The Canadian Entomologist (2021), **153**, 121–135
doi:10.4039/tce.2020.61

Published on behalf of the Entomological Society of Canada

FORUM

Semiochemicals for bark beetle (Coleoptera: Curculionidae) management in western North America: where do we go from here?

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(Received 04 March 2020; accepted 20 May 2020; first published online 27 November 2020)

Abstract

This paper is intended as an assessment of the state of knowledge and development of semiochemical methods for control of bark beetles (Coleoptera: Curculionidae) in western North America and as a road-map for future research and development in this field. It is based on a keynote presentation given at the symposium *Managing Bark and Ambrosia Beetles with Semiochemicals*, held in 2018 in Vancouver, British Columbia, Canada, at the Joint Meeting of the Entomological Society of America, the Entomological Society of Canada, and the Entomological Society of British Columbia. We describe currently available active ingredients, formulations, and release devices. Furthermore, we describe the most urgently needed new products and techniques, and constraints to their further development. Finally, we speculate about opportunities afforded by new advances in microbial synthesis of semiochemicals, streamlining of regulatory processing, and aerial application using unmanned aerial vehicles.

Introduction

Since the first discovery of a bark beetle pheromone more than a half century ago (Silverstein *et al.* 1966), much progress has been made in the development of semiochemicals for the management of bark beetles (Silverstein *et al.* 1968; Silverstein 1981; Wood 1982; Borden 1985, 1997; Seybold *et al.* 2000, 2018; Gillette and Munson 2009; Progar *et al.* 2014). Researchers have already identified semiochemicals for many of the most damaging bark beetle species, primarily in the Scolytine genera *Dendroctonus* Erichson (Coleoptera: Curculionidae) and *Ips* De Geer (Coleoptera: Curculionidae) but also in *Pityophthorus* Eichhoff (Coleoptera: Curculionidae) (Borden 1997; Seybold *et al.* 2000; El-Sayed 2020). Furthermore, new application techniques are continually being developed (Holsten *et al.* 2002, 2003; Gillette *et al.* 2006; Mafra-Neto *et al.* 2013; Fettig *et al.* 2015, 2016).

Bark beetles nevertheless continue to cause enormous losses to western North American forests, compromising forest productivity, biodiversity, and crucial forest carbon sinks (Bentz *et al.* 2009; Hicke *et al.* 2016; Morris *et al.* 2018). There are several options for managing bark beetle damage, including silvicultural treatments, insecticides, and semiochemicals (Gillette *et al.* 2014b). Semiochemical treatments often do not yield total control, but they are widely favoured over both insecticide treatments, which may have negative nontarget effects, and silvicultural methods, which are expensive and cumbersome (Progar *et al.* 2014). Although we do have effective

Subject editor: Andrew Graves

semiochemicals for management of some bark beetle species, many of these products are too expensive for widespread use. For example, one of the most effective repellents, conophthorin, is effective against many bark beetle species (Borden *et al.* 1998; Huber *et al.* 2000, 2001; Huber and Borden 2001a, 2001b; Graves *et al.* 2008), but its synthesis is currently prohibitively expensive for most forestry uses (Unelius *et al.* 2014). The search for improved semiochemical treatment methods is a multifaceted challenge requiring basic science to identify allomones, kairomones, and pheromones, laboratory and field bioassays to confirm behavioural activity, development of controlled-release devices to diffuse the active ingredients at an ethologically relevant rate during beetle flight, and regulatory approvals to make such products available for commercial development and use. The situation is further complicated by the fact that most applications occur on public lands in western North America, where human and environmental safety are paramount and treatment areas are often remote, rugged, and expansive.

Climate trends indicate a progressively worsening situation for forests globally, with drought and increasing temperatures expected to further stress forest ecosystems and exacerbate the negative impacts of bark beetles on forests (Raffa *et al.* 2008; Bentz *et al.* 2009, 2010; Jamieson *et al.* 2012; Kolb *et al.* 2016). There exists, therefore, an acute need for a more intensive focus on research and development of more effective and economical methods for tree protection, from the individual-tree level to the landscape level. Indeed, a recent meta-analysis established strong evidence for an overall treatment effect of anti-attractant treatments for the genera *Dendroctonus* and *Ips*, suggesting great promise for such a research investment (Schlyter 2012). In this paper, we focus primarily on the most damaging western North American bark beetles, the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) (Coleoptera: Curculionidae), the Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins) (Coleoptera: Curculionidae), the spruce beetle (*Dendroctonus rufipennis* Kirby) (Coleoptera: Curculionidae), and the western pine beetle (*Dendroctonus brevicomis* Le Conte) (Coleoptera: Curculionidae).

Release devices and active ingredients

The mostly commonly used release devices have been polymeric matrix reservoirs (bubble capsules, or "bubblecaps," and pouches) that release semiochemicals slowly and passively through a plastic membrane (Fig. 1A,B). Two newer release devices are flakes (Fig. 1C; Hercon Environmental Inc., Emigsville, Pennsylvania, United States of America) consisting of small laminated plastic or biodegradable chips with a pheromone-releasing layer in the middle, and SPLAT® (Fig. 1D), consisting of a spreadable wax-emulsion matrix incorporating semiochemicals (Specialized Pheromone & Lure Application Technology, ISCA Technologies Inc., Riverside, California, United States of America). In addition, there is a laminated pheromone-releasing polymer strip that can be hand applied from ground level. These release devices and their applications are summarised in Table 1. Currently registered active ingredients include verbenone (4,6,6-trimethylbicyclo[3.1.1]hept-3-en-2-one) and MCH (3-methylcyclohex-2-en-1-one). Currently available commercial products include: Verbenone – Beetleblock Verbenone (ChemTica USA, Durant, Oklahoma, United States of America), Disrupt MicroFlake® VBN (Hercon Environmental Inc., Emigsville, Pennsylvania, United States of America), Disrupt BioFlake® VBN (Hercon Environmental Inc.), Synergy Shield Verbenone Pouch and Bubble (Synergy Semiochemical Corp., Burnaby, British Columbia, Canada), Verbenone Pine Beetle Repellent Pouch (ISCA Technologies Inc.), and SPLAT® Verb Bark Beetle Repellent (ISCA Technologies Inc.) for *D. ponderosae* and other bark beetles; and MCH – Beetleblock MCH (ChemTica USA), Disrupt® MCH HA (Hercon Environmental Inc.), Disrupt MicroFlake® MCH (Hercon Environmental Inc.), MCH Douglas-fir/Spruce Beetle Repellent BC (ISCA Technologies Inc.), and Synergy Shield MCH Bubble and Double Bubble (Synergy Semiochemical Corp.) for *D. pseudotsugae* and *D. rufipennis*. In addition, there are several products in the development pipeline,

Table 1. Examples of commonly used release devices for bark beetle (Coleoptera: Curculionidae) semiochemicals.

Release device	Scale of use (ha)	Commonly targeted insects	References
Bubblecaps	<10	*Dendroctonus pseudotsugae*, *D. rufipennis*	Lindgren *et al.* 1989a, 1989b; Ross *et al*. 1996, 2002, 2004; Sánchez Martínez *et al.* 2012; Hansen *et al*. 2017, 2019
Pouches	<10	*D. ponderosae*	Lindgren *et al.* 1989a; Borden et al. 2003, 2006; Bentz *et al.* 2005; Progar 2005; Kegley and Gibson 2009; Kegley *et al.* 2010; Fettig *et al.* 2012a, 2012b
SPLAT®	<10	*D. ponderosae*, *D. pseudotsugae*	Mafra-Neto *et al*. 2013, 2014; Fettig *et al.* 2016; Foote *et al.* 2020
Plastic flakes	<10	*D. ponderosae*	Gillette *et al*. 2006, 2014a
Plastic flakes	≥10	*D. ponderosae*, *D. pseudotsugae*	Gillette *et al.*, 2009a, 2009b, 2012a, 2012b; Sánchez Martínez *et al.* 2012; Sánchez Martínez 2018
Biodegradable flakes	≥10	*D. ponderosae*	Gillette *et al.* 2009c

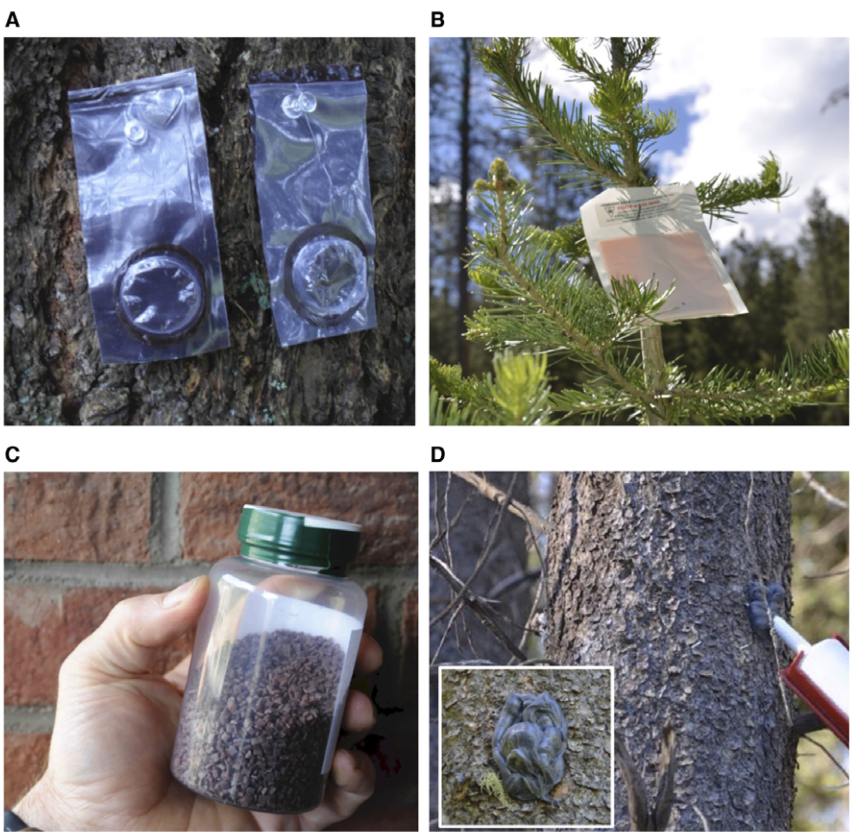

Fig. 1. Release devices for bark beetle semiochemicals include: **A**, bubbles (Synergy Semiochemical Corp., Burnaby, British Columbia, Canada); **B**, pouches (ISCA Technologies Inc., Riverside, California, United States of America); **C**, flakes (Hercon Environmental Inc., Emigsville, Pennsylvania, United States of America); and **D**, SPLAT® (ISCA Technologies Inc.). Photo credits: **A**, R.A. Progar, United States Department of Agriculture Forest Service; **B** and **D**, C.J. Fettig, United States Department of Agriculture Forest Service; and **C**, W. Murray, Department of Biological Sciences, San Jose State University, San Jose, California, United States of America.

Table 2. A summary of area-wide bioassays of pheromone-releasing flakes for bark beetle (Coleoptera: Curculionidae) management in western North America.

Site*	Year (plot size/no.)[†]	Treatment[‡]	Host species§	Beetle species‖	Beetle pressure[#]	% Reduction in attack	References
ID	2005 (20.2/5)	VBN	Pico	MPB	5.1	73	Gillette *et al.* 2009a
CA	2005 (20.2/5)	VBN	Pico	MPB	4.6	63	Gillette *et al.* 2009a
WY	2005 (4.05/5)	VBN	Pial	MPB	26.5	60	Gillette *et al.* 2012a
WA	2005 (4.05/5)	VBN	Pial	MPB	29.2	50	Gillette *et al.* 2012a
CA	2008 (4.05/5)	VBN	Pico	MPB	102.4	56	Gillette *et al.* 2012b
MT	2010 (2.02/5)	VBN	Pico, Pial	MPB	19.3	89	Gillette *et al.* unpublished
WA	2010 (0.81/3)	VBN	Pial	MPB	29.2	33	Gillette *et al.* 2012b
CO	2009 (32.4/1)	VBN	Pico	MPB	7.0	86	Gillette *et al.* 2009c
WA	2006 (4.05/5)	MCH	Psme	DFB	6.2	98	Gillette *et al.* 2009b
CH	2009 (1.0/4)	MCH	Psme	DFB	2.8	100	Sánchez Martínez *et al.* 2012

*CH, Chihuahua (Estados Unidos Mexicanos (Mexico)); CA, California; CO, Colorado; ID, Idaho; MT, Montana; WA, Washington; WY, Wyoming (United States of America).
[†]Year of treatment application (plot size in hectares per number of replicated plots).
[‡]VBN, verbenone; MCH, methylcyclohexenone.
[§]Pico, *Pinus contorta*; Pial, *Pinus albicaulis*; Psme, *Pseudotsuga menziesii*.
‖MPB, mountain pine beetle, *Dendroctonus ponderosae*; DFB, Douglas-fir beetle, *Dendroctonus pseudotsugae*.
[#]Beetle pressure was estimated using previous year attack rate, as measured by number of stems per hectares attacked.

including SPLAT® MCH for *D. pseudotsugae* (Foote *et al.* 2020), MCH + AKB for *D. rufipennis* (Hansen *et al.* 2019), SPLAT® Verb Plus for *D. brevicomis* (Fettig *et al.* 2012b), and a blend of limonene and conophthorin for the walnut twig beetle, *Pityophthorus juglandis* Blackman (Coleoptera: Curculionidae) (Audley *et al.* 2020).

Bubblecap, pouch, and SPLAT® releasers often provide good protection from beetle attack (Gillette and Munson 2009; Seybold *et al.* 2018), but results can vary depending on the semiochemical used, beetle population densities, stand structure, and tree stress, among other factors (Bentz *et al.* 1989, 2005; Huber and Borden 2001a, 2001b; Fettig *et al.* 2009b; Kegley and Gibson 2009; Kegley *et al.* 2010; Sánchez Martínez *et al.* 2012). 3-Methylcyclohex-2-en-1-one is generally much more effective for *D. pseudotsugae* than is verbenone for *D. ponderosae*, regardless of the release device. On its own, MCH has not been consistently effective against *D. rufipennis*, but MCH in conjunction with the new nonhost blend, AKB, has shown good efficacy in several studies (Hansen *et al.* 2016, 2017, 2019). The MCH + AKB blend will be commercially available in 2020 (Synergy Semiochemical Corp.). More recently, a nonhost blend used in conjunction with SPLAT® MCH has also shown great promise for use against *D. rufipennis* in Engelmann spruce, *Picea engelmannii* Parry ex Engelm. (Pinaceae) (Fettig *et al.*, unpublished). Verbenone alone has not proven to be consistently effective for protection of ponderosa pine, *Pinus ponderosa* Dougl. ex Laws. (Pinaceae), from *D. brevicomis* or *D. ponderosae* (Negrón *et al.* 2006; Fettig *et al.* 2009a). Verbenone in conjunction with a blend of nonhost volatiles, Verbenone Plus, has shown some promise based on studies in British Columbia, Canada and California, United States of America (Fettig *et al.* 2009b, 2012a, 2012b) but has yet to be commercialised. Light applications of MCH-flake releasers (371–1112 g/ha) over large areas yield good results for protection of Douglas-fir, *Pseudotsuga menziesii* (Mirbel) Franco (Pinaceae), from *D. pseudotsugae* (98–100% reduction in tree attack or mortality; Gillette *et al.* 2009b; Sánchez Martínez *et al.* 2012), and verbenone flakes show reasonably good reductions (33–89%) in tree attack by *D. ponderosae* in area-wide applications in several hosts, especially at low-to-moderate beetle populations (Table 2).

Needs and constraints

Future progress in the development of semiochemical methods for bark beetle management depends upon: (1) identification of new semiochemicals and blends; (2) assessment of the role of optical isomers in beetle behaviour; (3) development of less expensive methods for synthesising semiochemicals; (4) improvements in release-device performance (to include development and refinement of biodegradable releasers); (5) assessment and optimisation of various single-tree and area application tactics (*e.g.*, antiaggregation, trap-out, and push–pull); (6) improvements in application methods, particularly aerial application; and (7) regulatory streamlining to expedite the commercial availability of products to resource managers. Research to support these activities is expensive, but cost–benefit analyses for agricultural products indicate a cost–benefit ratio of \$2655 to \$26 548 (U.S. dollars) per dollar spent on research (Bento *et al.* 2016). Although benefits to forest health are more difficult to quantify than those to agricultural crops, concerns about carbon sequestration and climate change (Vose *et al.* 2018) support a different sort of valuation – one based on ecosystem services that depend on healthy, intact, and diverse forests.

The discovery and development of new semiochemical active ingredients is a laborious process involving isolation of headspace volatiles from insects and plants and assessment of their neurophysiological activity using electroantennogram detection (EAD), followed by identification of the behaviourally active compounds using analytical chemical instruments such as gas chromatography/mass spectrometry (GC/MS). Coupled GC–EAD assays may be conducted to confirm the neurophysiological responses to individual active ingredients. While GC–EAD yields information regarding which chemicals an insect is capable of perceiving, it cannot reveal the behavioural response (*i.e.*, is it attractive or repellent, or does it simply inhibit an insect's response to attractants?). Furthermore, GC–EAD cannot assess the activity of blends of chemicals on insect response, because with GC–EAD the chemicals are presented singly. The behavioural activity of individual active ingredients and blends at the level of the organism, therefore, requires exhaustive and often repetitive laboratory olfactometer and wind tunnel assays, followed by field trials to determine insect responses using both baited traps and baited trees, small stands, and eventually larger forest stands. In the latter stages of research, the responses of nontarget insects such as predators, parasitoids, and pollinators are conducted to assess the risk of unintended treatment effects.

As mentioned, MCH is extremely effective as a single-component semiochemical for the protection of *Ps. menziesii*, but more effective products are needed for all of the pine-killing species of *Dendroctonus* (where verbenone alone has not always been as effective as desired) and for *D. rufipennis* in Alaska, United States of America, where MCH + AKB is less effective (Hansen *et al.* 2019). Beetles such as fir engraver, *Scolytus ventralis* (Le Conte) (Coleoptera: Curculionidae), western balsam bark beetle, *Dryocoetes confusus* (Swaine) (Coleoptera: Curculionidae), and many *Ips* species also have the potential to cause landscape-scale tree mortality (Bentz *et al.* 2010) and, thus, present additional challenges for forest pest management using semiochemicals. These chemical–ecology challenges have typically been addressed by researchers in government and academia, but innovations in release device technology have usually been the domain of the semiochemical industry and are understandably largely market-driven. In more recent years, government agencies, academia, and industry have worked more closely on all aspects of bark beetle semiochemical innovation. As an example, the development of SPLAT® Verb, a highly effective flowable formulation, resulted from collaborations between government scientists and the semiochemical industry (Mafra-Neto *et al.* 2013; Fettig *et al.* 2015). Industry–government collaboration has also resulted in new active ingredient registration applications for Synergy Shield GVLM and AKB (Synergy Semiochemical Corp.) to be used as adjuvants for verbenone and MCH, respectively (David Wakarchuk, personal communication). Because bark beetle semiochemicals are often applied on public lands throughout western North America, there is a need for both biodegradable dispersible releasers and "discrete retrievable dispensers" that are made of polymeric matrix materials and are intended to be removed after depletion (United States Government Printing Office 2012).

In addition to these fine-scale issues, there remain substantial questions regarding the optimal tactics and strategies for bark beetle management using semiochemicals. For example, while antiaggregation methods using repellent semiochemicals (the "push" tactic; Gillette and Munson 2009) have been the most thoroughly tested approach, there remain unanswered questions about the comparative efficacy of other tactics, such as push–pull (a combination of attractant-baited traps or baited trees placed near areas treated with antiaggregation formulations; Borden *et al.* 2006; Gillette *et al.* 2012b; Hansen *et al.* 2019) and trap-out (using attractant-baited traps or baited trees to concentrate bark beetle populations; Bedard and Wood 1981; Gray and Borden 1989; Progar *et al.* 2010; Hansen *et al.* 2019).

Studies to resolve these questions require replicated and controlled tests over large areas where sources of heterogeneity (*i.e.*, stand structure, beetle populations, and tree stress) are difficult to measure and account for as covariates. Once all of these issues have been adequately resolved, the hurdles of regulatory approvals at multiple levels of government remain. These hurdles include fees for registration and costs of human and environmental health testing requirements, such as mammalian acute oral, dermal, and inhalation toxicities, and extensive avian, fish, host plant, and nontarget insect effects (United States Code of Federal Regulations 2019). Although testing to assess human and environmental effects of active ingredients is cumbersome and costly, forest trees are a minor use crop, which may make them commercially marginal for investment by industry. Some effective new active ingredients, therefore, remain unexplored by industry and unavailable for commercialisation and widespread use in forest pest management. The recent increasing movement of human populations into the wildland–urban interface, however, has resulted in an increased demand for green, safe, semiochemical solutions to manage bark beetles in those landscapes and may drive further development of commercially viable products.

New opportunities

Despite the obstacles described above, some promising avenues exist for overcoming constraints to semiochemical bark beetle management (Seybold *et al.* 2018). These include: (1) regulatory harmonisation across countries and agencies; (2) development of new biodegradable formulations for release devices; (3) advances in microbial synthesis of active ingredients; (4) transgenic plants that produce relevant semiochemicals; and (5) developments in unmanned aerial vehicle (drone) technology for application of semiochemicals to large expanses.

Regulatory harmonisation is an effort that began in North America decades ago with North American Free Trade Agreement support for harmonisation of biopesticide regulations across North America, to include the United States of America, Canada, and Mexico (United States Environmental Protection Agency 2016). In 1998, a technical working group comprising members from all three countries began to develop joint standards for assessing and registering biopesticides. In the intervening decades, initiatives have sprung up to harmonise these standards across continents and globally, including in Asia, Africa, North America, South America, and the European Union (Odong 2009; Food and Agriculture Organization of the United Nations 2013, 2019; Arora *et al.* 2016; Frederiksa and Wesselerb 2019). Furthermore, the Organisation for Economic Coordination and Development has developed a programme to harmonise pesticide testing and registration across member countries in Europe, the United Kingdom, North America, South America, and Oceania (Organisation for Economic Coordination and Development 2019). Although progress is slow, the increasing market share of biopesticides in the overall pesticide market, driven largely by consumer demands for residue-free produce and protection of biodiversity, has increased global attention to the need for regulatory streamlining for biopesticides (Olson 2015).

Advances in the development of biodegradable semiochemical-release devices have been driven largely by the medical market, but more recently greater attention has been given to the use of such

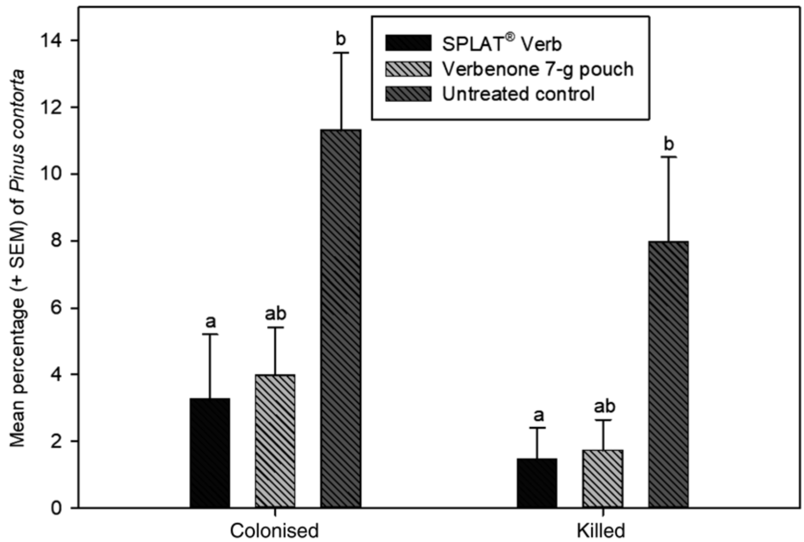

Fig. 2. Mean percentages (+SEM) of *Pinus contorta* colonised and killed by *Dendroctonus ponderosae* on 0.4-ha square plots treated with SPLAT® Verb (ISCA Technologies Inc., Riverside, California, United States of America) and 7-g verbenone pouches (ISCA Technologies Inc.), Caribou-Targhee National Forest, Idaho, United States of America, 2012–2013. Means (+SEM) followed by the same letter within group are not significantly different (Tukey's HSD; $P > 0.05$). Adapted from Fettig *et al.* (2015).

products in agriculture (Zada *et al.* 2009; Jadhav *et al.* 2011; Mafra-Neto *et al.* 2013, 2014). Sol–gel (Zada *et al.* 2009; Jadhav *et al.* 2011) and flowable semi-liquid (Mafra-Neto *et al.* 2013, 2014) formulations have obvious uses for individual-tree and small-stand applications where hand-applied releasers can be deployed easily. This type of product has demonstrated efficacy for use with bark beetle semiochemicals in individual-tree and small-area bioassays (Fig. 2). Release devices that can be aerially broadcast, such as semiochemical-releasing flakes, have been produced in a biodegradable laminated-flake formulation and have demonstrated efficacy over both small and large areas (Gillette *et al.* 2009c, 2012a, 2014a; Sánchez Martínez *et al.* 2012). Considering the overriding importance of biodegradable products for use on public lands, we encourage further research and development into these materials for use as semiochemical-release devices.

The need for cheaper, purer, and more effective active ingredients may soon be met using transgenic microbial pheromone "breweries" that harness genetically modified microbes (yeasts and bacteria) to produce chemically pure stereoisomers of semiochemicals at vastly reduced cost (Chang and Keasling 2006; Macek *et al.* 2008; Kirby and Keasling 2009; Bruce *et al.* 2015). Similarly, researchers in Sweden are developing transgenic *Nicotiana* (Solanaceae) plants that produce moth sex pheromones of high purity with minimum hazardous waste (Ding *et al.* 2014). While transgenic agricultural plants are already in widespread use for short-cycle crops (Bruce *et al.* 2015), we expect that transgenic forest trees are unlikely to be accepted on public lands in the foreseeable future because of public concerns about genetic pollution and unintended consequences for native forests (Strauss *et al.* 2015). On the other hand, research and development efforts to develop microbial synthesis of pharmaceuticals and biofuels have been underway for decades (Chang and Keasling 2006), and many of the drug and biofuel targets are based on isoprenoid compounds that are structurally similar to bark beetle pheromones (Seybold *et al.* 2006). We expect that semiochemicals produced by genetically engineered micro-organisms and forbs will be more readily accepted by the public and regulatory agencies for use on public lands than transgenic trees will be, because using microbe- and plant-produced semiochemical products poses little long-term ecological risk compared to introducing long-lived bioengineered trees to complex forest environments. Two further promising developments are the creation of CRISPR-Cas9 techniques (Doudna and Charpentier 2014) and "prime editing" (Anzalone *et al.* 2019) for more rapid and precise genome editing. The CRISPR-Cas9 techniques are particularly useful in genome editing of model organisms such as yeasts and bacteria, and these techniques are expected to generate much more efficient and rapid development of microbially produced isoprenoid compounds (Jakočiūnas *et al.* 2016). Prime editing is currently limited to human-disease applications but has great promise for a wider variety of targets. We hope that these new techniques will be adopted for the production of bark beetle semiochemicals, thereby reducing the cost and increasing the purity of semiochemicals available for use in forest pest management.

The use of drones in forestry is rapidly evolving for several kinds of applications (Hartley 2017). In the recent past, applications were limited by the technical limitations of drones to uses such as forest inventory, wildfire assessment, and forest health monitoring. For example, until recently, payload limits were as low as the 22-kg range, which would seriously limit the areas that could be reasonably treated with semiochemicals by drones (*e.g.*, verbenone flakes are currently labelled for application rates of 2.47–7.4 kg/ha of formulated product). Furthermore, until recently, battery life was insufficient to maintain flight for area-wide treatments, especially in remote areas of mountainous terrain. Obviously, there will always be a trade-off between payload weight and flight duration, but recent advances in "megadrones" and "quadcopters" have vastly increased payloads (up to 440 kg), and a newly developed drone with 18 rotors is specifically designed for application of pest management products such as pesticides, fertilisers, pheromones, and other semiochemicals (Volocopter, Bruchsal, Germany). Drone application of semiochemicals would appear to be ideally suited for forestry situations, where spatial constraints, remote locations, and steep terrain limit ground applications and the use of helicopters and fixed-wing aircraft (Hartley 2017). The technology is now available for testing in forest pest management applications (Hartley 2017; King 2017; Kislaya and Goutam 2019). Indeed, Anderson (2014) reports that, in 2014, agricultural drones were named the number-one breakthrough technology for that year. As such, we envision greater use of this technology in forest pest management in the future.

Conclusions

We emphasise that forest stand management, specifically thinning to increase tree and stand resistance and resilience, is still the lynchpin of bark beetle management (Wood *et al.* 1985; Gillette *et al.* 2014b). Stand management is considered indirect control, because it aims to minimise tree losses to bark beetles by focussing on stand conditions rather than by targeting the beetles themselves (Wood *et al.* 1985; Progar *et al.* 2013; Fettig and Hilszczański 2015). Nevertheless, in many situations, especially in high-value developed recreation settings (*e.g.*, campgrounds) or around homes in the wildland–urban interface, homeowners or resource managers are constrained from implementing stand treatments and must therefore rely on direct bark beetle control. Of all the direct control methods available to manage bark beetles (Fettig and Hilszczański 2015), semiochemical treatments are highly favoured because of their negligible effects on nontarget species, including other invertebrates, wildlife, and humans (Seybold *et al.* 2018). In the face of recent extensive bark beetle outbreaks in western North America (Bentz *et al.* 2009), it is our hope that new advances in the production of semiochemicals by microbes, regulatory streamlining, and unmanned aerial application will provide land managers with cheaper and more effective means to mitigate tree mortality attributed to bark beetles and its associated effects on a variety of resource objectives and ecological goods and services produced by forests.

Acknowledgements. Collaboration and cooperation have been essential to our past successes in the development and registration of semiochemicals for protection of this minor use crop. We applaud our many colleagues and cooperators who have contributed to this success. Critical among them are academic and government researchers, government resource managers in land management agencies at the state, provincial, *estadal*, and federal levels, the semiochemical industry, and private small- and large-scale landowners who have contributed their resources to this effort. In particular, we extend profound thanks to our forest health colleagues at all levels of government. We also thank A. Steven Munson (United States Department of Agriculture Forest Service, Forest Health Protection, Ogden, Utah, United States of America) for a very helpful review of this manuscript.

The authors wish to express their immense respect and gratitude for our deceased friend and colleague, Dr. Steven J. Seybold, whose contributions to our field are incalculable. He is sorely missed.

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Cite this article: Gillette, N.E. and Fettig, C.J. 2021. Semiochemicals for bark beetle (Coleoptera: Curculionidae) management in western North America: where do we go from here? The Canadian Entomologist, **153:** 121–135. https://doi.org/10.4039/tce.2020.61.