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Managing bark and ambrosia beetles (Coleoptera: Curculionidae: Scolytinae) with semiochemicals

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Abstract
On 14 November 2018, a symposium *Managing bark and ambrosia beetles with semiochemicals* was held 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. The focus was on the application of behavioural chemicals for management of bark and ambrosia beetles (Coleoptera: Curculionidae: Scolytinae) in conifers and hardwoods in North America and Europe. Contributors included nine invited speakers from Canada, Slovakia, and the United States of America who summarised the current state of knowledge and latest technologies and shared career-long experiences and insights. This special issue features publications derived from those presentations.

Bark and ambrosia beetles (Coleoptera: Curculionidae: Scolytinae) are among the most pernicious pests of forest and shade trees in the Northern Hemisphere (Figs. 1–2), and their cryptic (endophytic) habits have posed obstacles to their management for centuries from the level of individual trees to forested landscapes (Furniss and Carolin 1977; Fettig and Hilszczański 2015). They are taxonomically diverse organisms with a wide range of host fidelity (Wood and Bright 1992; Bright 2014). Populations of some species can increase rapidly (Bentz *et al.* 2009; Marini *et al.* 2017), and several notable tree-killing species appear to be capitalising on our changing climate (Bentz et *al.* 2010; Marini *et al.* 2012; Jakoby *et al.* 2019). During recent decades, substantial basic and applied research has been devoted to the development of effective tools and tactics for mitigating undesirable levels of tree mortality attributed to bark and ambrosia beetles (Bentz *et al.* 2020).

The genesis of the symposium *Managing bark and ambrosia beetles with semiochemicals*, and this special issue, was a synthesis published in the *Annual Review of Entomology* developed by a group of United States Department of Agriculture Forest Service research and development scientists from the western United States of America (Seybold *et al.* 2018). The synthesis highlighted the progress that has been made concerning the application of semiochemicals for management of conifer bark beetles in western North America. This team received substantial input from several Canadian colleagues, so it seemed appropriate to revisit the content of the synthesis article through a symposium format at an inspiring Canadian venue. Unlike the scope of the synthesis, we chose to expand the symposium programme to include presentations on ambrosia beetles,

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Fig. 1. California experienced a severe drought in 2012–2015 inciting a large bark beetle outbreak in the central and southern Sierra Nevada mountain range. At lower elevations, most of the tree mortality was attributed to western pine beetle (*Dendroctonus brevicomis*), a species that readily colonises drought-stressed ponderosa pine (*Pinus ponderosa* Douglas *ex* Lawson; Pinaceae) (Kolb *et al.* 2016). Photograph by Christopher J. Fettig, United States Department of Agriculture Forest Service.

which are major native, wood-boring pests of conifers in western Canada (Orbay *et al.* 1994) and also prominent invasive species of hardwoods in other parts of North America (Hulcr and Dunn 2011; Hughes *et al.* 2015; Coleman *et al.* 2019). The inclusion of hardwood pests also served to broaden the topic area of threatened habitats from forests to nurseries, ornamental plantings, orchards, urban landscapes, and forests.

Bark beetles and their semiochemicals have played a major role in the origin and development of the science of chemical ecology (Fig. 3). The functional terminology of signals involved in chemical ecology (*e.g.*, pheromone, allomone, kairomone, synomone) (Wood 1982; Seybold *et al.* 2018) found early illustrations in the primary and collateral behavioural activities of bark beetle aggregation pheromones during field testing in California, United States of America in the 1960s. Isolated or synthetic materials for two pine bark beetles, *Ips paraconfusus* Lanier and the western pine beetle (*Dendroctonus brevicomis* LeConte), attracted not only the target pest but also various natural enemies, while repelling competing bark beetles (Wood *et al.* 1967, 1968; Bedard *et al.* 1969). Verbenone [(1 *R*)-*cis*-4,6,6-trimethylbicyclo[3.1.1]hept-3-en-2-one], now regarded as a "universal" behavioural repellent (anti-aggregation pheromone) for many bark beetles (Seybold *et al.* 2018), was also identified as a pine bark beetle-associated natural product during this era of pioneering investigations (Renwick 1967).

The exquisite behavioural specificity elicited by some of the earliest isolated natural products relied on blends of optical isomers (enantiomers) of the components (Borden *et al.* 1976; Wood *et al.* 1976; Birch *et al.* 1980). In some instances, substantial amounts of both an enantiomer and its antipode were required to elicit the full behavioural response, whereas in other cases, the opposite isomer was inactive. With western populations of the pine engraver (*Ips pini* (Say)), the antipode interrupted the flight response to the behaviourally active enantiomer, (*R*)-(–)-ipsdienol (2-methyl-6-methylene-2,7-octadien-4-ol) (Birch *et al.* 1980). At the conclusion of this discovery period, it became clear that the semiochemicals that govern the diversity of behavioural interactions among bark and ambrosia beetles and the subcortical community (Fig. 4) may be useful to land managers as tools of integrated pest management and, specifically, in insect control (Silverstein 1981). Further research demonstrated the complexity of the olfactory environment within forests and that for widely distributed bark beetle species, there can be variability in

Fig. 2. *Xyleborus glabratus* Eichhoff (redbay ambrosia beetle) is native to Asia but was introduced into coastal forests of Georgia, United States of America, in 2002. This species vectors a wilt fungus (*Raffaelea lauricola* Harrington *et al*.; Ophiostomataceae) that has now resulted in mortality of hundreds of millions of redbay (*Persea borbonia*) with substantial negative consequences to these sensitive ecosystems (Evans *et al*. 2014). Of further concern, climate change may facilitate the northward spread of redbay ambrosia beetle to sassafras (*Sassafras albidum* (Nuttall) Nees; Lauraceae) in the central and northeastern United States of America (Nielsen and Rieske 2015). Photograph by Jason A. Smith, University of Florida (Gainesville, Florida, United States of America).

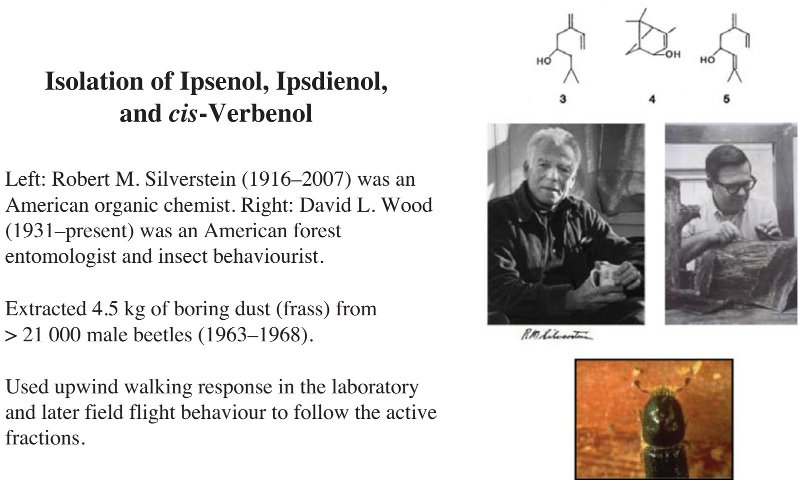

Fig. 3. Isolation and identification (1963–1968) of the aggregation pheromone of *Ips paraconfusus* Lanier (California fivespined ips) was a landmark step in the nascent science of chemical ecology (Silverstein *et al*. 1966; Tumlinson and Wood 2011). The three monoterpene alcohols that comprise the aggregation attractant of this pine bark beetle provided the first example of a multicomponent pheromone, whose elements work in synergy to elicit the behavioural response. It was also the first recorded instance of a pheromone that did triple duty as an allomone [repelling the competing *Ips latidens* (LeConte) and later the western pine beetle (*Dendroctonus brevicomis*) and red turpentine beetle (*Dendroctonus valens* LeConte)] and as a kairomone (attracting several bark beetle predators) (Wood *et al*. 1967, 1968; Paine and Hanlon 1991; Fettig *et al*. 2005).

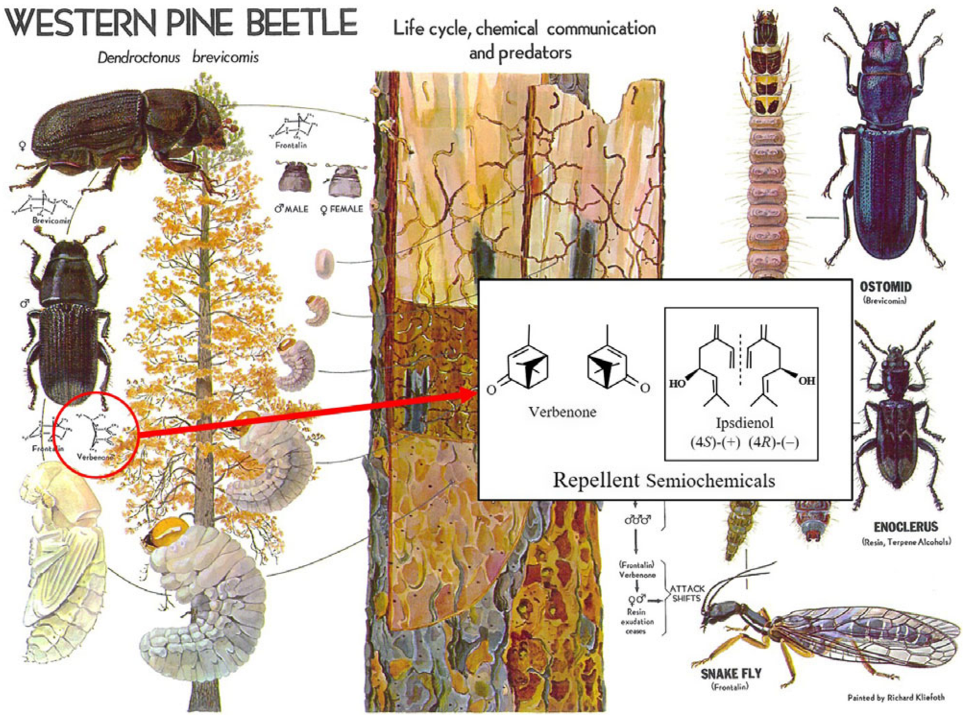

Fig. 4. Partial subcortical community of western pine beetle (*Dendroctonus brevicomis*) in ponderosa pine (*Pinus ponderosa*) illustrating semiochemical-guided interactions in which attractive pheromone components (*e.g.*, *exo*-brevicomin and frontalin) elicit aggregation behaviour, mating, and brood production, whereas repellent pheromone components [verbenone and (*S*)-(+)-ipsdienol] regulate intraspecific competition (Byers *et al.* 1984; Paine and Hanlon 1991). The latter also regulates population densities of competing bark beetles (as allomones), but attracts predators such as *Enoclerus lecontei* (Wolcott) (Coleoptera: Cleridae) and *Temnochila chlorodia* (Mannerheim) (Coleoptera: Trogositidae) (as kairomones). Modified from Boyce Thompson Institute of Plant Research.

the production and response to semiochemicals among populations, such that there are in essence olfactory dialects in different parts of the range.

Modern semiochemical-based tools and tactics for bark and ambrosia beetles range from monitoring and detection of native and invasive species to protection of individual trees and small landscapes. These approaches have been illustrated in depth in a series of case studies of four of the most damaging western North American bark beetles, mountain pine beetle (*Dendroctonus ponderosae* Hopkins), Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins), spruce beetle (*Dendroctonus rufipennis* (Kirby)), and *D. brevicomis* (Seybold *et al.* 2018). Application of pheromone-baited multiple funnel traps (Lindgren 1983) for the detection and evaluation of spread of the invasive *Orthotomicus erosus* (Wollaston) across urban areas of the southwestern United States of America and detection of the invasive *Pityophthorus juglandis* Blackman across the black walnut (*Juglans nigra* Linnaeus; Juglandaceae) "breadbasket" of the eastern United States of America are recent examples of the use of semiochemicals for revealing low-density and newly established populations (Seybold *et al.* 2015, 2018, 2019; Fig. 5). With the latter invasive species, volatiles from hosts and nonhosts, as well as verbenone, are under investigation to protect relatively high-value English walnut (*Juglans regia* Linnaeus) orchards in the Central Valley of California (Audley *et al.* 2016). In two other hardwood systems, redbay (*Persea borbonia* (Linnaeus) Sprengel; Lauraceae), a coastal species native to the southeastern United States of America, and in orchards of avocado (*Persea americana* Miller; Lauraceae), repellency of the invasive *Xyleborus glabratus* Eichhoff may figure prominently in future management (Martini *et al.* 2019).

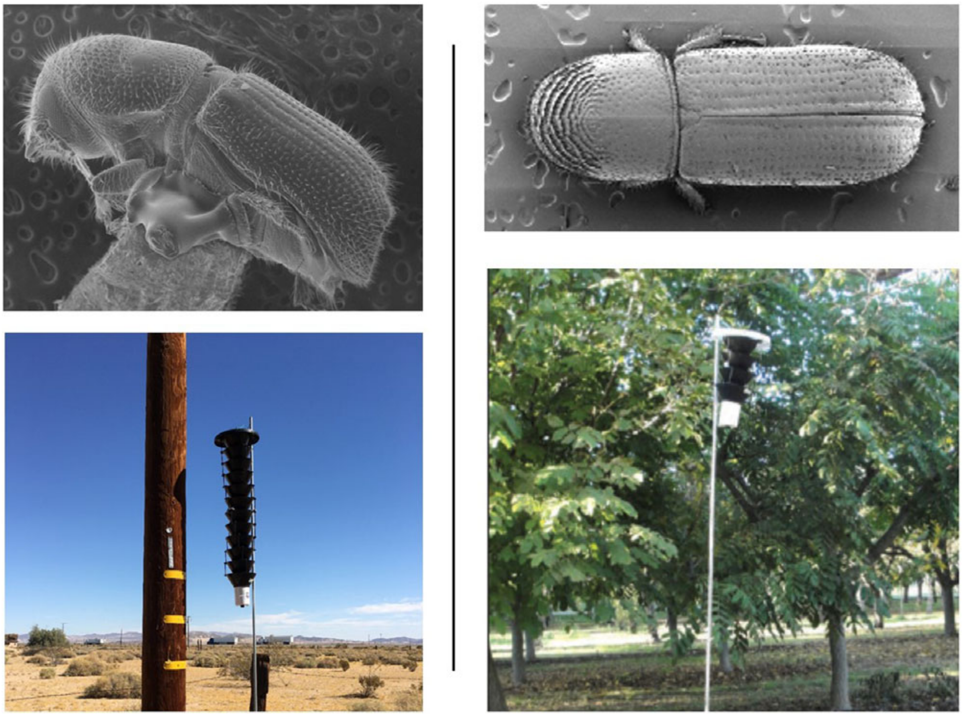

Fig. 5. Detection of populations of (left) *Orthotomicus erosus* and (right) *Pityophthorus juglandis* with aggregation pheromone-baited, multiple-funnel traps. These are two examples of detection of invasive bark beetle species through application of structurally similar pheromone components, 2-methyl-3-buten-2-ol and 3-methyl-2-buten-1-ol, respectively (both male-produced) (Seybold *et al*. 2013, 2015, 2016). Photographs by Megan A. Siefker, University of California (Davis, California, United States of America) (left), and Andrew D. Graves and Steven J. Seybold, United States Department of Agriculture Forest Service (right).

Development of effective semiochemical-based management tools and tactics for bark and ambrosia beetles is a tricky business. It not only requires strong knowledge of chemistry, chemical ecology, insect ecology, and forest ecology but also of the major semiochemical components of the system being studied and eventually the most efficacious blends, ratios, and release rates to impart the desired behavioural effect on the insect in the field. It involves substantial time, risk, and investment in research, development, and application, which are often significant barriers to success for minor use crops, such as pines, where returns on investments can be limited (Progar *et al.* 2014). Despite this, significant advances are being made ranging from increases in understanding of the biochemistry of pheromone production in beetles to commercialisation of novel products for field applications. This symposium highlighted some of these advances through presentations by nine distinguished speakers from three countries (Table 1), as we attempted to exercise deference to the joint meeting theme of *Crossing borders*. The symposium was bookended by keynote speakers John H. Borden and Nancy E. Gillette. Dr. Borden, who many regard as "the father of semiochemical-based management of bark and ambrosia beetles" took a typically refreshing approach by eschewing a PowerPoint presentation. Rather, he narrated his thoughts through a letter that he composed to a fictitious prospective graduate student. Dr. Gillette, who braved the smoke of wildfires in northern California for a day trip to Vancouver (British Columbia, Canada), shared insights and experiences from her remarkable career focussed on management of multiple forest insect systems with semiochemicals. Dr. Gillette's and Dr. Borden's visions of the path forward will likely shape future contributions to the field.

Table 1. Contributors to the symposium *Managing bark and ambrosia beetles with semiochemicals* held at the Joint Meeting of the Entomological Society of America, the Entomological Society of Canada, and the Entomological Society of British Columbia, *Crossing borders: entomology in a changing world*, 14 November 2018, Vancouver, British Columbia, Canada.

Contributor	Co-authors (if any)	Title
John H. Borden		Management of bark and ambrosia beetles with semiochemicals: letter to a prospective graduate student
Dezene P.W. Huber	Christopher J. Fettig, Kelsey Jones, Maya Evenden, and John H. Borden	Nonhost volatiles and bark beetle foraging: from concept to operational use
Brian T. Sullivan	Holly L. Munro and Kamal J.K. Gandhi	Managing the southern pine beetle with semiochemicals: past and present
Darrell W. Ross		Using MCH to protect trees and stands from Douglas-fir beetle infestation
Rastislav Jakuš	Marek Turcani, Roman Modlinger, Peter Surovy, Anna Jirosova, Ivana Tomaskova, Miroslav Blazenec, Alexander Gurtsev, C. Rikard Unelius and Fredrik Schlyter	Conceptualisation and preliminary results on semiochemical-based bark beetle management under climate stress, project EXTEMIT-K, for the Eurasian spruce beetle in Europe
Christopher M. Ranger		Applied chemical ecology for managing ambrosia beetles in ornamental nurseries and urban landscapes
Eveline Stokkink	John H. Borden	Semiochemical-based IPM of ambrosia beetles in BC's forest industry: implemented in 1982 and still running
Jason A. Smith		Host volatiles and other semiochemicals as potential repellents for redbay ambrosia beetle in mixed hardwood stands and avocado orchards
Nancy E. Gillette	Christopher J. Fettig and Steven J. Seybold	Semiochemical-based tools for management of bark and ambrosia beetles: where do we go from here?

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