing (October 2020) (Higuera and Abatzoglou, 2021), are suffering increasing tree mortality due to bark beetle outbreaks of unprecedented scale in some forest systems (Vose et al., 2018). Warmer temperatures foster longer, more intense periods of drought, which in turn reduce trees' vigor and capacity to defend themselves against many wood-boring insects (Freeman, 2017; Mietkiewicz et al., 2018; Negrón and Popp, 2018), while simultaneously promoting conditions favorable to wood-boring beetle outbreaks, accelerating insect development (Negrón and Popp, 2018), extending flight periods (Lill, 2019; Puikkonen, 2019), increasing overwintering survival (Miller and Werner, 1987; Hart et al., 2017), and even producing larger beetles and larger populations of fertile female beetles (Puikkonen, 2019). One of the world's most valuable tropical crops, coffee, is expected to suffer higher infestation rates from its chief insect pest, the coffee berry borer (CBB), *Hypothenemus hampei* Ferrari, as global temperatures rise, expanding the range of the insect and increasing the number of generations produced over each coffee crop season (Jaramillo et al., 2009, 2011).

At the same time that these challenges are emerging, effective management tools for

destructive arthropods are becoming scarce. Conventional chemical insecticides have formed the backbone of arthropod control for much of the last century, for both public health and agricultural applications. In recent decades, however, ample evidence has arisen to indicate that unrestricted pesticide use is technically, environmentally, and culturally unsustainable. Because arthropods reproduce so rapidly and in such large numbers, they are readily capable of responding to selective pressures in their environment, including evolving tolerances to chemical agents applied to suppress their populations. Applications of even the most effective pesticides lose their effectiveness over time as natural selection confers physiological or behavioral resistance to the chemical active ingredient (AI) (Martini et al., 2012; Mota-Sanchez and Wise, 2021). One particularly alarming instance of this phenomenon is the increasing frequency of mosquito resistance to pyrethroids, a group of synthetic insecticides designed to mimic the biological activity of pyrethrins, found naturally in chrysanthemum flowers (Bond et al., 2014). Pyrethroids have played a critical role in vector control since the 1970s (Kupferschmidt, 2016). They are the only insecticides approved for use in long-lasting insecticide-treated bed nets and the primary agent used in indoor residual insecticide sprays, both of which tactics are pillars of the World Health Organization's (WHO) global strategy to eliminate malaria (World Health Organization, 2015; Larson et al., 2016). In 2012, the WHO estimated that if pyrethroids were to lose most of their efficacy, 55% of the benefits of vector control would be lost (World Health Organization, 2012). Pyrethroid resistance was rarely observed until the last decade when cases began to appear across Africa with alarming speed (Kupferschmidt, 2016); in 2018, the WHO reported widespread resistance in the sub-Saharan countries most impacted by malaria (World Health Organization, 2018).

Public acceptance of conventional pesticide use has declined over recent decades. Many

insecticidal chemicals have been linked to a range of health and environmental risks, particularly older classes with neurotoxic modes of action, such as organochlorine, organophosphate, and carbamate insecticides. Regulations regarding the use of these chemicals on crops have generally tightened globally in the last few decades, with lower tolerances for maximum pesticide residues exported produce, mandated delays between pesticide application and entry of workers into treated fields, and even total bans on some chemistries. For example, the chlorinated cyclodiene pesticide, endosulfan, was once one of the most effective tools available to coffee growers seeking to manage CBB (Ingram, 1968; Vega et al., 2015) but has since been banned in 70 countries, including Brazil, the United States, and the member states of the European Union, on account of its negative environmental impacts and the threat its continued use would pose to agricultural workers (U.S. Environmental Protection Agency, 2010; European Commission, 2016). Nonselective chemical insecticide applications also can lead to the emergence of other pest problems. Thacker (2002) estimated that approximately half of the arthropod species that are currently considered pests only emerged as pests as a result of unintended effects of insecticide usage, such as the removal of predators and other natural enemies that would otherwise have acted as a natural check against such secondary outbreaks.

Considering the hazards and limitations of traditional pest control methods and the growing challenges presented by a warming world, there is a clear need to develop more lastingly effective, safe, and sustainable strategies to mitigate the impacts of harmful insects on human health and prosperity. This chapter will discuss three cases of a method of insect control that does not rely on traditional pesticides to reduce impacts: pheromone- or semiochemical-based repellents to protect agricultural and forestry resources. While repellents have been broadly used to protect people from hematophagous arthropods

(ticks, mosquitoes, other biting flies), their commercial use in agriculture and forestry is comparatively rare. The technologies described herein demonstrate the feasibility of agricultural and/or forestry pest management by means of semiochemical-based repellents in situations made more challenging or likely to become more frequent as climate change continues to reshape ecosystems around the world. *CBB Repel* is a repellent designed to deliver effective, long-lasting control of CBB in coffee plantations. CBB Repel can be applied alone or in combination with strategic insecticide applications, where the volatiles of the spatial repellent flush the insects out of the interior of the coffee berries where they feed and breed, making them more susceptible to pesticide treatments. Adoption of CBB Repel could help coffee growers to cope with the increasing populations of CBBs fostered by warming climates in tropical and subtropical regions. *SPLAT Verb* contains the bark beetle antiaggregation pheromone verbenone in a viscous thixotropic fluid matrix that increases in firmness following application, which when applied to the bark of pine trees protects them and their neighboring trees from colonization by host-seeking mountain pine beetle (MPB), *Dendroctonus ponderosae* Hopkins. This product has been tested in multiple pine species and multiple locations in the Western United States, including high-altitude stands of whitebark pine, *Pinus albicaulis* Engelmann, a critical tree species in North American mountain ecosystems that is being threatened by climate-driven changes. *Beetle Guard*, utilizing semiochemical repellents, has applications in both forestry and agriculture, as it has been developed to prevent attack by multiple species of ambrosia beetles known to colonize a broad range of tree species that include endangered or ecologically important species and specialty food crops. The redbay ambrosia beetle (RAB), *Xyleborus glabratus* Eichhoff, for example, is a serious threat to the native Lauraceae species that characterize coastal forests of the Southeastern United States and has

also severely impacted the avocado industry in Florida.

15.2 Coffee berry borer, *Hypothenemus hampei* (Ferrari)

15.2.1 Background

Coffee is the world's most widely consumed beverage and the most valuable export crop produced in the tropics (Davis et al., 2012). Globally, the coffee industry is worth over 100 billion USD a year and supports the livelihoods of roughly 100 million people (Bunn et al., 2015; Davis et al., 2019; Schiffman, 2019). Two main species are cultivated: Arabica coffee, *Coffea arabica* (L.), and robusta coffee, *C. canephora* (Pierre ex A. Froehner), with Arabica being the chief crop grown, accounting for 60%–70% of the world's commercial production (Davis et al., 2012). Both species originated and flourished in the humid forests of Africa (Davis et al., 2006) but are currently grown in 80 countries over an area of >10 million ha (FAOSTAT, 2014). A third species, *C. liberica* (Bull ex Hiern), is grown around the world, but this crop is used almost exclusively as grafting rootstock for Arabica and robusta coffee rather than for actual bean production (Davis et al., 2019). The majority of commercially traded coffee, around 70%, is produced on farms ≤2 ha in size, partly because of the high-altitude environment required for Arabica beans to thrive, which renders larger-scale growing operations impossible (Davis et al., 2019; Knowledge@Wharton, 2019).

In terms of crop productivity, coffee has proven to be highly sensitive to changes in climate. The ideal mean annual temperature range for Arabica has been estimated at 18–24°C, depending on the location (Alègre, 1959; Teketay, 1999; Davis et al., 2012). Temperatures above 30°C, if sustained for too long, can severely stress the crop, slowing its growth and creating such defects as stem tumors and yellowing of the leaves (Franco, 1958; Davis et al., 2012).

Accelerated fruit development also occurs at higher than optimal temperatures, reducing the quality of the beverage produced from the brewing of the ground beans (Camargo, 1985; Davis et al., 2012). This presents an uncertain future for the coffee industry in many locations, as the Intergovernmental Panel on Climate Change estimates that average global temperatures will increase by at least 1.8°C and as much as 4°C by 2100 (IPCC, 2007; Davis et al., 2012). Such an increase will impact coffee production in a variety of ways, including causing more frequent extreme weather events (i.e., heat waves or frosts, floods, or droughts) that are detrimental to crop quality and productivity (Conde et al., 2006; Gay et al., 2006). In Veracruz, Mexico, for example, where coffee is grown on over 153,000 ha by 67,000 producers, winter frosts led to nearly complete destruction of coffee plants in 1970 (Gay et al., 2006). Because of the limited range of geographies and conditions over which coffee can be cultivated properly, climate-driven challenges may affect large proportions of the market simultaneously, limiting or disabling supply chains and driving coffee prices up (Worland, 2018). Wild *Coffea* species are also threatened by these changes, with an estimated 60% (75 out of 124 identified species) currently at risk of extinction (Knowledge@Wharton, 2019). While these species are not commercially cultivated for coffee production, coffee growers rely on the genetic diversity of wild plants for cross-breeding, to make their crops more resistant to drought, pests, or disease, which is ever more critical in the face of growing variability in conditions (Knowledge@Wharton, 2019). The drying up of this genetic reservoir could therefore make Arabica and robusta crops more susceptible to these stresses, while at the same time warmer temperatures enable fungal diseases such as stem rust to thrive (Knowledge@Wharton, 2019). These collective impacts are projected to cut the global land area capable of producing coffee by half across all scenarios (Schiffman, 2019). In some areas, such as the

Colombian mountain region, these changes are already underway. Cultivated coffee area in this region has decreased by 20% since the 1990s, with almost 40,500 ha (4% of the total area) lost in an 18-month span (2018–2019) (Schiffman, 2019). Daylight hours have been shortened by 19% as cloud cover has increased, which in some cases has hindered coffee productivity, and extremes in precipitation and outbreaks of insect pests and fungal diseases have become more common (Schiffman, 2019).

The CBB, is the most damaging pest on coffee worldwide; indeed, it is the only organism in the world known to feed solely on coffee beans (Fig. 15.1A–D). This feeding behavior is enabled by the presence of gut bacteria that detoxify caffeine (1,3,7-trimethylxanthine), a purine alkaloid that is both distasteful and toxic to most herbivorous insects, and also break down the large carbohydrate molecules that comprise coffee berries (Ceja-Navarro, 2015; Vega et al., 2015). Infestation of a coffee berry is typically initiated by a single individual, a founder female beetle, which bores into the endosperm of the berry starting around 8 weeks after crop flowering and continuing to the harvest (Centre for Agriculture and Biosciences International, 2016). She creates galleries within the berry in which she lays 2–3 eggs daily for a period of 20 days, but she does not leave the berry after this oviposition period has ended, remaining within the fruit to tend her brood (University of Hawaii, 2018). After hatching, CBB larvae also feed on the endosperm and at maturity practice sibling mating. Female beetles, more common than males at a ratio of 10:1 (Waterhouse and Norris, 1989; Baker et al., 1992), leave their berry of origin ready to infest other berries and begin rearing their own young, while males never leave the berry (Centre for Agriculture and Biosciences International, 2016). Each infested berry may contain up to 100 CBB spanning three generations, and reproduction continues even after berries have dropped to the ground, making these berries a major source of continuing infestation of the crop (Centre for

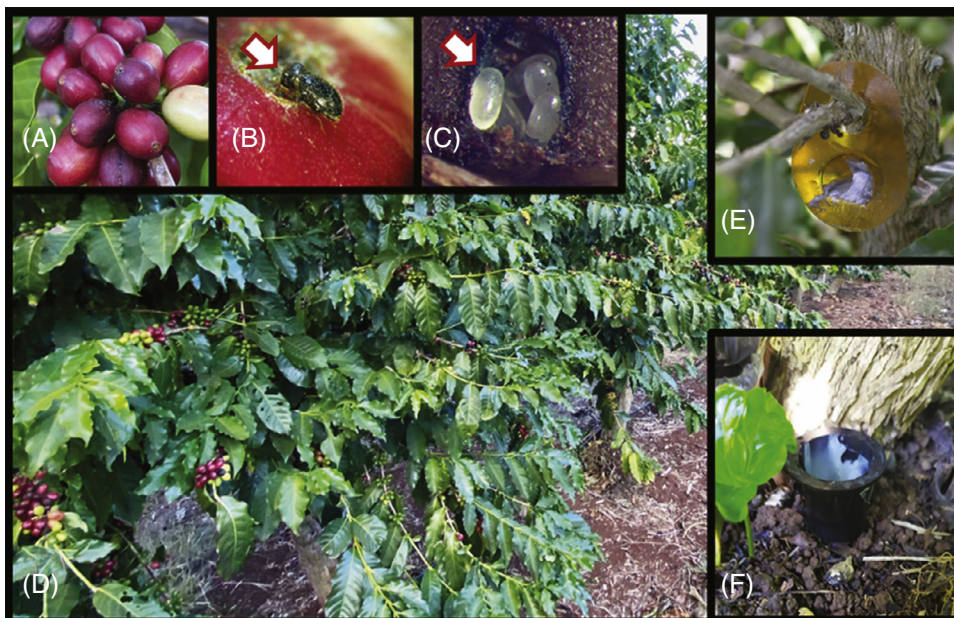


FIG. 15.1 (A) Coffee beans susceptible to the attack of (B) adult female coffee berry borers, *Hypothenemus hampei*, that penetrate the bean and (C) oviposit, creating new foci of CBB infestation in the field (D). Frequently, each infected coffee bean hosts a multigenerational colony of CBB that is well protected from predators, external pesticide applications, and potential desiccation. The use of CBB Repel in the field induces female CBB to leave infested coffee beans, exposing themselves to these dangers in the environment. Furthermore, CBB Repel seems to reduce the likelihood that CBB females will deposit eggs in the protected field. Although CBB Repel has been designed to be applied as dollops to the base of the plant and or the soil, the tests described herein used 3-g dollops of the formulation applied inside containers. CBB Repel, a gray paste, was placed as 3-g dollops inside (E) prototype plastic orange containers clipped to the coffee branches or (F) black plastic containers placed on the ground at the base of the plant. Credits: (A and D) Mafra-Neto; (B and C) Wright; (E and F) Borges. CBB, coffee berry borer.

Agriculture and Biosciences International, 2016; University of Hawaii, 2018). One study found that 1.5–2 million CBB per ha emerged from fallen berries in Colombian coffee plantations after pruning (Byers, 1992; Baker, 1999).

Damage caused by CBB feeding on coffee berries renders the infested beans unsaleable, reduces the quality and yield of the remaining crop, and can lead to bacterial or fungal infestations and premature drop of immature berries (Sponagel, 1994; Damon, 2000; Duque, 2000; Duque-Orrego, 2002; Duque and Baker, 2003; Vega et al., 2009). Left uncontrolled, CBB infestation rates can reach 50%–100%, essentially eliminating crop yield, enabled by the pest's rapid

generation time (Le Pelley, 1968; Mathieu et al., 1999; Vega et al., 2015; Centre for Agriculture and Biosciences International, 2016). Under favorable temperatures, adult CBB can emerge in as little as 30 days, producing multiple generations in a single season (Baker et al., 1992). Global losses due to CBB infestations have generally been estimated at 500 million USD each year (Vega et al., 2003), but recent evaluations conducted in Brazil place the pest's annual impact in that country alone at 215–358 million USD (Oliveira et al., 2013; Yong, 2015), suggesting that the half-billion USD toll is likely an underestimation of CBB's real global impact. Native to Central Africa, CBB has since been introduced to every country in the

world where coffee is produced except Nepal and China, with Puerto Rico and Hawaii being the most recently infested areas (2007 and 2010, respectively) (Jaramillo et al., 2011). In the first 5 years after the pest's introduction in Puerto Rico, coffee values dropped by approximately 12.6 million USD, a 33% decrease, and 1200 coffee farms were abandoned (U.S. Department of Agriculture (USDA), 2014; Mariño et al., 2017). CBB's first appearance in Hawaii occurred on Kona Island, but it has since spread to Hawaii Island, Maui, and Oahu, putting at risk a coffee industry valued at >49 million USD in the 2015–2016 season (Hawaii Department of Agriculture website, 2017a, 2017b).

Climate change is expected to worsen the impacts of CBB on coffee. Jaramillo et al. (2009, 2011) projected that an increase in average temperatures of 1–2°C would alter CBB's geographic range, quicken the insect's development process, and increase its number of generations per season. These predictions were followed only 2 years later by reports from Tanzania that CBB had been detected at altitudes 300 m above the limit where they were detected 10 years previously (Le Pelley, 1968; Mangina et al., 2007; Jaramillo et al., 2011). The warm, dry conditions created by a La Niña event occurring in East Africa in 2011 contributed further to the problem, sparking a series of CBB infestations across the area (Jaramillo et al., 2011).

Control measures for CBB rely on cultural practices such as replacement of traditional burlap coffee bags with bags made of synthetic fiber (which are less likely to be infested by CBB), varying storage methods for harvested berries, timely pruning and removal of all unharvested berries from coffee trees and the ground, and proper sanitation in processing mills (Department of Agriculture, State of Hawaii, 2014; Centre for Agriculture and Biosciences International, 2016; University of Hawaii, College of Tropical Agriculture & Human Resources, 2018). Like many other bark beetles, CBB is a challenging pest to manage using traditional chemical insecticides due to its

internal feeding behavior. As these beetles spend most or all of their lives within the coffee berry where they hatched, they are shielded from contact by insecticide sprays, and are only susceptible to these toxins during a limited window of time, before adult females have burrowed into the endosperm (Centre for Agriculture and Biosciences International, 2016).

Until recently, growers had two reliable weapons in their pesticidal arsenal against CBB, the organochlorine insecticide, endosulfan (6,7,8,9,10,10-hexachloro-1,5,5a,6,9,9a-hexahydro-6,9-methano-2,4,3-benzodioxathiepine-3-oxide) and the organophosphate, chlorpyrifos [0,0-diethyl 0-(3,5,6-trichloro-2-pyridinyl)-phosphorothioate] (Baker et al., 2002). Introduced in the 1950s, endosulfan possesses characteristics that make it ideal for use against CBB and led to its rapid adoption by coffee growers around the world. Rather than inducing toxicity on physical contact, this chemical exerts fumigant effects, improving its efficacy against internal-feeding CBB (Vega et al., 2015). However, the use of endosulfan for CBB management has since fallen victim to the twin banes of conventional pesticides: deregistration and development of resistance. CBB resistance to endosulfan was first reported in 1989 (Brun et al., 1989), and as data accumulated regarding its negative health and environmental impacts, governments have acted to restrict or eliminate its use (Cone, 2010). Endosulfan has been banned in 70 countries, including the United States and the member states of the EU (Lubick, 2010; U.S. Environmental Protection Agency, 2010; Janssen, 2011; European Commission, 2016). Chlorpyrifos is in the process of meeting the same fate. The pesticide was banned in Europe in April 2016, and the United States was prepared to follow suit later that year—proposing to revoke tolerances for chlorpyrifos on any crop (U.S. Environmental Protection Agency, 2016)—before reversing itself following the 2017 change in the US federal administration, though the compound has been banned for use in California by 2021. The loss of

these chemicals leaves coffee growers with a critical shortage of effective tools to manage CBB, which in some cases has translated into substantial economic losses. The ban on endosulfan in Brazil in 2013 brought an end to four decades of the pesticide's use against CBB in that country. Compounded by a heavy rain season and improperly maintained sanitation programs, this ban facilitated the largest CBB infestation in recent history in Brazil, resulting in coffee crop losses of 5%–30% (Szal, 2017).

The confluence of factors threatening the coffee industry—a changing climate creating conditions harmful to the crop and favorable to its pest, emergence of resistance to previously effective pesticides, and removal of entire classes of control agents by regulatory agencies—serves as a prime example of the challenges faced by agricultural producers in the modern age and highlights the need for more integrated, sustainable methods of arthropod pest control. Rather than continuing to rely on conventional chemical toxins to suppress or eradicate pest populations, many pest control developers have focused on the use of behavior-modifying chemicals, or semiochemicals, to reduce crop damage. Diverse semiochemical-based strategies for agricultural pest control have been developed and tested in the field: the use of attractant lures for mass trapping; the application of toxic baits in an attract-and-kill method; push–pull strategies, employing arthropod repellents to push pests away from crops and attractants to pull them toward a trap; and mating disruption, a technique that consists of the deployment of sex pheromones to interfere with male arthropods' ability to detect and orient to female mating partners. These techniques have been applied successfully in several cropping systems and against many insect pests including codling moth, *Cydia pomonella* L., tephritid fruit flies (e.g., oriental fruit fly, *Bactrocera dorsalis* Hendel, melon fruit fly, *Bactrocera cucurbitae* Coquillett, and Mediterranean fruit fly, *Ceratitis capitata* Wiedemann), and carob moth, *Ectomyelois*

ceratoniae Zeller, but the use of insect semiochemicals as repellents in agriculture is comparatively rare.

Several compounds have been evaluated for potential repellency against CBB. A blend of two volatiles produced by *Coffea* plants, (Z)-3-hexenyl acetate and (Z)-3-hexenol, was found to repel CBB adults, as was (*E,E*)- α -farnesene, a sesquiterpene produced by CBB-infested coffee berries (Borbón et al., 2000; Castro et al., 2017; Vega et al., 2017). A field trial in Hawaii revealed that application of a bubble capsule formulation of (*E,E*)- α -farnesene reduced the number of CBB captured in traps baited with standard methanol/ethanol lures by 80%, compared with traps baited with the lure alone (Vega et al., 2017). However, the compound is highly reactive and can be degraded by photochemical and air oxidation, limiting its usefulness in coffee-growing regions, which are generally characterized by intense sunlight and frequent rainfall (Anet, 1969; Spicer et al., 1993; Vega et al., 2017). Nonhost compounds from several plants, including *Lantana camara* (L.), *Allium sativum* (L.), *Capsicum frutescens* (L.), *Moringa oleifera* (Lam.), *Piper* spp., and *Tilesia baccata* (L.) Pruski, have also demonstrated some repellency to CBB (Giraldo and Valencia, 2000; Henao, 2008; Santos et al., 2010; Santoro et al., 2011; Benavides and Góngora, 2015; Castro et al., 2017), but the extracts used are expensive and have generally failed to maintain their efficacy under field conditions (Schmutterer, 1990; Gurr et al., 2004; Nicholls, 2009; Castro et al., 2017).

Verbenone [4,6,6-trimethylbicyclo [3.1.1]hept-3-en-2-one], an antiaggregation pheromone of some species of *Dendroctonus* bark beetles has been developed as a patented alternative semiochemical-based repellent for the management of CBB in coffee (Mafra-Neto et al., 2016). Antiaggregation pheromones function to prevent the influx of new colonizing beetles on a particular substrate to a degree that would be unsustainable and thus harmful to the colony's members. In the case of CBB, higher concentrations of

semiochemicals produced by larvae or emerged adults may signal overcrowding within an infested coffee berry, causing founder females to avoid that fruit (Vega et al., 2011). The antiaggregation semiochemicals of other bark beetles, including frontalin, (Z)-3-hexenol, methylcyclohexenone (3-methylcyclohex-2-en-1-one) and verbenone, have shown some degree of repellency toward CBB in several trials (Borbón et al., 2000; Vega et al., 2015; Vega, et al., 2017). A 2014 field trial in a Kenyan coffee plantation revealed that frontalin reduced CBB attraction to methanol-ethanol lures. Traps containing both the lure and frontalin captured 77% fewer CBB than traps with the lure alone (Njihia et al., 2014; Vega et al., 2017). CBB also has been shown to avoid verbenone and α -pinene, leading Jaramillo et al. (2013) to recommend intercropping coffee plants with those that produce repellent conifer monoterpenes (Vega et al., 2015). In laboratory and field trials, verbenone has been shown to act as a repellent to CBB and *Xylosandrus compactus* (Eichhoff), another beetle pest of coffee in Hawaii (Burbano et al., 2011; Jaramillo et al., 2013). To date, however, semiochemical-based repellent strategies have yet to be successfully commercialized or incorporated into area-wide control programs for CBB. The utility of insect repellents in general has often been limited by practical shortcomings, including relatively limited residual effectiveness in the field (a result of the volatility of most repellent AIs), loss of efficacy to environmental degradation, and the resulting need for frequent reapplications, challenges that would be especially daunting to coffee growers given the already high costs of their operations.

15.2.2 Repellent trials

To create a technically and commercially viable repellent for CBB in coffee, Mafra-Neto et al. (2016) incorporated verbenone into a wax-based controlled-release emulsion technology, specialized pheromone & lure application technology (SPLAT) manufactured by ISCA, Inc.,

Riverside, CA. The base SPLAT emulsion, which has been discussed at length in previous publications (Fan and Singh, 1989; Stelinski et al., 2006; Teixeira et al. 2010; Lapointe and Stelinski, 2011; Mafra-Neto et al., 2013, 2014), is a shear-thinning, thixotropic fluid that becomes thinner and less viscous when agitated by stirring or vibration but thickens when at rest. This characteristic makes the formulation amenable to the application using a broad range of manual or mechanized equipment and allows the user to designate a desired application rate or quantity. After the point source is applied, the aqueous component of the formulation evaporates, leaving the active components (AIs, additives incorporated to stabilize the formulation and/or refine release rates, etc.) securely attached to the application surface. Most SPLAT formulations become secure and resistant to rain within 3 h of application. The release rate of an AI from SPLAT can be modulated by altering one or more of several factors of the formulation, AI, or application process, including size of the AI molecule, AI concentration, composition, proportion, and order of addition of nonactive components of the matrix, temperature at varying stages of the formulation process, and size of the point source. Most SPLAT-based products developed to date have an active field life ranging from 2 weeks to 6 months.

Trials with CBB Repel (Fig. 15.1E and F) began with a series of laboratory assays to assess the response of CBB adults to varying doses of a prototype SPLAT formulation containing 20% verbenone: 0.1, 0.25, 0.5, 1.0, and 3.0 g (four replicates per dose). Ten coffee berries infested with a known number of beetles were placed in a Petri dish or watch glass in the center of a 50-L plastic container filled with soapy water to a depth of 5 cm. Containers were placed ≥ 20 m away from each other to prevent cross-contamination of any volatiles emerging from the prototype repellent, and each container was covered with a fabric net to prevent insects from escaping. Point sources of CBB Repel were applied in

a small plastic holder affixed to the side of the 50-L container. Each container was checked for emergence of CBB from infested berries at 5, 15, and 30 min and 2, 5, 10, and 22 h after the start of the bioassay. Exposure to CBB Repel caused CBB to dislodge from the inside of the bean; after 22 h, significantly more adults emerged from fresh berries exposed to 0.1 g and 0.25 g doses than the control.

These results suggested an interesting mechanism by which CBB Repel might be used to reduce the impacts of CBB on coffee crops. The repellent could be applied at an appropriate interval before a planned insecticide application to flush the beetles out from the berries, increasing their exposure to the toxins and making pest suppression interventions more efficacious and efficient. Even in the absence of such insecticide treatment, exiting coffee berries would likely reduce the survival of female adult beetles simply by exposing them to the hazards of the environment (e.g., predation, microbial pathogenic infection, dehydration, or starvation) as a result of exposure to CBB Repel. Such a repellent might also dissuade female CBB from ovipositing in fruit in an area treated with verbenone, further reducing crop damage. To determine whether the effects observed in the lab could be induced at larger scales outside a contained environment, preliminary field trials were conducted in areas of Brazil experiencing high CBB pressure. In the first of these trials, a set of 10 × 10-m plots were randomly assigned to receive either no treatment (control) or a single application of CBB Repel. Rates of damage to coffee berries were assessed in each plot, revealing that treatment with CBB Repel significantly lowered berry damage in treated plots after 60 and 90 days compared to untreated control to a similar degree as treatment with chlorpyrifos.

However, because these data showed relatively low infestation rates across the experimental area (both treatment and control plots), limiting the certainty of any conclusions regarding the efficacy of the repellent, a second field

trial was performed in coffee plantations (Red Catuai variety) at Alegre/ES region (20° 46' 03" S, 41° 35' 23" W, elevation 687 m). Replicates were set up in a block design with six 10 m × 10 m² plots per block, and each plot spaced at least 25 m apart within the block. Four treatments were installed: (1) CBB Repel, (2) CBB Repel + chlorpyrifos, (3) chlorpyrifos, and (4) control. Ten 3-g point sources of CBB Repel were placed in the top half of the coffee plant once at the beginning of the trial. Positions of each treatment within a block were randomly selected. To evaluate the efficacy of each treatment, a monitoring trap (baited with 200 mL of 1:1 methanol: ethanol) was placed in the center of each plot and checked every 2 weeks for CBB captures. Chlorpyrifos was applied via backpack sprayer 1–3 days after trap installation and reapplied every 2 weeks until the end of the trial. Coffee berries were sampled 15 days after experimental setup and collected on a monthly basis thereafter. One hundred randomly selected coffee berries from 20 randomly selected plants were collected in each plot and evaluated for larval and adult infestation. Treatments remained in place until the end of the season when the crop was harvested. No significant difference was observed in CBB infestation rate (number of insects detected in damaged fruit) or percentage of berry damage among any of the evaluated treatments for the first, second, and third months of the trial. In the fourth month, however, coffee berries in plots treated with CBB Repel with or without chlorpyrifos had significantly fewer insects within damaged fruit than control plots. There were no significant differences among CBB Repel, CBB Repel + chlorpyrifos, and chlorpyrifos alone in the number of insects within damaged fruit. Coffee berries in plots containing CBB Repel, CBB Repel + chlorpyrifos, and chlorpyrifos alone displayed significantly less damage than control plots. No significant differences were observed in damage rate among CBB Repel, CBB Repel + chlorpyrifos, and chlorpyrifos alone. These data suggest

that the CBB Repel prototype applied a single time at the beginning of the season has the same suppressive effect on CBB field populations and coffee berry damage as a biweekly chlorpyrifos spray regimen sustained throughout the season and that CBB Repel retains its capacity to alter female beetles' behavior for a period of at least 90 days in the field.

Following some adjustments to the formulation to improve flowability, rainfastness, repellency, and field longevity, Borges et al. proceeded to evaluate CBB Repel in a series of field trials representing a range of severity levels in CBB infestation, with or without additional insecticide treatments (personal communication, unpublished results). Two experimental areas, 2.7 and 4.5 ha in size, were selected in Cabo Verde, Minas Gerais, Brazil, to represent midlevel infestations based on monitoring for CBB infestation in fruit, while a third (Serrana, São Paulo; 1.8 ha) and fourth area (Arceburgo, Minas Gerais; 5.25 ha) represented low and high infestation scenarios. Three treatments were evaluated at each site: (1) CBB Repel alone, with no additional insecticide applications; (2) CBB Repel with a single application of chlorpyrifos, 3–5 days after the repellent application; and (3) control, represented by the grower's standard insecticide regime for CBB. Four replicates were made per treatment, with one replicate in each experimental area (Area 1 plots: 0.9 ha; Area 2 plots: 1.5 ha; Area 3 plots: 0.6 ha; Area 4 plots: 1.8 ha). For both treatments using CBB Repel, 3 kg of the formulation was applied per ha, distributed in point sources of 3 g each (1000 point sources per ha), contained within a plastic dispenser pinned on a branch in the middle of the coffee plant. This was done to preclude any damage to the crop, as some trials with CBB Repel prototypes have shown some phytotoxic effects when applied directly to plant leaves. CBB Repel was applied in November during the period between the blooming of the crop and the greening of the coffee beans ('*chumbinho*' stage). No reapplications were made throughout

the trial period, which continued until the harvest. The effect of each treatment was assessed by dissecting 200 fruits randomly sampled from each plot and inspecting them for signs of CBB-induced damage, starting 15 days after treatment application and continuing monthly. Sampling took place on December 19, 2016, January 3, February 6, March 6, April 10, and May 6, 2017.

In Experimental Area 3, characterized by the lowest CBB-infestation rate of any site used in this trial, no significant difference was observed in the percentage of damaged fruit among the three treatments. Fruit damage was relatively low at this site, likely correlated to the sparse presence of the pest, ranging from 0.5% to 1.5%. Treatment effects were clearer at the sites experiencing higher infestation rates. In Areas 1 and 2, characterized by midlevel pest pressure, and in Area 4, the high-level infestation site, treatment with CBB Repel suppressed crop damage below the rate of damage detected in plots treated with the grower's standard insecticide regime. No significant difference was observed in the level of crop damage reduction between plots treated with CBB Repel alone and those treated with a combination of CBB Repel and chlorpyrifos, except in Area 4, where the latter treatment appeared more effective in reducing damage. This suggests that interventions using CBB Repel alone effectively suppress CBB crop damage in the field. The largest reduction in damage observed with the use of CBB Repel over the course of the trial was 8%, which at the contemporaneous price of raw coffee fruit (Hawaii, 2016/2017), would translate into a gross financial gain for the grower of nearly 2300 USD per ha.

In addition to the trials conducted in Brazil, CBB Repel has also been tested in Hawaiian coffee plantations in collaboration with Dr. Mark Wright's Insect Ecology and Integrated Pest Management Laboratory (University of Hawaii at Manoa). In June of 2019, a field trial was installed on two orchards at Dole Coffee

Plantations, Haleiwa, Oahu, comprising a total of 50.6 ha, separated by a distance of 1 km. These orchards had rows running in rough alignment with an N-S parallel, with standard planting distances. Trees were 2–3 m tall at the start of the trial. CBB Repel was applied on a grid pattern, with one 25-g point source applied to the trunk of a tree (1.5 m above the ground) every second row, with five treated trees in each row. This produced a treated area of approximately 40 × 38 m. Control plots under grower's best CBB pest control practices were established at the same size, located at least 11 m upwind from the treatment blocks. Eight CBB traps baited with a methanol-ethanol lure were installed at even spacing in each treated area (four traps per plot, two on one border, and two in the middle row). Thirty trees in the middle three rows of each treatment or control block were randomly selected for sampling, and one fruit-bearing branch per tree was subsampled. For each of these branches, all coffee fruit present were counted and classified as "attacked" or "not attacked" by CBB. Assessments of CBB trap captures and fruit evaluations were made every 2 weeks, with traps emptied and all captured insects transported to the laboratory for counting.

Although there was no significant difference in the numbers of CBB captured in traps (Treatment mean = 214.8 per trap; Control mean = 453.9 per trap, $F_{7,8} = 1.21$, $P = .39$) there were differences in the rate of berry infestation across the treatments. As with the previous trials, CBB Repel-treated plots exhibited significantly lower rates of berry infestation than control plots ($F_{1;1} = 171.36$, $P < .0001$). Rate of CBB infestation increased significantly over the duration of the trial ($F_{6;6} = 13.52$, $P < .0001$) but remained consistently lower in the CBB Repel treatment blocks than in the control. Some caution should be exercised in interpreting these results, as individual trees in each block were treated as replicates, rather than using means of infestation levels per block,

which may have resulted in an underestimation of error. However, the patterns appear to be robust, with 2021 field results corroborating these trends.

15.2.3 Future directions

The effects of global climate change are making profitable coffee production more challenging on multiple fronts. Higher temperatures, if sustained for too long during the growing season, can stress coffee plants and reduce the quality of the crop. The warming climate is driving wild *Coffea* species—which provide cross-breeding stock vital to maintaining the health and resilience of *Coffea arabica* crops—to extinction and creating favorable conditions for diseases such as stem rust and insect pests such as CBB. The ban on endosulfan in many geographies and the tenuous regulatory status of chlorpyrifos has exacerbated the latter threat by creating a shortage of viable control options for CBB in coffee. These challenges will be particularly difficult to deal with for the small-holder farms (≤ 2 ha) that comprise the majority (~70%) of the coffee industry, a fact that is illustrative of a general trend in the socio-economic consequences of climate change: The worst of these impacts tend to fall heaviest on those of lower economic status who have the fewest resources to draw on to cope with them.

CBB has been shown to respond well to certain spatial repellent compositions. The studies reported here demonstrate that a strategy using CBB Repel, alone or in combination with traditional pesticide sprays, can effectively reduce crop damage inflicted by CBB. While the application of a "flush and kill" strategy—applying CBB Repel to drive the beetles out of the coffee berries where they live, feed, and breed, to make them more vulnerable to insecticide treatment—requires further evaluation in the field, this approach holds the potential not only to improve the efficacy of CBB control but also to enable more precise, targeted pesticide

applications, reducing the amount of toxic chemical applied in the field over the course of a growing season. As the agronomic use of CBB Repel is being assessed under different conditions and geographies, its developers have commenced the registration of the product with the US EPA and in other countries of interest. Product launch of CBB Repel is expected to take place in key coffee-growing geographies starting in the next few years.

15.3 *Dendroctonus* bark beetles: mountain pine beetle, southern pine beetle, Douglas-fir beetle, and spruce beetle

15.3.1 Background

North American forests have had a difficult time of it lately, to put it mildly. At the peak of the fire season in the late summer and early fall of 2020, there were >8200 wildfires burning across California alone, consuming over 1.6 million ha of forest—more than double the previous record set in 2018—killing 31 people, forcing >96,000 to evacuate, and destroying >8400 structures (as of October 7, 2020) (Peñaloza, 2020; Stelloh, 2020). Factors contributing to these destructive events include the years-long drought affecting the area, a particularly dry 2019/2020 winter, an abundance of fuels resulting from 100 years of fire suppression programs, record heat waves, and a series of freak lightning storms accompanied by little to no rain (Rogers, 2020; Stelloh, 2020). All available data indicate that these challenges to forest health, diversity, and productivity are expected to continue for the foreseeable future, suggesting that the severity of the 2020 fire season across the American West may become more of the new norm (Vose et al., 2018). Since global temperatures began to be monitored and recorded in 1880, the 10 hottest years on record have all occurred since 1998 (Rogers, 2020). As this pattern continues, heat waves are expected to become more intense and more

common, and drought risk and severity are projected to increase across the Western United States, particularly in the Southwest, even as heavy precipitation and flooding become more frequent in other regions (Cook et al., 2018; Gray and Merzdorf, 2019).

In addition to these direct impacts on forest ecosystems, climate change is facilitating another threat to North American coniferous forests in the form of mass outbreaks of tree-killing bark beetles. While most bark beetle species (Coleoptera: Curculionidae) feed on dead or dying trees, several are aggressive tree killers that colonize living trees to feed on their nutritive phloem tissues and to gain a place of shelter to lay eggs and rear their brood. Conifer trees have evolved a number of natural defense mechanisms to deter attacks by wood-boring insects, specifically by producing large volumes of resin to drown or encapsulate attacking insects; and by altering the chemical composition of their tissues to release insecticidal compounds (Franceschi et al., 2005; Hain et al., 2011). Systemic resistance can also be induced so that future attacks are more easily defended against. Aggressive bark beetles, such as MPB, southern pine beetle (SPB), *Dendroctonus frontalis* Zimmerman, Douglas-fir beetle (DFB), *Dendroctonus pseudotsugae* Hopkins, and spruce beetle (SB), *Dendroctonus rufipennis* Kirby, have in turn evolved a sequence of semi-chemical-mediated mass attack behaviors to overwhelm these defenses by sheer numbers.

Following a similar trend as forest wildfires, outbreaks of aggressive bark beetles have become more common in recent decades, resulting in the deaths of billions of conifer trees over millions of ha of North American forests (Bentz et al., 2009, 2010; Mattson et al., 2019; Foote et al., 2020). Recent outbreaks of MPB (Fig. 15.2A), which attacks several North American pine species (lodgepole pine, *Pinus contorta* Douglas ex Loudon, ponderosa pine, *Pinus ponderosa* Lawson & C. Lawson, sugar pine, *Pinus lambertiana* Douglas, and whitebark pine, among others) (Furniss and Carolin, 1977; Keane, 2001; Wood

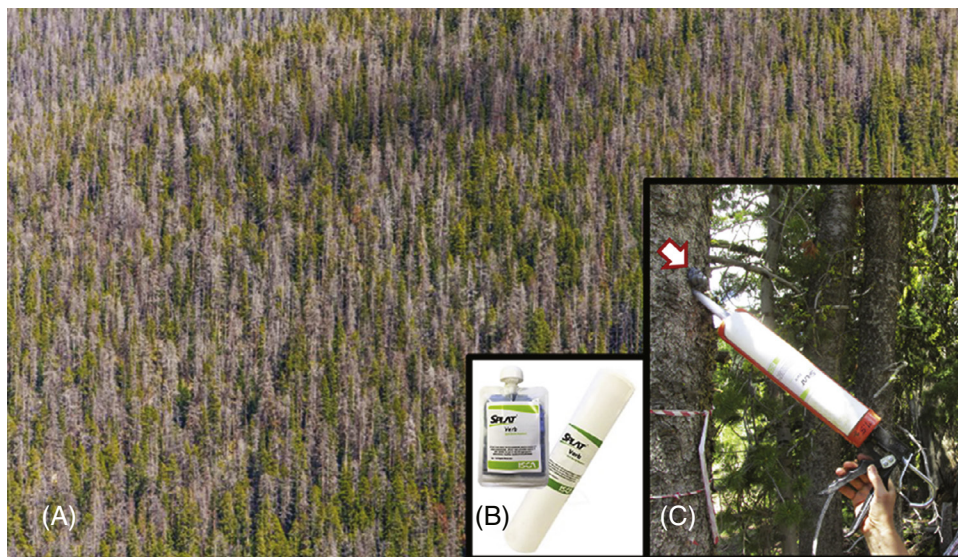


FIG. 15.2 (A) Example of a study area that has been devastated by bark beetles. SPLAT Verb can be used to protect single trees or stands of trees from attack by bark beetles repelled by verbenone. The product is sold in (B) multidose caulking gun cartridges or in a single application squeeze-bag. (C) A dollop of SPLAT Verb (indicated by white arrow) is applied directly to a tree trunk using a caulking gun. The dollop eventually biodegrades, eliminating the need for crews to return to the site to retrieve plastic pouches. Credits: (A, B) ISCA Technologies, Inc.; (C) Fettig. *SPLAT*, Specialized Pheromone & Lure Application Technology.

et al., 2003; Schwandt and Kegley, 2004), have been responsible for the loss of billions of trees across over 27 million ha of western North American forests (Fettig et al., 2020). Such outbreaks typically begin with the colonization of trees that are physically compromised, stressed by injury, overcrowding, disease, or old age, but as the density of the beetle population grows, even healthy trees may be infested. The most severe outbreak of MPB on record, occurring in Western Canada, affected over 20 million ha of pine forests (McIntosh and Macdonald, 2013; Walton, 2013; Dhar et al., 2016).

Southern pine beetle (SPB) is the most destructive pest of southern yellow pine species, particularly in forests across the southeastern United States, Mexico, and Central America (Fig. 15.3A) (Billings, 2011b). Outbreaks of this species are not only destructive on a large scale—according to USDA Forest Service estimates, over the course of eight outbreaks from

1973 to 2004, SPB caused a total of 3.57 billion USD in damage—but are also unpredictable (Waldron, 2011). SPB populations can remain low for long periods, then explode in outbreaks that kill thousands of trees and can last 2–3 years, only coming to an end when there are no suitable host trees left or environmental conditions render the affected region inhospitable to the beetles (Hain et al., 2011). Currently, the most severe impacts of SPB outbreaks are felt in the Southern United States, where ~80.9 million ha of forest is nearly a third (30%) composed of pine species susceptible to infestation by SPB. However, outbreaks have recently occurred much farther north (Guldin, 2011). Since 2010, outbreaks in New Jersey, where SPB-susceptible pitch pines, *Pinus rigida* Mill., are the dominant pine species (Crocker, 2012), have impacted ~11,000 ha of forests (Ferguson et al., 2013; Strom et al., 2015). In 2015, SPB was detected along a front >320 km long, stretching from



FIG. 15.3 (A) A pine forest infested with southern pine beetle, *D. frontalis*. The infestation is directional, expanding from the center to the borders. Attacked trees in the center are gray, dead, and defoliated, whereas canopies fade and trees show different senescent colors, from brown, red, and yellow to light green approaching the edges of the infestation. (B) SPB Repel dollop (white arrow) being applied to a pine tree. Credits: (A) Tanner; (B) Fettig. *SPB*, Southern pine beetle.

Long Island to Martha's Vineyard and Cape Cod (Schlossberg, 2016). Additional infestations have been found in Bear Mountain State Park in New York, in Rhode Island, Massachusetts, and Connecticut (Schlossberg, 2016).

DFB and SB are the most destructive pests of the trees they are named for, Douglas-fir (*Pseudotsuga menziesii* Mirb.) and spruce (*Picea* spp.) (Fig. 15.4A) (Furniss and Carolin, 1977). Occurring from Southern Canada to Northern Mexico, DFB was once fairly limited in its impact on North American forests, its populations maintained at low levels by the availability of stressed, dying, or dead trees in a given landscape and only reaching outbreak levels in the aftermath of destructive events such as windstorms or wildfires (State of Colorado, 2016). DFB-induced tree mortality is now on the rise in many locations, even in some of the healthier forests of the United States (Dickson, 2019; Harper, 2019). In the Pacific Northwest, for example, historical annual tree mortality rates associated with DFB infestations fluctuated between 1% and 5% but have now risen to 30%–50% (Bible, 2001; Larson et al., 2008; Freeman, 2017). SB is the most broad-ranging

bark beetle in North America and the leading cause of death for mature spruces (Holsten et al., 1999; Raffa et al., 2008; Mietkiewicz et al., 2018), colonizing all spruce species within their range, including white spruce, *Picea glauca* Moench, Sitka spruce, *Picea sitchensis* Bong., and Engelmann spruce, *Picea engelmannii* Parry ex Engelm., and destroying 333–500 million board feet of timber each year (Oatman, 2013). As with DFB, research suggests that current SB outbreaks are causing unusually high rates of spruce mortality, nearly 90%, compared to the historically typical 20%–30% (Salvail, 2019). SB has infested more than 49,370 ha of spruce forests in Utah (3 million trees killed) and caused losses of >100 million board feet of timber in Arizona, 2 billion in Alaska, 25 million in Montana, and 31 million in Idaho (Holsten et al., 1999). Outbreaks continue in British Columbia, Alaska, Colorado, Idaho, New Mexico, Utah, and Wyoming (Hansen et al., 2019; Murkowski, 2019). According to USDA Forest Service estimates, >364,000 ha of Alaskan spruce forest has become infested with SB on the Kenai Peninsula and in the Susitna River Valley, and nearly 204,000 ha in Matanuska-Susitna, in

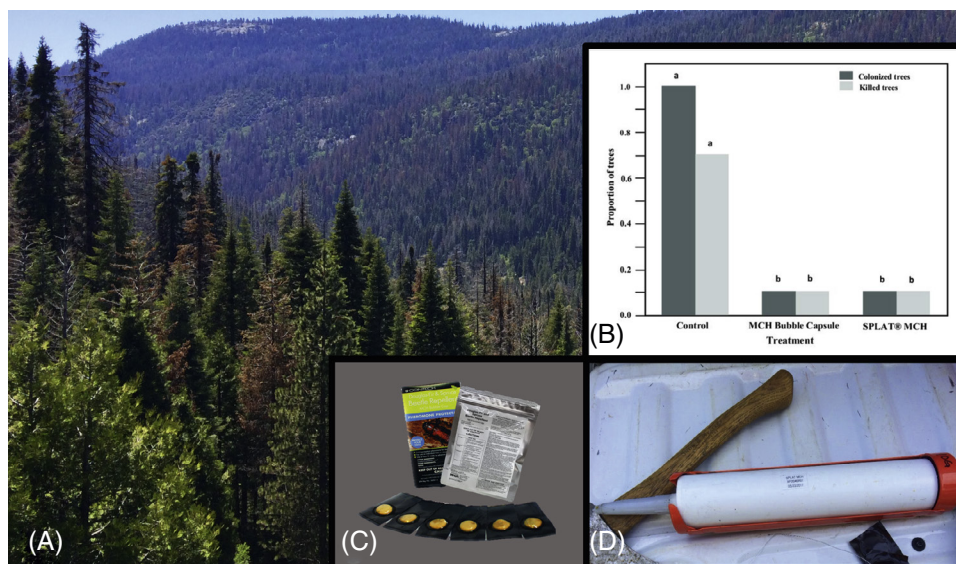


FIG. 15.4 (A) Douglas-fir forests devastated by bark beetles. (B) A higher proportion of Douglas-fir trees were colonized or killed when untreated (control), than when treated either with MCH bubble capsules, or the prototype SPLAT MCH formulation. (C) Commercial ISCA/Contech plastic MCH bubble capsules. (D) Prototype biodegradable MCH Repel. Credits: (A–C) ISCA Technologies, Inc.; (D) Fettig. *MCH*, 3-methylcyclohex-2-en-1-one.

addition to the 1.2 million ha of spruce forest damaged in the last major SB outbreak, which ended in 2004 (Murkowski, 2019; O'Malley, 2019).

The impacts of bark beetle outbreaks are not limited to the destruction of timber. They also complicate long-term forest stewardship by disrupting logging plans and change tree stocking levels and age distributions. Forests enduring beetle infestations also may be more likely to burn, as beetle-killed trees have higher emissions of flammable terpenes from foliage and create an abundance of combustible fuels (State of Colorado, 2016; Giunta et al., 2016). Widespread tree mortality increases soil erosion, reduces soil stability, and impacts water yields by eliminating transpiration from dying and dead trees and by exposing snow to rapid melting in the spring, consequently increasing water inputs to rivers and lakes and causing flooding (Holsten et al., 1999; State of Colorado, 2016).

As is the case with the effects of global climate change in general, the influence of

rising temperatures on bark beetle outbreaks and their impact on forest health are complicated, varying with geography and tree species. In some cases, prolonged drought increases the risks of severe bark beetle outbreaks by placing trees under chronic stress, reduces their general vigor, and impedes their capacity to repel beetle attacks through resin outflow (Waldron, 2011; Kolb et al., 2016; Freeman, 2017; Mietkiewicz et al., 2018; Negrón and Popp, 2018). Shorter, warmer winters may increase overwintering survival in more locations, allow beetle populations to move into higher elevations or more northerly territories as shown by SPB, and also may lead to an additional generation each year (Miller and Werner, 1987; Ungerer et al., 1999; Bentz et al., 2010; Hain et al., 2011; Hart et al., 2017). Other impacts of current climate trends include accelerated insect development, longer, and more unpredictable flight periods, larger populations of fertile female beetles, and larger insect body

size (Negrón and Popp, 2018; Lill, 2019; Puikonen, 2019). These changes may also alter host selection in a destructive way, as unusually large beetle infestations may result in attacks on younger, smaller-diameter trees than would ordinarily not be targeted, reducing the number and size of the next generation of mature trees (Raffa et al., 2008; Hart et al., 2014; Mietkiewicz et al., 2018).

Attempts to control bark beetle pests are hampered by the scale over which outbreaks occur, as well as by the remote, sensitive natural environments constituting susceptible forests. Removal of infested material, stand thinning, creation of felled-tree buffer zones, and preventative insecticide treatments may be effective against some species if implemented properly, but these techniques may be too costly and labor-intensive to be applied at the scale of a bark beetle outbreak (Billings, 1980; Mitchell et al., 1983; Fiddler et al., 1989; Amman and Logan, 1998; Johnstone, 2002; Billings, 2011a; Fettig et al., 2014; Fettig and Hilszczanski, 2015). Insecticide treatments have a further disadvantage in terms of the negative impacts they can have on the environment and their negative connotations in the minds of the public. One of the most commonly employed chemical agents for bark beetle control, the carbamate insecticide, carbaryl (1-naphthyl methylcarbamate), must be applied as a bark drench over each treated tree to the point of runoff, to a height where the bole diameter is too small to sustain beetle larvae; this level of coverage typically requires 15–30 L of insecticide solution per tree (DeGomez et al., 2006; Fettig et al., 2006; Fettig et al., 2008; Fettig et al., 2013). Because of the risks of exposure to this toxic chemical (headaches, memory loss, muscle weakness, and cramps, vomiting, bronchoconstriction, blurred vision, convulsions, coma, and respiratory failure), carbaryl applications require all application personnel to wear personal protective gear and use special application equipment that may be difficult or impossible to move across

rugged forest terrain (Bond et al., 2016). Carbaryl treatments are not effective against all bark beetle species. SPB, for instance, can rapidly break down the insecticide into its metabolites and then excrete them (Ragenovich and Coster, 1974; Zhong et al., 1994; Fettig et al., 2009; Cancelliere, 2016a, 2016b).

The search for more effective, sustainable methods of bark beetle control has found fertile ground in the same set of chemical compounds that enable these insects to cause such widespread and substantial damage: the semiochemicals that mediate mass attack behavior (Seybold et al., 2018; Gillette and Fettig, 2021). To successfully colonize a living tree, aggressive bark beetles must recruit enough insects (hundreds to thousands, depending on the species, size, and vigor of the host tree) to the selected host to overwhelm its defenses and penetrate the phloem beneath the outer bark (Gara et al., 1965; Hain et al., 2011). This beetle battle cry, as it were, takes the form of aggregation pheromones released by the insects, such as (Z)- and (E)-verbenol, frontalin, and *exo*-brevicomin (Pitman et al., 1969; Conn et al., 1983; Miller and LaFontaine, 1991; Billings, 2011b; Sullivan, 2011), amplified by the release of certain kairomones from the tissues of the plant being colonized (e.g., α -pinene, myrcene) (Miller and Lindgren, 2000; Billings, 2011b; Sullivan, 2011). Toward the end of a successful mass attack, once the tree is fully colonized, beetles begin releasing antiaggregation pheromones to deter incoming beetles, which might otherwise result in overcrowding that would be harmful to the larval brood within the tree. Antiaggregation pheromones are interpreted by host-seeking beetles as an indication that a target tree is already fully occupied and therefore unsuitable for further colonization (Seybold et al., 2018; Gaylord et al., 2020).

The functionality of antiaggregation pheromones offers a valuable opportunity to manipulate the behavior of bark beetles in such a way as to reduce the destruction they inflict on forests. Verbenone is the most commonly deployed

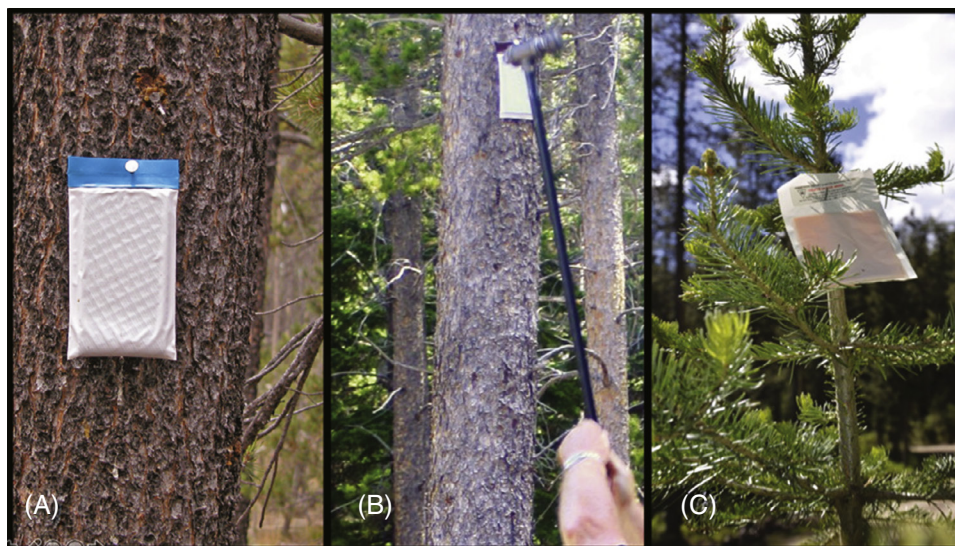


FIG. 15.5 (A) Plastic pouch containing verbenone nailed to a tree. (B) A verbenone pouch being nailed to a tree trunk. (C) A verbenone pouch stapled to a young fir tree. Credit: Fettig.

antiaggregation pheromone in bark beetle management, particularly against MPB, and has been used by forest scientists and managers for decades to protect trees and forest stands in high-value or high-visibility locations, such as residential or recreational areas and seed orchards (Amman et al., 1989; Ross and Daterman, 1995; Seybold et al., 2018; Fettig et al., 2020). Multiple verbenone-based repellents are registered in the United States and Canada, including plastic bubble capsules, pouches, and pheromone-impregnated flakes. While these products have delivered effective control in many cases, treatment failures are common (Progar et al., 2014; Seybold et al., 2018), attributed to inconsistent or insufficient release of the pheromone (Bentz et al., 1989), photoisomerization of verbenone to chrysanthenone (2,7,7-trimethylbicyclo[3.1.1]hept-2-en-6-one, a compound with no known impact on bark beetle behavior, therefore of no use as a repellent) (Kostyk et al., 1993), and a limited range of repellency, especially when beetle populations are high (Miller, 2002). In addition to these technical shortcomings,

device-type repellents like pouches and bubble caps (Fig. 15.5) present practical challenges, as they must be removed from many forested areas after the beetle flight period ends. Plastic pheromone flakes may be broadcast more quickly over larger areas than discrete devices and are less conspicuous in the environment, but they tend to have short release periods (Seybold et al., 2018; Gillette and Fettig, 2021) while introducing plastic pollutants to treated environments.

15.3.2 Repellent trials

An alternative verbenone-based repellent was developed starting in 2011: SPLAT Verb (Fig. 15.2B and C), a flowable controlled-release formulation designed to improve the efficiency of application and ensure a more consistent and effective release rate of the pheromone AI, so that a single application of the repellent would be sufficient to protect treated trees from bark beetle colonization for an entire flight period (Fettig et al., 2015). Because SPLAT Verb is comprised entirely of food-safe ingredients and

biodegrades within a year of application, point sources of this formulation do not require retrieval from the field as do plastic verbenone products (Fettig et al., 2020). SPLAT Verb was first tested for its capacity to protect lodgepole pine from attack by MPB, beginning with a pilot study conducted in July 2011 in Bridger-Teton National Forest, Wyoming. A prototype SPLAT formulation containing verbenone was applied as four large point sources spaced evenly around the bole of 21 randomly selected healthy, non-MPB infested lodgepole pines. Twenty-one pines were treated with roughly 533 g of the SPLAT formulation (32 g verbenone/tree), and six were treated with 650 g of formulation (39 g verbenone/tree). Thirty additional healthy lodgepole pines were left untreated and used as controls. All trees used in the experiment, both SPLAT Verb-treated and untreated control, received a commercial MPB tree bait, manufactured by Contech Inc. (Delta, BC, Canada, since acquired by ISCA, Inc. Riverside, CA, US), to ensure sufficient pest pressure to evaluate any treatment effect. One year after the treatment, control and treated trees were assessed for crown fade, an indication of a successful mass attack and tree death. Results of the assessment indicated that the SPLAT Verb prototype delivered a high degree of protection against MPB. While 28 out of 30 untreated control trees were killed by MPB, a mortality rate of 93.3%, all SPLAT Verb-treated trees remained alive and healthy 1 year after treatment.

While the level of efficacy demonstrated by the initial Bridger-Teton study was encouraging, the high AI loading rate was cost-prohibitive for a viable commercial product. The prototype formulation, therefore, underwent further refinement to reduce its content of verbenone and ensure a steady, consistent release rate, followed by an additional study in the same area. This second trial was conducted according to a similar protocol as the initial study but with an AI application rate equivalent to the dose of verbenone used in pouch formulations: 7 g of

verbenone AI per tree. The reduction in AI loading rate showed no significant impact on the level of tree protection provided. As with the first trial, 100% of SPLAT Verb-treated trees survived with no signs of MPB colonization 1 year after application of the repellent, while 93.3% of untreated trees died (Fettig et al., 2015). Assessments of trees growing near SPLAT Verb-treated trees also displayed a reduced frequency of MPB attack. No trees growing within 11 m of SPLAT Verb-treated trees were found to have been successfully colonized, compared to 61 infested trees growing within 11 m of control trees (Fettig et al., 2015).

A small stand-level trial was performed on a series of 0.4-ha plots in the Caribou Targhee National Forest, Idaho. A SPLAT Verb formulation containing 10% verbenone was compared to Contech verbenone pouches (7 g AI) applied according to manufacturers' instructions along a 9.1×9.1 m grid, and untreated control. SPLAT Verb was applied in such a manner as to achieve an equivalent AI rate/area as the verbenone pouch treatment. At this equivalent rate, SPLAT Verb delivered more effective protection of treated stands than verbenone pouches compared to the untreated control (Fettig et al., 2015). When a final assessment of tree mortality on the experimental plots was made in July 2013, eight trees in SPLAT Verb-treated plots had died as a result of the MPB attack, compared to 15 trees killed in pouch-treated plots and 49 trees killed in untreated plots. In another small-scale stand study in the Beaverhead-Deerlodge National Forest, Montana, fewer trees were colonized by MPB on 0.41-ha experimental plots treated with 2.5 kg and 3.5 kg of SPLAT Verb [250 g and 350 g of verbenone] and the 7-g verbenone pouch [50 pouches/plot, 350.0 g of verbenone/plot] compared to the untreated control. No significant difference was observed between 1.5 kg of SPLAT Verb [150 g of verbenone] and the untreated control. Fewer trees were killed by MPB on experimental plots treated with 1.5, 2.5, and 3.5 kg of SPLAT Verb and the verbenone

pouch compared to the untreated control. No other significant differences were observed among treatments. Collectively, these data suggest that lower doses of SPLAT Verb can be used for tree protection than previously considered and at a substantial cost savings that could make this strategy economically viable for area-wide management of MPB (Fettig et al., 2020). A third study on SPLAT Verb (7 g verbenone/tree) was conducted in Darby, Montana, on ponderosa pine but was confounded by the presence of two additional bark beetle pests at the trial site, western pine beetle, *Dendroctonus brevicomis* LeConte, and pine engraver beetle, *Ips pini* Say (Fettig et al., 2016).

SPLAT Verb was registered for use against MPB in lodgepole pine in 2014 and went on to become the first semiochemical-based control product for bark beetles to be successfully commercialized in the past 20 years. It has since been tested in several other pine species, including sugar pine in Stanislaus National Forest and Yosemite National Park, California—where SPLAT Verb provided complete or nearly complete protection of treated trees (<5% mortality in Stanislaus, 0% mortality in Yosemite compared to ≥60% mortality in untreated, baited control trees (Fettig et al., 2016)—and whitebark pine, a foundational species that provides multiple crucial functions in subalpine ecosystems, including wildlife habitat and watershed protection (Progar et al., 2021). Whitebark pine densities have declined by as much as 90% in some locations as a result of MPB infestations and white pine blister rust to the extent that it has been considered for inclusion under the Endangered Species Act (Progar et al., 2021). Small stand studies were conducted in whitebark pine in the Southern Cascade Range in northern California and in the Strawberry Mountain Range in central Oregon (Progar et al., 2021). Survival rates were 4%–7% higher in plots treated with SPLAT Verb, compared to 2%–3% higher with verbenone pouches. SPLAT Verb and verbenone pouches delivered roughly equivalent levels of

protection in small and medium trees at the Oregon trial site, but for large trees, survival was significantly higher in plots treated with SPLAT Verb (93%) than in those treated with pouches (82%) (Progar et al., 2021).

The developers of SPLAT Verb advanced similar repellents for other bark beetle pests, including SPB, DFB, and SB. SPB has proven a particularly difficult pest to manage by semiochemical means, as most studies have indicated it does not respond to verbenone in the same way as MPB. The reason for this difference can likely be found in the chemical nature of verbenone, which occurs in two enantiomeric forms. The “R” enantiomer of verbenone, also written as (–)-verbenone, is the more common of the two and is easier and less expensive to synthesize than its opposite, “S” or (+)-verbenone but has not been shown to be an effective repellent for SPB. Multiple studies have demonstrated that SPB responds more readily to verbenone blends containing higher proportions of the (+) isomer, which costs tens of thousands of USD per kg, compared to low hundreds for a kg of the (–) isomer (Mafra-Neto 2020, unpublished data). Commercial high-volume synthesis of verbenone typically produces only 9% (±3%) of the (+) isomer, while most verbenone repellent formulations contain about 12% (+)-verbenone (Bunt et al., 1980; Salom et al., 1995), far short of the 30% that the current literature suggests is the minimum necessary for an effective SPB repellent (Strom and Clarke, 2011). In their efforts to develop an analogous product to SPLAT Verb for SPB (Fig. 15.3B), ISCA scientists first developed a novel synthetic method for production of high purity (+)-verbenone that reduced the cost of the final product to 1200 USD/kg, 29x less expensive than the current price of purchase (35,000 USD/kg). Further optimization of the synthetic pathways has allowed ISCA to produce (+)-verbenone at costs similar to that of (–)-verbenone.

Work to develop a semiochemical repellent for SPB is ongoing, but several field trials with

SPLAT formulations containing (+)-verbenone have been completed. A trapping study in the Bienville National Forest in Mississippi showed significant inhibitory effects of the (+)-verbenone repellent on the SPB population. Significantly fewer SPB were trapped in baited traps treated with the repellent than in control traps (baited with no repellent). Three spot-suppression trials, evaluating the repellent's capacity to disrupt growing SPB infestations, were also conducted in Mississippi, the first in the Bienville National Forest and the second and third in the Homochitto National Forest. At Bienville, five SPB infested spots were treated with SPLAT containing (+)-verbenone [17.5 g/tree applied to unin-fested trees in a buffer creating a barrier (avg. 3 treated trees deep) separating the area of spot growth from the area without infested trees, where the growth of SPB infection was predicted to progress], while another five spots were left untreated. Three out of five repellent-treated spots exhibited significantly reduced infestations. Two treated spots were considered completely successful (0 untreated trees attacked beyond the buffer zone), and the third was considered partially successful (<10 trees colonized). More than 10 trees were infested in the remaining two spots, but in both cases, the breach of the barrier that led to treatment failure occurred at its narrowest points, where there was a gap in treated trees or the barrier was only one or two trees deep. This result can be interpreted as an indication that the cause of the treatment failure at these sites may be attributable to faulty application rather than an ineffective repellent formulation.

Similar problems were encountered in the first trial conducted at the Homochitto Forest, where only one repellent treatment was determined to have been completely successful in SPB spot disruption (three considered partially successful, and one considered a treatment failure); as with the Bienville trial, all breaches of the repellent barrier occurred at its narrowest points. A second trial at Homochitto addressed

the application difficulty by increasing the depth of the barrier to a ubiquitous minimum of three trees around the spot head and all currently infested trees. Of the three SPB infestations treated, two achieved partially successful spot disruption, while a third achieved completely successful disruption. According to a mathematical model developed by one of ISCA's collaborators on this project, Dr. Stephen Clarke at the USDA Forest Service, to predict the likelihood and direction of expansion of a given SPB spot, 60% of the spots treated in these trials were either slowed or contained by the presence of the (+)-verbenone barrier.

To develop an effective repellent for DFB and SB, a different semiochemical AI was required, 3-methylcyclohex-2-en-1-one (MCH), which serves an analogous function in the chemical ecology surrounding a mass attack on trees in these two species as verbenone does in MPB and SPB infestations. Repellent bubble capsules that release MCH have been commercially available for tree protection against DFB since 1999 and are used to treat several thousand ha of high-value forest annually at a cost of 200 USD per ha (2 USD per tree) (Ross et al., 2001, 2015; Brookes et al., 2016; Hansen et al., 2019). The cost of this repellent treatment is significantly lower than for carbaryl treatments and significantly reduces environmental impact (Gillette and Munson, 2009; Strom and Clarke, 2011). However, as with verbenone pouches, MCH bubble caps are not suitable for larger-scale management programs, as their application and post-season removal are labor-intensive (Fig. 15.4C). They are also not consistently effective against SB (Zogas, 2001). MCH Repel (Fig. 15.4D), a controlled-release formulation similar to SPLAT Verb, incorporating MCH, was developed to correct these issues and field tested against DFB in Idaho and New Mexico (Foote et al., 2020) and against SB in Wyoming and Alaska. A field trial performed in the Boise National Forest in Idaho demonstrated that both MCH Repel and MCH bubble capsules

significantly reduced DFB attacks on Douglas-fir trees and subsequent levels of tree mortality compared to the untreated control and that there was no significant difference between MCH bubble capsules and MCH Repel (Fig. 15.4B) (Foote et al., 2020).

MCH Repel was also tested in two stand-level trials in the Boise National Forest and the Cibola National Forest in New Mexico. Results from the New Mexico trial indicated that MCH Repel was as effective as MCH bubble capsules. Both MCH treatments significantly reduced the proportion of trees attacked and killed by DFB compared to untreated control plots, with no significant difference between MCH treatments (Foote et al., 2020). The Idaho trial found that neither MCH treatment significantly reduced DFB attack and that only MCH bubble capsules significantly reduced tree mortality due to DFB attack compared to untreated control plots, though no significant difference in tree mortality was observed between MCH Repel and bubble capsule treatments (Foote et al., 2020). As this contradicts the findings of multiple studies on MCH bubble capsule efficacy against DFB, the authors of the study attributed this result to the use of a strong three-component attractant in the trial, which has not been used in previous studies (Ross and Daterman, 1994, 1995; Ross et al., 1996, 2002; Ross and Wallin, 2008; Brookes et al., 2016; Foote et al., 2020).

Repellents combining MCH Repel with nonhost volatiles were tested against SB in 2019 in white spruce in Alaska and in Engelmann spruce in Wyoming. Preliminary results from Wyoming suggested that MCH Repel + acetophenone + (*E*)-2-hexen-1-ol and (*Z*)-2-hexen-1-ol, and MCH Repel + AKB [linalool, β -caryophyllene and (*Z*)-2-hexen-1-ol] were effective for protecting individual trees and small groups of trees from mortality attributed to SB (Hansen et al., 2019, Fettig et al., USDA Forest Service, unpublished data). The best performing MCH Repel prototype with nonhost volatiles, applied at 3.5 and 7 g MCH per tree,

reduced spruce mortality due to SB attack in Wyoming to 0 and 8%, compared to 100% mortality in untreated trees at the same site. However, no evaluated MCH Repel treatment was effective in Alaska (Fettig et al., USDA Forest Service, unpublished data). In the summer of 2020, the manufacturers of SPLAT Verb and all other bark beetle repellents described in this section, ISCA, Inc., obtained its latest Phase II grant from the USDA Small Business Innovation Research (SBIR) program to continue research and development on SPLAT-based MCH repellents for DFB and SB, which will include continued field trials to assess the capacity of these semiochemical techniques to deliver effective protection of North American forests at the individual tree, small stand, and area-wide scale.

15.3.3 Future directions

As with CBB in commercial coffee, the warming global climate is creating conditions more challenging to the health of North American forests and more favorable to their most damaging insect pests, bark beetles in the *Dendroctonus* genus. More frequent and severe droughts and other extreme weather events place conifer trees under chronic stress, leaving them more vulnerable to insect attacks. Aggressive *Dendroctonus* species are expanding their territories northward and into higher altitudes, enabled by higher average temperatures to survive the winter at higher rates. Warmer temperatures also accelerate insect development and foster larger, more fertile populations of female beetles, allowing outbreaks to multiply faster. Some species are altering their attack behaviors as they move into new areas. Infestations of SPB in the northern United States do not progress with the same directionality as in their native southern range, making them less predictable and harder to treat effectively. As these shifts continue and an ever-increasing area of forest biomass is lost to bark beetle outbreaks, deforestation, and widespread wildfires, some forests

may be converted from carbon sinks (systems that absorb more carbon than they release) to carbon sources. A critical resource for mitigating the effects of anthropogenic carbon emissions could therefore become a worsening factor for climate-related problems.

Forests represent both a challenge and an opportunity for semiochemical-based pest management technologies. As most pheromones and other semiochemicals used for insect control are nature-identical and selective in their mode of action, they are considered safer for people and other nontarget species, and therefore better suited for use in sensitive, diverse forest environments. This is in contrast with agricultural pest control applications, where semiochemical techniques must compete directly with cheaper, faster-acting broad-spectrum pesticides. However, the field environment over which bark beetle outbreaks take place poses a significant challenge for a pest control application of any kind. Previous bark beetle repellents have failed to deliver consistent tree protection due to difficulties achieving a sufficient release rate and period, degradation of the AI through environmental exposure, and insufficient range of active repellency.

The repellent products described here, SPLAT Verb, SPB Repel, and MCH Repel, have completed field trials demonstrating the resolution of many of these previous shortcomings in bark beetle control products. SPLAT Verb was registered in 2014 following field trials demonstrating effective repellency in lodgepole pine and has since been tested in multiple additional pine species, including the high-altitude foundational species, whitebark pine. Mafra-Neto et al. are also engaged in field trials exploring aerial application methods for SPLAT Verb using fixed-wing aircraft, helicopters, or unmanned aerial vehicles to apply the repellent to larger and/or more remote areas than can be treated effectively using manual application. Evaluations of SPB Repel demonstrated that a repellent using (+)-verbenone partly or completely

disrupted SPB infestations, though in several cases, the treatment buffer zone proved too narrow to entirely prevent spot expansion. Continuing development on SPB Repel will focus on determining how to most effectively disrupt the linear expansion of SPB infestations in the southern regions of their range and evaluation of new methods of application to combat the atypical and unpredictable SPB outbreaks observed in the north. MCH Repel achieved an equivalent level of tree protection against DFB infestation as MCH bubble capsules in field trials conducted in New Mexico and Idaho, though a stand-level trial in the Boise National Forest revealed no significant treatment effect on tree mortality, likely due to the potent lure deployed in the trial. A series of prototype MCH Repel formulations containing nonhost volatiles delivered effective protection of Engelmann spruce trees in Wyoming but not of white spruce trees in Alaska.

Because the MCH Repel formulation is biodegradable, breaking down within 1–2 years, it will not require postflight removal, giving it a decided advantage where such retrieval is costly and labor-intensive. Continuing trials on MCH Repel will include field studies assessing the efficacy of MCH Repel against DFB and SB at larger scales and in a wider range of habitats across the lower 48 states, as well as field trials in Alaska with lower SB infestation rates. Mafra-Neto et al. expect full registration and product launch of MCH Repel as a control product for DFB with the US EPA within the next year.

15.4 Ambrosia beetles: redbay ambrosia beetle, black stem borer, and polyphagous shot hole borer

15.4.1 Background

The first section of this chapter discussed the use of a semiochemical-based repellent against a major pest of commercial agriculture, the CBB, whose impacts are expected to increase as a

result of global climate change, while the second deals with a group of insects exerting expanding influence on North American forest ecosystems. The subjects of this section, ambrosia beetle pests, have harmful impacts on both forestry and commercial agriculture. Ambrosia beetles are in the same subfamily as bark beetles (Scolytinae), and display some of the same attack behaviors and ecology, boring beneath the bark of host trees to create galleries for themselves and their offspring. However, unlike bark beetles, ambrosia beetles do not directly feed on the wood tissues themselves; instead, they use these galleries as a substrate for the cultivation of the symbiotic “ambrosia” fungi they rely upon for sustenance (Batra, 1966, 1967; Beaver, 1989; Castrillo et al., 2011; Ploetz et al., 2013). Adult ambrosia beetles introduce the fungi to the interior tissues of their host tree, providing them with a suitable sheltered environment and an abundant food supply. Typically, ambrosia beetle species in their original native habitats limit their attacks to dead or dying trees, serving as nature’s recyclers. For reasons not completely understood, some invasive ambrosia beetles also may infest healthy living trees (Kuhnholz et al., 2001; Reding et al., 2010; Castrillo et al., 2011; Ploetz et al., 2013; Wilson et al., 2014). In these instances, the transmitted fungus disrupts the transport of water and nutrients throughout the plant’s vascular system, inflicting serious and, in some cases, lethal damage. Some species also transmit secondary pathogenic fungi or bacteria (Beaver, 1989; Whitney, 1982; Hiji et al., 1991; Castrillo et al., 2011).

The RAB is an example of an introduced ambrosia beetle species attacking living and healthy hosts in its new environment (Fig. 15.6B and C). RAB transmits the deadly fungal pathogen *Raffaelea lauricola* (Harr., Fraedrich & Aghayeva) (Fig. 15.6D), which causes laurel wilt disease in trees in the family Lauraceae. Infection with the disease can result from as few as 100 fungal spores and disrupt xylem tissue function in as little as 3 days after the initial

inoculation (Inch and Ploetz, 2012; Inch et al., 2012; Ploetz et al., 2013). Symptoms of laurel wilt include withering of leaves, branch death, and blackening of sapwood; in some cases, infection with *R. lauricola* can be lethal to the tree. Most species of Lauraceae native to the United States are susceptible to infection with laurel wilt (Fig. 15.6A and E), including redbay, *Persea borbonia* L., swamp bay, *Persea palustris* Rafinesque, avocado, *Persea americana* Mill., sassafras, *Sassafras albidum* Nutt. (Fraedrich et al., 2008; Mayfield et al., 2008; Smith et al., 2009; Hughes et al., 2011), and several other commercially, culturally, and ecologically important species in the Coastal Plain forests of the southeastern states (Fraedrich et al., 2011; Ploetz et al., 2011; Ploetz et al., 2013).

Since RAB was first detected in the United States in 2002 in Georgia (Haack, 2002), it has spread rapidly throughout the South, killing millions of redbay and swamp bay trees (Cameron et al., 2015). Laurel wilt was detected in Northern Florida in 2005 and in the southern regions of the state in 2011, causing widespread mortality in redbay growing across Florida, Georgia, and South Carolina (Fraedrich et al. 2008; Kendra et al., 2013; Hughes et al., 2015). An estimated one-third of redbay in the United States (>300 million trees) have already been killed by infestation with *R. lauricola* (Hughes et al., 2017b). RAB attacks multiple *Persea* spp., including California laurel, swampbay, sassafras, and endangered Lauraceae species like pondspice, *Litsea aestivalis* L., and pondberry, *Lindera melissifolia* Walter (Fraedrich, 2008; Fraedrich et al., 2011; Hughes et al., 2011; Peña et al., 2012). Lauraceae trees are key riparian species protecting rivers, lakes, and other bodies of water across continental North America. The reduction of protective vegetation or the sudden degradation of the woody key species in riparian areas greatly increases the risk of habitat degradation and soil erosion and loss through fire, wind, and rain effects. Laurel wilt is also of concern to the avocado industry. The fungus *R. lauricola* has already been reported on avocado

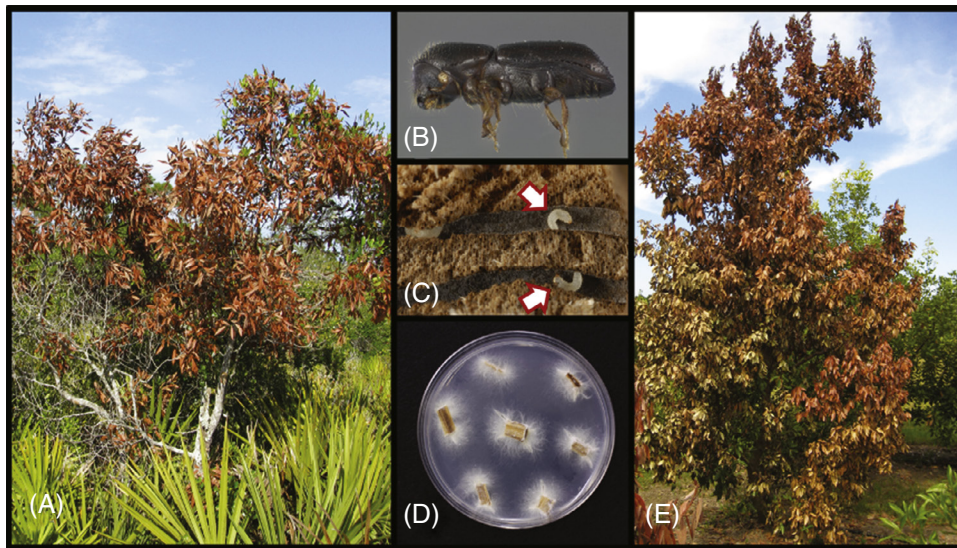


FIG. 15.6 (A) The native Lauraceae species that characterize coastal forests of the southeastern United States, including redbay, as well as agricultural crops such as (E) avocado, have been severely impacted by the invasive redbay ambrosia beetle (RAB), *X. glabratus*. (B) Adult RAB females oviposit preferentially onto Lauraceae trees, where (C) the larvae tunnel beneath the bark. During oviposition, RAB inoculates its host tree with (D) the deadly fungal pathogen *R. lauricola*, which invariably causes a widespread fungal infection that overwhelms the tree defenses, ultimately killing it. Credits: (A and E) Martini; (B and C) Buss; (D) Hughes.

in Florida, the second-largest producer of avocado in the country. Avocados were grown on roughly 2350 ha in Florida in the 2018–2019 season, producing a total yield of 13,900 tons (13,620 tons utilized, with an estimated value of 15.3 million USD) (USDA National Agricultural Statistics Service (NASS), 2019). In the case of avocado, the fungus is transmitted to the host through other ambrosia beetle species that acquire fungal spores through lateral transfer from an infected laurel tree (Carrillo et al., 2014), so in this crop, control of laurel wilt needs to focus on the ambrosia beetle group rather than on a specific species (Rivera et al., 2020). If the pest and its pathogenic symbiont were to spread to California, the economic impacts would be far larger. According to estimates by the USDA National Agricultural Statistics Service, a total of 171,000 tons of avocados were produced in California over 19,000 ha, with a utilized production value of 383 million USD (169,100 tons) (USDA

National Agricultural Statistics Service (NASS), 2019). Laurel wilt disease distribution has been moving westwards, and it has been confirmed in Arkansas, Louisiana, and Texas (USDA, 2015).

Black stem borer (BSB), *Xylosandrus germanus* (Blandford), an ambrosia beetle native to eastern Asia that was introduced to the United States in 1932, has become one of the most serious pests of nurseries and landscapes across the Southern, Midwest, Upper northwestern, and Northeastern United States (Gill et al., 1998; Mudge et al., 2001; Rabaglia et al., 2006). BSB preys on more than 200 species in 51 families, including beech, *Fagus*, oak, *Quercus*, *Magnolia*, maple, *Acer*, black walnut, *Juglans nigra* L., ash, *Fraxinus*, cedar, *Cedrus*, grape, *Vitis*, pecan, *Carya illinoensis* Wangenh, plum, *Prunus*, willow, *Salix*, dogwood, *Cornus*, chestnut, *Castanea*, apple, *Malus domestica* Borkh., cherry, *Prunus*, peach, *Prunus persica* L., pear, *Pyrus*, and rose, *Rosa* (Weber and McPherson, 1983; Oregon State University, 2007; Ranger et al., 2010; Centre

for Agriculture and Biosciences International, 2020). Virtually any woody plant is vulnerable to infestation by BSB, though it does show some preference for deciduous species over conifers (Weber and McPherson, 1983; Oregon State University, 2007; Ranger et al., 2010; Centre for Agriculture and Biosciences International, 2020). It also displays a preference for saplings and small-diameter trees, making it a particular threat to ornamental nursery and orchard industries. BSB is also highly mobile, capable of flying distances of 2 km or more, and can travel even farther if humans provide assistance by transporting infested wood (Grégoire et al., 2001; Centre for Agriculture and Biosciences International, 2020). Because this species practices sibling mating, only a few mobile female beetles are required to produce an active infestation (Centre for Agriculture and Biosciences International, 2020). Infestations by BSB, along with its symbiotic fungal

partner, *Ambrosiella grosmanniae* (McNew, Mayers, and Harr) produce discoloration and blistering in the bark of infested trees and disruption of the vascular system, leading to wilting, dieback, and eventually mortality (Fig. 15.7A and B). BSB also transmits pathogenic *Fusarium* spp. fungi, known to cause dieback, stem cankers, sprouting, and may lead to tree death (Anderson and Hoffard, 1978; Weber, 1980; Centre for Agriculture and Biosciences International, 2020). In recent years, BSB has expanded its impacts in orchard crops, including apples, apricots, and plums in Michigan, and apples in Ohio, North Carolina, and New York (Oregon State University, 2007; Lehnert, 2015). In 2013, apple growers in Western New York began to see significant numbers of trees (up to 30%) collapsing in their orchards. By the end of 2013, hundreds of apple trees had to be removed and destroyed, and 50 more infestation sites have since been identified, extending all the way to

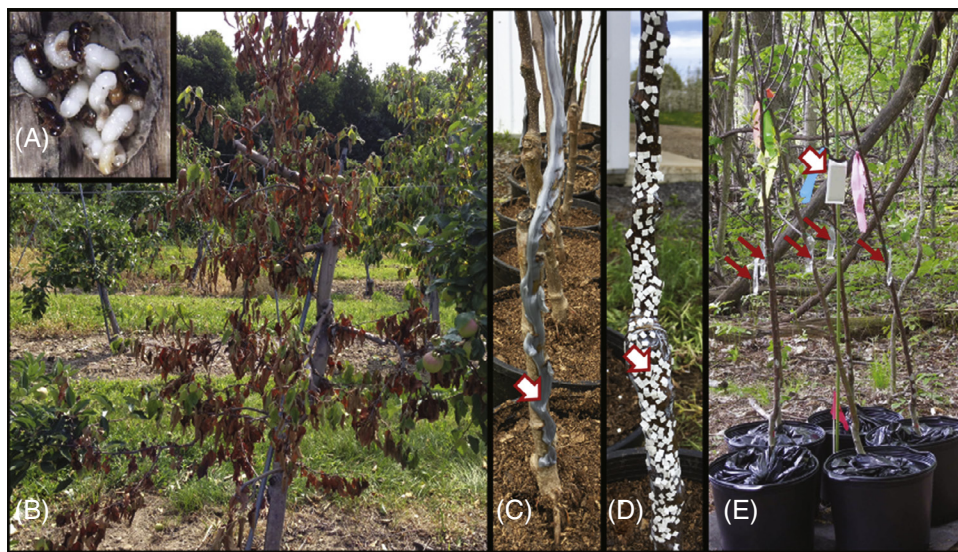


FIG. 15.7 The black stem borer (BSB), *X. germanus*, is an invasive species that preys on more than 200 plant species in 51 families, including important crops like pome and stone fruit, nuts, and grapes. BSB creates (A) galleries hosting adults and brood, and in the process inoculates the host tree with a symbiotic fungus, *A. grosmanniae*, which accelerates the senescence of the infested plant. (B) An infested apple tree shows signs of decline during early summer, with dead branches and brown leaves. Field trials reported here used potted apple trees with trunk applications of (C) SPLAT Verb (indicated by white arrow), or (D) Verbenone Disrupt Micro-Flakes VBN (indicated by white arrow). (E) A group of potted trees treated with individual ethanol lures (indicated by red arrows) plus a central verbenone dispenser (indicated by white arrow). Credits: (A, C, D, and E) Agnello; (B) Biltonen. SPLAT, Specialized Pheromone & Lure Application Technology.

Long Island (Agnello et al., 2017). The pest had apparently been present in the forests around these orchards for several years before colonizing the orchard trees (Lehnert, 2015). The reason for this shift in behavior is currently unknown.

In 2003, an additional invasive ambrosia beetle species was found in Whittier, California (Boland, 2016; Seybold et al., 2016; Chen et al., 2017). It was initially misidentified as tea shot hole borer, *Euwallaeceae fornicatus* (Eichhoff), only to be revealed as a new species in the same genus through genetic analysis (Eskalen et al., 2013). Seven years later, this species—now assigned the moniker of polyphagous shot hole borer—was implicated in the deaths of a large number of box elder trees in Long Beach (University of California; Pest and Diseases of Southern California Oaks, 2014). The beetle's range expanded to four other counties in Southern California, Ventura, San Bernardino, Riverside, and Orange County, becoming a serious pest of multiple hardwood species in urban and wild forests (Chen et al., 2017). Over 200 species are known to be susceptible to infestation by polyphagous shot hole borer, with 41 species classified as true reproductive hosts (in which beetles are successful in creating galleries and cultivating their fungal gardens), including coast live oaks, *Quercus agrifolia* Née, willow, big leaf maple, *Acer macrophyllum* Pursh, sycamore, *Platanus occidentalis* L., California box elder, *Acer negundo* L., Castor bean, *Ricinus communis* L., English oak, *Quercus robur* L., and blue palo verde, *Parkinsonia florida* Benth. ex A. Gray S. (Oregon State University, 2007; University of California; Pest and Diseases of Southern California Oaks, 2014; Aguilar, 2016; Boland, 2016). Like BSB, polyphagous shot hole borer transmits *Fusarium* spp. fungi, causing a condition called *Fusarium* dieback, characterized by damage to the xylem and phloem tissues, discoloration of the leaves and wood, wilting, branch dieback, and possible mortality (Oregon State University, 2007; Eskalen et al., 2012, 2013; Freeman et al., 2013; Eatough Jones and Paine,

2015). According to an estimate by the Orange County Parks staff, polyphagous shot hole borer has killed 1.4 million USD worth of trees. This pest's broad host range could make it a substantial threat in California, where major agricultural centers, wildland forests, and urban landscapes—many of them dominated by tree species that serve as reproductive hosts for the borer—often all exist in the same region (Eskalen et al., 2013). Nearly half (48%) of street trees in Southern California are species vulnerable to *Fusarium* dieback, and six of these, including American sweetgum, *Liquidambar styraciflua* L., one of the most common street trees, are confirmed reproductive hosts for polyphagous shot hole borer (Eskalen et al., 2013).

Management options for ambrosia beetles are limited. Because these insects spend so much of their time shielded within their host trees, they are protected from topical insecticide treatments such as bark drenches, and because they do not feed directly on the plant tissues, most systemic treatments have little to no impact on them, either (Wilson et al., 2014; Centre for Agriculture and Biosciences International, 2020). In addition, the beetles' small size makes them difficult to detect until after they have inflicted visible damage to the tree, making proper timing of insecticide applications very difficult (Reding et al., 2010). Treatment for the fungal infestations ambrosia beetles transmit can be equally challenging. The only available treatment for laurel wilt, for example, is preventative injection with the fungicide propiconazole (1-[[2-(2,4-dichlorophenyl)-4-propyl-1,3-dioxolan-2-yl]methyl]-1,2,4-triazole), a costly and labor-intensive process that is not suitable for area-wide treatment, such as in the southeastern forests where RAB thrives (Gitau et al., 2013; Ploetz et al., 2017). There is no cure for a tree already infested with laurel wilt; infested trees typically die within weeks. Cultural control practices are currently the most commonly recommended method for preventing ambrosia beetle infestations, including removal and destruction of infested trees (typically by burning, chipping and solarization, or

heat sterilization) and eliminating transport of potentially infested wood (Buffam and Lucht, 1968; Denlinger and Yocum, 1998; Wang et al., 2000; McCullough et al. 2007; Spence et al., 2013; Wilson et al., 2014). However, in the case of the RAB, this method is only applied by avocado growers, not by forest managers. Most have limited resources and lack the time and people to scout for laurel wilt trees, and to remove and dispose of them properly. In theory, the surest method of tree protection is to maintain their health, and with it their capacity to defend themselves from wood-boring insects, but this simple strategy is becoming more challenging with changing environmental conditions, such as the years-long drought in California, resulting in large swaths of severely stressed forests.

15.4.2 Repellent trials

Following on the success of ISCA's SPLAT Verb against MPB, in 2014, Mafra-Neto et al. began the development of Beetle Guard, a controlled-release repellent combining SPLAT Verb with additional repellent semiochemicals. As with bark beetles, verbenone has been shown to have an inhibitory effect on certain ambrosia beetle species. Dodge et al. (2017) demonstrated that verbenone pouches significantly reduced the number of polyphagous shot hole borers and Kuroshio shot hole borers attracted to quercivorol [(1S,4R)-4-Isopropyl-1-methyl-2-cyclohexen-1-ol], a known attractant to these species, to the extent of almost eliminating the lure's effect. Similar behaviors have also been documented in BSB (Ranger et al., 2013, 2014; Van DerLaan and Ginzl, 2013), where verbenone combined with terpinolene (1-methyl-4-propan-2-ylidene-cyclohexene) reduced attraction to ethanol, a volatile emitted by stressed trees commonly used as a monitoring lure for ambrosia beetles (Grégoire et al., 2001; Oliver and Mannion, 2001; Reding et al., 2010; Centre for Agriculture and Biosciences International, 2020). Methyl salicylate, also released by plants stressed by injury or

infection (Shulaev et al., 1997), has been tested as a semiochemical repellent against a broad array of harmful insect species, including the yellow fever mosquito, (Dekker et al., 2011) and black bean aphid *Aphis fabae* Scopoli (Hardie et al., 1994). The ambrosia beetles *X. glabratus*, *Xyleborus bispinatus*, and *Xyleborus volvulus* were also repelled by methyl salicylate in laboratory conditions (Hughes et al., 2017a; Rivera et al., 2020).

Prototype formulations of Beetle Guard, including those containing methyl salicylate and both (–) and (+) verbenone isomers, have also been field-tested against BSB in New York apple orchards, under the supervision of one of ISCA's research partners, Dr. Art Agnello (Department of Entomology, Cornell University, New York, NY). Several treatments were evaluated based on trap capture rates and damage to the crop (Fig. 15.7C–E), including SPLAT Verb (commercial formulation described in the first section of this chapter), with or without chlorpyrifos treatment; two prototype formulations of Beetle Guard, combining verbenone and methyl salicylate; Verbenone Disrupt Micro-Flakes with or without chlorpyrifos treatment; chlorpyrifos treatment alone; blank flakes (no repellent AI), and untreated control. SPLAT formulations were applied to young apple trees using a caulking gun at 35 g/tree (3 testing sites/treatment × 6 trees/treatment per site = 18 trees per treatment). Trap captures in the treated areas showed a relatively normal adult flight occurrence, indicating active BSB populations at these sites, but assessments of damage indicated that the rate of infestation was low at two out of three sites, perhaps due to abundant rain during the season. Treatments utilizing SPLAT Verb, with or without chlorpyrifos, failed to provide effective protection for treated trees from beetle attack, but both Beetle Guard treatments completely prevented crop damage.

Several ISCA repellent formulations also have been field-tested against RAB. A series of large-scale experiments were conducted from November 2016 to October 2017 at three

locations in North-central and Northwest Florida, selected for their recent history of laurel wilt infestation (Martini et al., 2020). The north-central trial sites were located at the Historic Haile Homestead in Gainesville and Ichetucknee Springs State Park in Fort White, while the northwestern trial was established at the Edward Ball Wakulla Springs State Park in Quincy. Each site comprised five blocks, assigned in a randomized complete block design to receive one of six treatments: (1) SPLAT Verb, single application; (2) Beetle Guard, single application; (3) SPLAT Verb double application; (4) Beetle Guard double application; (5) asymptomatic redbay without SPLAT Verb or Beetle Guard treatment, serving as a negative control; and (6) nonhost tree without SPLAT Verb or Beetle Guard treatment, also serving as a negative control (Martini et al., 2020). All SPLAT Verb and Beetle Guard treatments were applied via caulking gun to live redbay trees, as four 17.5-g point sources spaced evenly around the circumference of the trunk (70 g formulation/tree). Reapplications were made at the same rate and in the same pattern for treatments 3 and 4, totaling 140 g/tree over the course of the trial (Martini et al., 2020). At the Historic Haile Homestead and Ichetucknee Springs State Park, treatment blocks were separated by at least 20 m, and by 50 m at Edward Ball Wakulla Springs State Park (Martini et al., 2020). Treatment impacts were assessed based on trap capture rates of adult beetles, obtained through the placement of sticky card traps on all experimental trees, and monitoring of the trees for symptoms of laurel wilt. Traps were replaced and monitoring assessments were made every 2 weeks. To cope with a high frequency of 0 beetle capture rates at the two north-central locations, cumulative totals of all beetles captured over the course of the trial were used for data analysis (generalized linear model with Poisson distribution, treatment, and location as explanatory variables), while separate analyses were implemented for the northwestern site.

First and second application data were also analyzed separately at the Wakulla site, using a general linear mixed model (library MASS, function glmmPQL), with treatment and time as explanatory variables and block numbers as the random variable. A Poisson distribution was used for the first application, a negative binomial distribution for the second ($\theta=0.160$). Combined data on tree mortality from all three trial sites were subjected to Cox' survival analysis (Martini et al., 2020).

Trap monitoring revealed high RAB populations at Wakulla State Park, and low populations at Historic Haile Homestead and Ichetucknee Springs State Park (Martini et al., 2020). This was likely due to differences in pest infestation history among the different locations. While Historic Haile Homestead and Ichetucknee Springs State Park have been infested with RAB for several years, the first RAB was found in Wakulla State Park in November 2016. The Wakulla trial began in February 2017, when RAB populations were increasing, and in late September populations increased exponentially in the aftermath of Hurricane Irma. After the first application at Wakulla, traps placed on SPLAT Verb-treated trees showed significantly lower capture rates of RAB than those on control trees ($t\text{-value} = 3.763$, $P < .001$). Treatment with Beetle Guard showed no such effect, as there was no significant difference from control ($t\text{-value} = 3.763$, $P < .001$). Similar results were obtained following the second treatment applications (for treatments 3 & 4): trees treated with SPLAT Verb once or twice captured significantly fewer beetles than control ($t\text{-value} = 2.257$, $P = .035$; $t\text{-value} = 3.194$, $P = .005$), while no significant difference was observed for trees treated with Beetle Guard once or twice ($t\text{-value} = 1.649$, $P = .115$; $t\text{-value} = 0.36$, $P = .718$). SPLAT Verb's treatment effect was not significantly different between the single and double treatment. As expected, significantly fewer beetles were captured on nonhost trees compared to untreated host trees ($t\text{-value} = 3.837$, $P = .001$) (Martini et al., 2020). The Ichetucknee trial site had a

significantly higher RAB population, as measured by trap captures, than the Haile site (1.6 ± 0.79 ; 0.46 ± 0.10 , respectively). As at the Wakulla site, significantly fewer beetles were captured in traps placed on trees treated with a single (z value = 2.331, $P = .020$) or double application of SPLAT Verb (z value = 2.120, $P = .034$) than in control traps (Martini et al., 2020). Beetle trap captures on trees treated with Beetle Guard were not significantly different from the control, whether applied once (z value = 0.343, $P = .732$) or twice (z = 1.287, $P = .198$) (Martini et al., 2020). By the end of the trial, 40% of redbay trees that received no repellent treatment across the three trial sites suffered fatal infestations of laurel wilt. In trees treated with single or double applications of SPLAT Verb, only 13% died from the disease. Survival analyses that included trials from Martini et al. (2020) as well as new trials conducted in 2018, showed a significant decline in mortality due to laurel wilt when trees were treated with SPLAT Verb (Martini et al., 2020).

These results contradicted previous findings by Hughes et al. (2017a) and Martini et al. (2020), which demonstrated repellency of Beetle Guard against RAB in lab tests, and in small-scale field trials when applied to cut logs. To further elucidate the impact of Beetle Guard in the field vs. in the lab, an additional field trial was conducted in May 2018 against ambrosia beetle vectors of *R. lauricola* in avocado, *X. volvulus* (Fabricius) and *X. bispinatus* (Eichhoff) (Rivera et al., 2020). A 4-ha avocado orchard in Homestead, Florida, planted with the West Indian variety of the crop, was selected as the trial for its known incidence of laurel wilt infestation. Trees at this site were treated with fungicide, and any trees showing symptoms of laurel wilt were removed from the orchard, resulting in a low infestation rate at the time of the trial. A neighboring orchard, separated by a dirt road and a distance of ~10 m, was subject to unknown control practices; trees growing therein had visible symptoms of laurel wilt. This situation allowed for an effective assessment of the efficacy of the evaluated

repellents (deployed alone or as part of a push-pull strategy), as the presence of a presumably large beetle population from the neighboring orchard would ensure high pest pressure on the tested treatments. The first trial conducted at this location evaluated the effects of SPLAT Verb or Beetle Guard, each applied alone, compared to untreated control; and assessed whether their repellency extended beyond a range of 1 m. SPLAT formulations were applied as eight 1-g point sources to each tree in a 3×3 tree plot (0.05 ha/plot, five replicates per treatment). Four unbaited sticky traps were placed in each replicate plot, two on each of a pair of trees. One trap was placed 5–10 cm away from the applied Beetle Guard point source, and the other was placed 1–1.5 m away. Traps were collected and replaced every 10 days for 1 month, and all ambrosia beetles captured were counted.

A second trial was conducted in June 2018, testing a push-pull strategy using verbenone or methyl salicylate as a repellent (push) and ethanol as an attractant (pull) (Rivera et al., 2020). The experiment was installed in a split-plot design, with the “pull” as whole plot factor at two levels: (1) control, (2) ethanol dispensers (Synergy Semiochemicals, Burnaby, BC, Canada) and “push” as the split-plot factor at three levels: (1) control, (2) Beetle Guard, and (3) SPLAT Verb. Treatments were replicated three times. SPLAT applications were made in an identical manner as in the repellent trial, with a buffer row separating plots from each other. In the block assigned for treatment with ethanol, dispensers were applied to the buffer row separating the plots treated with SPLAT Verb and Beetle Guard. Two additional ethanol dispensers were placed on each west-facing border of the plot, to establish the “pull” whole plot factor. Unbaited sticky traps were placed at the west-facing edge of the control plots, facing the unmanaged avocado orchard neighboring the test site. As in the repellent trial, traps were placed at differing distances from SPLAT Verb or Beetle Guard point source (5–10 cm vs 1–1.5 m) and were

checked for ambrosia beetles every 10 days.

Trap capture data from the first field trial (repellent only) indicated that treatments had no overall effect on the number of ambrosia beetles caught in the field, with the exception of sentinel traps placed close to SPLAT Verb and Beetle Guard point sources, in which reduced captures were observed compared to controls ($F_1 = 3.37$, $P = .0682$) (Rivera et al., 2020). The number of beetles captured 20 days after treatment was significantly higher than captures at 10 or 30 days after treatment ($F_2 = 3.45$, $P = .0340$). No statistical difference was observed between traps placed close or far from SPLAT Verb and Beetle Guard point sources at 10 or 30 days after treatment, but analysis within treatment times at 20 days revealed that traps placed nearer to the repellent captured fewer beetles than control traps ($F_1 = 4.75$, $P = .0429$) (Rivera et al., 2020). Reduced capture rates were also observed at 20 days after treatment in traps placed close to point sources of Beetle Guard than in traps placed farther away or in control traps. No difference was observed between the “far” placed traps and control with either the SPLAT Verb or Beetle Guard formulations. In the push–pull trial, significant interaction was observed between the effects of the applied repellents (SPLAT Verb and Beetle Guard) and attractants (ethanol) in traps placed near treated trees (Rivera et al., 2020). Significantly fewer beetles were trapped in push–pull-treated plots than in the controls at 10 and 30 days after treatments were applied, using either SPLAT Verb or Beetle Guard as the “push” factor. This effect was not seen at the 20-day interval, likely because the beetle population across the treated site was lower at this time. In plots treated with the SPLAT Verb-based push–pull system, no beetles were captured. As in the repellents-only trial, no significant difference was observed in the number of beetles captured in “far”-placed traps and control traps in push- or push–pull-treated plots (Rivera et al., 2020). These results suggest that the push–pull system was more effective at

reducing trap capture rates of ambrosia beetles but only when traps were placed fewer than 10 cm away from the applied repellent. At the current stage of these products’ development, SPLAT Verb and Beetle Guard would need to be applied to every avocado tree in a given field to provide effective protection of the crop.

15.4.3 Future directions

Impacts of ambrosia beetle pests, while currently less well known and less visible than those of bark beetle pests, have both expanded and worsened in the last few decades. The appearance of RAB in Georgia in 2002 was followed by devastating ecological effects throughout the Lauracea-dominated forests of the American South. The fungal pathogen transmitted by this species, *R. lauricola*, or laurel wilt, has killed off an estimated one-third of the redbay trees in the United States and now threatens commercial avocado crops in Florida. BSB, presumably present for years in the forests around New York apple orchards without impacting them, has now spilled over into these orchards, introducing the deadly fungal disease, *Fusarium dieback*. A similar *Fusarium* pathogen has also appeared in Southern California with the emergence of a previously unknown ambrosia beetle species, polyphagous shot hole borer in that area, resulting in the loss of roughly 1.4 million USD in trees.

As with bark beetles, the sensitive natural environments where ambrosia beetle outbreaks occur demand a selective, ecologically sound approach to manage these pests. Beetle Guard provides a means of protecting susceptible trees from attack by ambrosia beetles without the application of toxic chemicals, instead relying on a combination of repellent semiochemicals, including the bark beetle antiaggregation pheromone, verbenone, and a kairomone produced by stressed or injured plants, methyl salicylate. Field trials with Beetle Guard are ongoing. The results obtained from these

studies provide evidence of the potential of a repellent strategy to deliver effective tree protection from ambrosia beetle attack—in trials against BSB in New York apple orchards, Beetle Guard completely suppressed crop damage by the target pest (Agnello et al., 2021)—as well as illumination of the importance of rigorous field testing. Beetle Guard displayed relatively high levels of repellency toward RAB when tested in lab trials, but results in the field were less consistent. Field studies in North Central and Northwestern Florida demonstrated that treatment with SPLAT Verb significantly decreased the number of RAB adults captured in baited traps, and decreased mortality due to laurel wilt. When tested in an avocado system, both SPLAT Verb and Beetle Guard were efficient in repelling beetle species responsible of laurel wilt. Additional trials evaluating both repellents, SPLAT Verb and Beetle Guard, alone or as part of a push-pull mechanism, revealed that the latter strategy was more effective in suppressing trap capture, but that both strategies were limited to a close range of activity.

Further work on Beetle Guard will include optimization of the agronomic application of the formulation to protect trees of interest, including avocado. Additional field trials will assess Beetle Guard's capacity to prevent or reduce attack by other invasive ambrosia beetle species of concern in the United States, including BSB in apples and polyphagous shot hole borer in urban forest environments.

15.5 Conclusion

Decades of reliance on a single tactic for agricultural pest control—cover sprays of broad-spectrum chemical pesticides like DDT, organochlorines, and organophosphates—have revealed the weaknesses of any such simplistic approach. As insects are infinitely varied and adaptable, so too must be the methods employed

to minimize their detrimental impacts on human health and prosperity. The resources offered by the field of arthropod chemical ecology, by the myriad chemical signals by which arthropods perceive and respond to various aspects of their environment, present an equally vast array of opportunities to investigate such means of mitigation, which has been previously underutilized, especially in agriculture and forestry applications. The repellent technologies described in this chapter, CBB Repel, SPLAT Verb, SPB Repel, MCH Repel, and Beetle Guard, have proven effective in field trials against seven beetle pest species of agriculture and forestry: *H. hampei*, *D. ponderosae*, *D. frontalis*, *D. pseudotsugae*, *D. rufipennis*, *X. glabratus*, and *X. germanus*. A similar repellent formulation is also being evaluated by Mafra-Neto et al. against darkling beetle, *Alphitobius diaperinus* Panzer, a major pest of the poultry industry. The varied applications for these semiochemical repellents in forestry, orchard crop agriculture, and animal husbandry demonstrate the largely untapped potential of insect semiochemicals in general to effect suppression of pest impacts without the introduction of large quantities of toxic chemicals.

This potential efficacy is, surprisingly, not limited to the insect world but can be deployed against other pest organisms as well. The wide-ranging utility of insect pheromones has been demonstrated by a recent collaborative project between ISCA Technologies and Wright et al. (2018), during which an alarm pheromone produced by honeybees in response to a perceived threat to the hive was examined for its impact on African bush elephants, *Loxodonta africana* Blumenbach. Elephants pose a threat to human communities in Africa by causing damage to farmland and infrastructure and may interfere with conservation priorities by trampling through preserved environments (Ngama et al., 2016; Cook et al., 2017; Wright et al., 2018), but because elephants are themselves members of a

protected species, means to minimize or prevent these impacts are limited. Elephants' natural aversion to African honey bee, *Apis mellifera scutellata* Lepeletier, colonies opens an opportunity to repel these animals away from sensitive areas without harming these animals and without the time and investment required to establish complete hives around the areas to be protected. When a crude approximation of the honey bee alarm pheromone (comprising a blend of isomyl acetate and 2-heptanone in equal proportions) was applied in field trials in the Greater Kruger Park Associated Private Nature Reserves, Limpopo Province, South Africa, incorporated into a prototype SPLAT formulation (20% AI blend by volume) and applied in 25-g point volumes in weighted white socks hung from tree branches, elephants responded not by bolting in fear, which could have created its own problems, but by stopping, turning in the direction of the semiochemical plume, and extending their trunks toward it before calmly moving away from the formulation (Wright et al., 2018).

The diversity of potential applications for repellent semiochemicals is an enormous asset in attempts to mitigate the impacts of destructive arthropods, which heretofore has not been accurately represented in the range of control applications adopted on a broad commercial scale. Arthropod repellents have been readily developed and adopted to protect people from blood-feeding arthropods such as ticks, mosquitoes, and other biting flies for much of the latter 20th and early 21st centuries, but relatively few analogous methods have been successful in agriculture or forestry applications. The studies reported herein provide strong evidence that the utility of pheromone- or semiochemical-based repellents is not limited to vector management but may also prove more broadly efficacious and cost-effective in meeting the challenges of pest control in the age of anthropogenic climate change, whether in regard to public health, agriculture, or natural resource management.

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