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Semiochemical-mediated host selection by *Xylosandrus* spp. ambrosia beetles (Coleoptera: Curculionidae) attacking horticultural tree crops: a review of basic and applied science

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Abstract

Exotic ambrosia beetles (Curculionidae: Scolytinae) in the tribe Xyleborini include destructive pests of trees growing in horticultural cropping systems. Three species are especially problematic: *Xylosandrus compactus* (Eichhoff), *Xylosandrus crassiusculus* (Motschulsky), and *Xylosandrus germanus* (Blandford). Due to similarities in their host tree interactions, this mini-review focuses on these three species with the goal of describing their host-selection behaviour, characterising associated semiochemicals, and assessing how these interactions relate to their management. All three of these *Xylosandrus* spp. attack a broad range of trees and shrubs. Physiologically stressed trees are preferentially attacked by *X. crassiusculus* and *X. germanus*, but the influence of stress on host selection by *X. compactus* is less clear. Ethanol is emitted from weakened trees in response to a variety of stressors, and it represents an important attractant for all three species. Other host-derived compounds tested are inconsistent or inactive. Verbenone inhibits attraction to ethanol, but the effect is inconsistent and does not prevent attacks. Integrating repellents and attractants into a push–pull management strategy has been ineffective for reducing attacks but could be optimised further. Overall, maintaining host vigour and minimising stress-induced ethanol are keys for managing these insects, particularly *X. crassiusculus* and *X. germanus*.

Introduction

Ambrosia beetles (Coleoptera: Curculionidae) represent about 3400 species within the Scolytinae and 1400 species within the Platypodinae (Hulcr *et al.* 2015). These beetles, and especially those belonging to the tribe Xyleborini, are recognised as extremely successful invaders worldwide (Hulcr and Stelinski 2017). Around 50% of nonnative scolytines established in North America and Europe are within the tribe Xyleborini (Haack *et al.* 2013; Rassati *et al.* 2016b; Gomez *et al.* 2018), including some serious pests of trees growing in natural and managed habitats (Agnello *et al.* 2015; Ranger *et al.* 2016; Hulcr and Stelinski 2017). Key traits that contribute to the invasion success of xyleborine ambrosia beetles also make them particularly challenging

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pests to manage. These include a broad host range, cryptic wood-boring behaviour, an association with fungal symbionts, haplodiploid reproduction, and sib-mating (Kirkendall *et al.* 1993; Normark *et al.* 1999; Dole *et al.* 2010; Hulcr and Stelinski 2017). Adult female xyleborines tunnel into the heartwood of trees to create galleries where they cultivate fungal symbionts and rear offspring (Hulcr and Stelinski 2017). Symptoms of infestation include sawdust “toothpicks” and sap emerging from the tunnel entrances, branch and twig dieback, and death of saplings and small trees (Greco and Wright 2015; Ranger *et al.* 2016).

Three species of xyleborine ambrosia beetles are especially problematic in nurseries, orchards, groves, and plantations: these are black twig borer, *Xylosandrus compactus* (Eichhoff); granulate ambrosia beetle, *Xylosandrus crassiusculus* (Motschulsky), and black stem borer, *Xylosandrus germanus* (Blandford) (Chong *et al.* 2009; Greco and Wright 2012, 2015; Agnello *et al.* 2015, 2017; Ranger *et al.* 2015b, 2016). *Xylosandrus compactus* is native to Asia but has been introduced to parts of Africa, Europe, New Zealand, North America, the Pacific Islands, and South America (Rabaglia *et al.* 2006; Garonna *et al.* 2012; Gomez *et al.* 2018; CABI 2019a). Since being first reported in Florida in 1941, *X. compactus* has become established in 13 states in the midwestern, southeastern, and southern United States, as well as in Hawaii (Rabaglia *et al.* 2006, 2019; Chong *et al.* 2009; Gomez *et al.* 2018). *Xylosandrus crassiusculus* is native to southeast Asia but is now established in parts of Africa, Central America, North America, Oceania, and South America (Storer *et al.* 2017; CABI 2019b). Since being first reported in South Carolina in 1974, *X. crassiusculus* is now established in 31 states in the northeastern, mid-Atlantic, southeastern, southern, and midwestern United States, along with Hawaii and the Canadian province of Ontario (Anderson 1974; Rabaglia *et al.* 2006, 2019; Haack *et al.* 2013; Gomez *et al.* 2018). *Xylosandrus germanus* is native to southeast Asia but is now established in Europe, Great Britain, and North America (Ito *et al.* 2008; CABI 2019c; Inward 2020). Since being first detected in New York in 1932 (Felt 1932), *X. germanus* has spread to 34 states in the northeastern, mid-Atlantic, southeastern, southern, midwestern, and northwestern United States, along with the Canadian provinces of British Columbia, Nova Scotia, Ontario, and Québec (Rabaglia *et al.* 2006, 2019; Gomez *et al.* 2018; CABI 2019c).

Three species of fungi have been reported as mycangial symbionts of *X. compactus*, including *Ambrosiella xylebori* Brader (Ceratocystidaceae), *Ambrosiella macrospora* (Francke-Grossman) Batra, and *Fusarium solani* (Martius) Saccardo (Nectriaceae) (Bateman *et al.* 2016). *Ambrosiella roeperi* T.C. Harrington & McNew is the mycangial symbiont of *X. crassiusculus* (Harrington *et al.* 2014; Mayers *et al.* 2015), and *Ambrosiella grosmaniae* C. Mayers, McNew & T.C. Harrington is the symbiont of *X. germanus* (Mayers *et al.* 2015). A variety of secondary microorganisms can also be transported on the cuticle or in the mycangium, some of which can be tree pathogens (Kinuura 1995; Dute *et al.* 2002; Carrillo *et al.* 2014; Bateman *et al.* 2016; Juzwik *et al.* 2016; Malacrino *et al.* 2017).

The goal of this review is to describe the host-selection behaviour of these three *Xylosandrus* spp., characterise the associated semiochemicals, and assess how such interactions relate to managing these destructive insects of horticultural tree crops. Possible reasons why these pests, which are restricted to dying or dead host substrates in their native habitats, began attacking apparently healthy trees in horticultural production systems following their introduction into North America are also discussed.

Host-selection behaviour

Host range

A broad range of woody species are attacked by *X. compactus*, *X. crassiusculus*, and *X. germanus*, including horticultural plants and trees growing in ornamental nurseries, tree fruit orchards, coffee plantations, and avocado groves (Burbano *et al.* 2012; Carrillo *et al.* 2012; Greco and Wright

2012, 2015; Agnello *et al.* 2015; Ranger *et al.* 2015b, 2016). Over 120 host species have been recorded for *X. crassiusculus*, and both *X. compactus* and *X. germanus* have more than 200 host species (Schedl 1963; Ngoan *et al.* 1976; Hara and Beardsley 1979; Weber and McPherson 1983; Chong *et al.* 2009; Greco and Wright 2012, 2015; Ranger *et al.* 2016; Vannini *et al.* 2017). Although both deciduous and coniferous species are attacked by these three *Xylosandrus* spp., reports of damage generally involve thin-barked deciduous species (Ngoan *et al.* 1976; Greco and Wright 2012, 2015; Agnello *et al.* 2015; Ranger *et al.* 2015b, 2016). Trees ranging in age from sapling to maturity are attacked, but *X. crassiusculus* and *X. germanus* will also attack recently cut stumps and logs (Soné *et al.* 1998; Oliver and Mannion 2001; Zach *et al.* 2001; La Spina *et al.* 2013; Greco and Wright 2012, 2015; Coyle *et al.* 2015; Reed *et al.* 2015; Ranger *et al.* 2016; Rassati *et al.* 2016a, 2020; Galko *et al.* 2018). Stems and trunks are preferred over branches by both *X. crassiusculus* and *X. germanus* (Reding *et al.* 2010; Ranger *et al.* 2015a, 2019). In contrast, *X. compactus* preferentially attacks branches and twigs, but it will also infest stems, large branches, and trunks (Ngoan *et al.* 1976; Hara 1977; Chong *et al.* 2009; Greco and Wright 2012, 2015; Gugliuzzo *et al.* 2019a, 2019b).

Influence of host quality

The majority of ambrosia beetle species use dying or dead hosts (Hulcr and Stelinski 2017), but some species, including *X. crassiusculus* and *X. germanus*, preferentially attack stressed or weakened trees (Kühnholz *et al.* 2001; Ranger *et al.* 2016). Both *X. crassiusculus* and *X. germanus* have been reported to attack apparently healthy trees that show no visible symptoms of stress (Weber and McPherson 1984). However, physiologically stressed trees can visually appear healthy while emitting stress-associated volatiles (*i.e.*, ethanol) that signal their vulnerable state to generalist ambrosia beetles (Ranger *et al.* 2010, 2013a, 2015b). Studies described herein demonstrate the preference of *X. crassiusculus* and *X. germanus* for trees in the early stages of physiological stress over healthy trees. Despite having a broad host species range, *X. crassiusculus* and *X. germanus* function more like specialists when influenced by hosts in a weakened condition, such that certain species and individual trees are attacked in a nonrandom fashion within diverse horticultural production systems (Ranger *et al.* 2015b). *Xylosandrus compactus* reportedly attacks both apparently healthy and physiologically stressed trees (Masuya 2007; Oliveira *et al.* 2008; Chong *et al.* 2009; Greco and Wright 2012, 2015; Vannini *et al.* 2017), but colonisation success has not been compared under controlled conditions to determine the influence of host condition.

In support of anecdotal field observations from ornamental nurseries where poor drainage preceded attacks on flood-intolerant *Cornus florida* L. (Cornaceae) trees (Ranger *et al.* 2013a, 2016), studies under controlled conditions have demonstrated that flood stress predisposes trees to attack by *X. crassiusculus* and *X. germanus*. Ott (2007) induced attacks by *X. crassiusculus* and other ambrosia beetles within one to nine days of initiating flood stress of container-grown *Quercus alba* Linnaeus (Fagaceae) saplings; notably, the trees appeared healthy as attacks were initiated. Similarly, more *X. germanus* were attracted to and landed on flood-stressed *C. florida* trees over nonflooded trees (Ranger *et al.* 2013a). Moreover, *X. germanus* began landing on *C. florida* trees within one day of flooding, whereas no attacks occurred on nonflooded control trees. During subsequent free-choice experiments, *X. crassiusculus* and *X. germanus* readily distinguished among flooded trees varying in their tolerance of flood stress and preferentially attacked flood-intolerant deciduous tree species over flood-tolerant species (Ranger *et al.* 2015a). When *X. crassiusculus* and *X. germanus* were caged to stems of flooded or nonflooded *C. florida* trees, foundresses established fungal gardens and produced offspring only in stems of flooded trees. Additional studies further support the preference of *X. crassiusculus* and *X. germanus* for thin-barked tree species subjected to flood stress, including *Cercis canadensis* Linnaeus (Fabaceae), *Malus domestica* Borkhausen (Rosaceae), and *Styrax japonicus* Siebold (Styracaceae) (Frank and Ranger 2016; Ranger *et al.* 2016, 2020; Agnello *et al.* 2017; Frank *et al.* 2017; Werle *et al.* 2019).

The influence of drought stress on host selection by pioneering ambrosia beetles is less clear. Anecdotal field observations by Hara and Beardsley (1979) noted that *Croton reflexifolius* Kunth (Euphorbiaceae) and *Acacia koa* Gray (Fabaceae) trees stressed by drought and transplanting were especially vulnerable to *X. compactus*. Reduced sap production associated with drought and transplanting stress has been surmised to influence the host selection and colonisation success of *X. compactus*. Similarly, Greco and Wright (2015) observed *X. compactus* attacking coffee plants stressed by a lack of water and fertiliser. Compared to flood-stressed trees, drought-stressed *C. florida* were only mildly attractive and sustained few attacks by *X. crassiusculus* and *X. germanus* (Ranger and Schultz, unpublished data). Because the growth of ambrosia beetle fungal symbionts within host tree galleries is likely influenced by the moisture content of the tissue, additional studies are warranted to characterise the extent to which drought stress influences host selection and colonisation success.

Low-temperature stress also influences the host-selection behaviour of *X. crassiusculus* and *X. germanus*. Anecdotal field observations indicated that stress from low temperatures preceded attacks by *X. germanus* on *Quercus rubra* L. (Fagaceae), *Acer pseudoplatanus* L. (Sapindaceae) (Heidenreich 1960), *S. japonicus* (Meyer 1992), *Fagus sylvatica* Linnaeus (Fagaceae) (Grégoire *et al.* 2001; La Spina *et al.* 2013), *Acer palmatum* Thunb. (Sapindaceae), *Cercis canadensis* Linnaeus, *Cladrastis kentukea* (Dumont de Courset) Rudd (Fabaceae), *Liriodendron tulipifera* Linnaeus (Magnoliaceae), *S. japonicus*, and *Zelkova serrata* (Thunberg) Makino (Ulmaceae) (Ranger *et al.* 2015a). Controlled experiments by La Spina *et al.* (2013) demonstrated that *X. germanus* was more attracted to bark tissue of *F. sylvatica* trees experimentally injured by freezing compared to noninjured tissues. Similarly, *X. crassiusculus* and *X. germanus* rapidly began attacking and establishing galleries in container-grown *C. canadensis*, *C. florida*, *Malus pumila* Mill., and *S. japonicus* trees that were experimentally freeze-stressed, while no attacks occurred on noninjured trees (Ranger *et al.* 2019). Attacks on freeze-stressed trees occurred disproportionately on the upper stem and into the canopy, whereas attacks on flood-stressed trees were more prevalent on the lower portion of the stem. This phenomenon is likely a function of a physiological stressor influencing the tissue-specific production of stress-induced volatiles.

Girdling and herbicide damage can also predispose trees to attack by *X. crassiusculus* and *X. germanus*. Dodds and Miller (2010) attracted *X. germanus* to trap trees by injecting trunks of *Pinus resinosa* Aiton (Pinaceae) with the herbicide dicamba. Similarly, Reed *et al.* (2015) induced attacks by *X. crassiusculus*, *X. germanus*, and a variety of other ambrosia beetles by first mechanically girdling the trunk of *Juglans nigra* Linnaeus (Juglandaceae) trees and then treating the wounded tissue with glyphosate. *Xylosandrus crassiusculus* and *X. germanus* represented the majority of nearly 17 000 insects reared from logs harvested from these trees (Reed *et al.* 2015).

Anecdotal observations indicate that stress caused by fungi and bacteria can predispose trees to attack by *Xylosandrus* spp. beetles. However, few studies have directly tested this association. Early observations by Buchanan (1940, 1941) indicated that *X. germanus* was attracted to elm, *Ulm* sp., infected with Dutch elm disease, *Ceratostomella ulmi* (Schwarz) (Ophiostomataceae). Similarly, *Fusarium* sp. cankers on stems of black walnut, *Juglans nigra* L. (Kessler 1974; Weber and McPherson 1985), and tulip poplar, *Liriodendron tulipifera* L. (Anderson and Hoffard 1978), were associated with attacks by *X. germanus*. Cultivars of *Malus* × *domestica* Borkh. trees infected with fireblight, *Erwinia amylovora* (Burrill) (Erwiniaceae), were also attacked by *X. germanus*, and Hall *et al.* (1982) proposed the beetles were attracted to the trees due to the infection but were not vectors of the pathogen. Symptomatic *J. nigra* trees infected with the causal agent of 1000 cankers disease, *Geosmithia morbida* Kolařík, Freeland, Utley, and Tisserat (Bionectriaceae), and *Persea* spp. (Lauraceae) infected with laurel wilt, *Raffaelea lauricola* Harrington & Fraedrich (Ophiostomataceae), were attacked by *X. crassiusculus* (Juzwik *et al.* 2016). Recently, Rassati *et al.* (2020) reported that infection of *Castanea sativa* (Miller) (Fagaceae) logs by chestnut blight (*Cryphonectria parasitica* (Murrill) Barr) (Cryphonectriaceae) influences host-selection behaviour in the xyleborine *Anisandrus dispar*

F., but not in *X. germanus*. The combination of root infection by *Phytophthora cinnamomi* Rands (Peronosporaceae) and flood stress also influences the host-selection behaviour of *X. crassiusculus* and *X. germanus* (Addesso *et al.* 2018; Brown *et al.* 2019). Future work should focus on understanding the extent to which beetles are attracted to volatiles that may arise from the interaction of pathogens with their woody hosts. Similarly, the impact of abiotic and biotic tree stressors on host selection by *X. compactus* should be examined under controlled experimental conditions.

Stress-induced volatile emissions

The aforementioned abiotic and biotic stressors can induce the production and emission of stress-associated volatiles, and at least some of these may influence the behaviour of *Xylosandrus* spp. ambrosia beetles. For instance, physiologically stressed trees emit higher amounts of acetaldehyde, acetic acid, acetone, ethane, ethanol, ethylene, and methanol (Kimmerer and Kozłowski 1982; Millar *et al.* 1986; Kimmerer and MacDonald 1987; Holzinger *et al.* 2000; Copolovici and Niinemets 2010; Ranger *et al.* 2013a, 2015a, 2015b, 2019). Roots subjected to little or no oxygen, such as those subjected to flooding, will switch from aerobic to anaerobic cellular respiration, which leads to the production of acetaldehyde as an intermediate metabolite (Kimmerer and Kozłowski 1982; Kreuzwieser *et al.* 1999). Acetaldehyde is converted into ethanol, which is then transported from the roots to the stem and leaf tissues and emitted through the epidermis (Kreuzwieser *et al.* 1999). Addesso *et al.* (2018) observed that ethanol was emitted from *C. canadensis* trees one day after being flooded. Similarly, higher levels of ethanol were detected three days after flooding within stems of flood-intolerant tree species, including *C. canadensis*, *C. florida*, *Prunus serrulata* Lindley (Rosaceae), and *S. japonicus*, compared to flood-tolerant tree species, such as *Acer saccharinum* Linnaeus (Sapindaceae) and *Quercus bicolor* Willdenow (Fagaceae) (Ranger *et al.* 2015a). Emissions of acetaldehyde, acetic acid, and ethanol were also detected from stems of *C. florida* at 7 and 14 days after initiating flooding (Ranger *et al.* 2013a).

An inability of cells to take up O₂ due to injury from low-temperature stress can induce the production and emission of ethanol from the bark epidermis (Kimmerer and Kozłowski 1982; Forney *et al.* 2000; Obenland *et al.* 2003). For instance, ethanol emissions were initiated within 1 day after freeze stress of *S. japonicus*, peaked at 4 days, and continued to be detected after 19 days (Ranger *et al.* 2019). Correspondingly, attacks by *X. germanus* were initiated within 1 day after experimentally imposing freeze stress on *C. florida* and peaked by 4–7 days.

Ethanol was demonstrated to be associated with cankers of *Phytophthora ramorum* Werres *et al.* (Peronosporaceae) on infected stems of *Quercus agrifolia* Née (Fagaceae), which then attracted the generalist ambrosia beetle, *Xyleborinus saxesenii* (Ratzeburg) (Kelsey *et al.* 2013). A similar interaction has not yet been characterised for *Xylosandrus* spp. However, fireblight infection of *M. domestica* could induce the emission of ethanol and thereby attract *Xylosandrus* spp. ambrosia beetles, warranting additional studies as it pertains to rapid apple decline (Agnello *et al.* 2015).

Semiochemistry

Attractants

Ethanol is the most studied host-derived kairomone that attracts *X. compactus*, *X. crassiusculus*, and *X. germanus*. During field trapping studies, a positive correlation was demonstrated between ethanol emissions from lures and trap captures of *X. germanus* (Klimetzek *et al.* 1986). A positive correlation was demonstrated between concentration of ethanol injected into *Magnolia virginiana* Linnaeus (Magnoliaceae) and attacks by *X. germanus* and other ambrosia beetles (Ranger *et al.* 2012), along with a positive correlation between ethanol concentration within stems of flooded

trees and attacks (Ranger *et al.* 2015a). Several studies have demonstrated that ethanol is a long-range attractant for *X. compactus* (Miller and Rabaglia 2009; Burbano *et al.* 2012) and *X. crassiusculus* (Miller and Rabaglia 2009; Reding *et al.* 2011; Werle *et al.* 2019).

Pressurised injections of ethanol into *M. virginiana* L. induced more attacks than acetaldehyde, acetone, and methanol under field conditions (Ranger *et al.* 2010). Ethanol injection into 16 species of deciduous trees from 11 families also induced ambrosia beetle attacks under field conditions (Reding *et al.* 2017). Baiting trees with ethanol-induced attacks on specific trees, however, immediately ceased upon removal of the ethanol cue (Ranger *et al.* 2015b). Irrigating container-grown trees with solutions of ethanol also induces attacks by *X. germanus* and other ambrosia beetles (Ranger *et al.* 2012, 2018). Stem sections (*i.e.*, bolts) soaked in aqueous solutions of ethanol are readily attacked by *X. germanus* and other ambrosia beetles when deployed under field conditions (Reding and Ranger 2019; Rassati *et al.* 2020). Ethanol-soaked bolts were generally more attractive to *X. germanus* than ethanol-baited traps, suggesting that additional host-derived compounds emitted from the bark might enhance the attraction to ethanol (Reding and Ranger 2019).

Xylosandrus germanus efficiently located and attacked ethanol-injected trees, but rarely landed on adjacent trees not emitting ethanol, and never attacked these neighbouring trees (Ranger *et al.* 2015b). A spatial analysis of trees attacked by *X. germanus* within ornamental nurseries revealed that only certain tree species or cultivars, and only certain individuals within these host species or cultivars, were attacked (Ranger *et al.* 2015a). Stress-induced ethanol was present within the tissues of those attacked trees, which further supports the role of ethanol as a long-range attractant that assists *X. germanus* in efficiently locating vulnerable trees.

Ethanol within host tissues acts as a boring cue for ambrosia beetle species that are attracted to it; Kelsey *et al.* (2013) reported fourfold more ambrosia beetle attacks on sapwood tissues infused with ethanol compared to the opposite side of the same log which did not receive ethanol treatment. Ethanol within host tissues also appears to be associated with favourable environments for adult foundresses to establish fungal gardens and produce offspring (Ranger *et al.* 2018). *Xylosandrus germanus* attacked trees baited with ethanol lures, but only superficial tunnels were created, and no fungal gardens or broods were produced unless the living stem tissues contained ethanol introduced through irrigation with ethanol solutions. Ethanol incorporated into growing media promotes the growth of the fungal symbionts of *X. germanus* (*i.e.*, *A. grosmanniae*) and *X. crassiusculus* (*i.e.*, *A. roeperi*) but inhibits the growth of “weedy” fungal garden competitors, such as *Aspergillus* sp. (Trichocomaceae) and *Penicillium* sp. (Trichocomaceae) (Ranger *et al.* 2018).

The presence of ethanol as a potent antimicrobial agent within host tissues may reduce interspecific competition among different species of ambrosia beetles. Rassati *et al.* (2020) demonstrated that ethanol in wood tissue might facilitate niche-partitioning among xyleborine ambrosia beetles. In a field experiment involving ethanol-soaked logs, *X. germanus* and *X. saxesenii* were differentially attracted to increasing ethanol concentrations in wood tissues, whereby the number of entry holes decreased with increasing ethanol concentration for *X. germanus* and increased for *X. saxesenii* (Rassati *et al.* 2020). Ethanol concentration in wood tissues also differentially affected colonisation success of *X. germanus* and *X. saxesenii*, in that the number of galleries with brood chambers in ethanol-soaked logs was higher for *X. germanus* than for *X. saxesenii*, even though the attack rate was largely higher for the latter species.

A few other host-derived compounds are weak and inconsistent attractants for *X. compactus*, *X. crassiusculus*, and *X. germanus*. Conophthorin, ((*E*)-(±)-7-methyl-1,6-dioxaspiro[4.5]decane), is associated with the bark of deciduous tree species (Francke *et al.* 1995; Byers *et al.* 1998; Huber *et al.* 1999; Huber and Borden 2001; Zhang *et al.* 2002), functions as a pheromone component of some bark beetles (Birgersson *et al.* 1995; Dallara *et al.* 2000; DeGroot and DeBarr 2000), and is produced by symbiotic fungi of bark beetles (Dickschat 2017; Zhao *et al.* 2019). Conophthorin has been associated with variable effects on *Xylosandrus* spp., either increasing or decreasing

attraction. Kohnle *et al.* (1992) demonstrated that conophthorin decreased attraction of *X. germanus* to ethanol-baited traps, but Dodds and Miller (2010) reported that conophthorin enhanced attraction of *X. germanus* to girdled trap trees. VanDerLaan and Ginzel (2013) reported that conophthorin enhanced attraction of *X. crassiusculus* to ethanol but had a negligible effect on *X. germanus*. Conophthorin in combination with ethanol elicited larger electroantennogram amplitudes than ethanol alone, and conophthorin enhanced attraction of *X. germanus* to ethanol under field conditions (Ranger *et al.* 2014). Conophthorin decreased attraction of *X. germanus* to ethanol-baited traps deployed in Oregon but had no effect on trap captures of *X. germanus* in New Hampshire or Michigan (Miller *et al.* 2015). Conophthorin also had no effect on *X. compactus* and *X. crassiusculus* during field trapping studies conducted in Georgia (Miller *et al.* 2015).

(-)- α -Pinene has also exhibited inconsistent effects on the attraction of *X. compactus*, *X. crassiusculus*, and *X. germanus*. (-)- α -Pinene did not enhance the attraction of *X. compactus*, *X. crassiusculus*, or *X. germanus* to ethanol in field trapping studies (Miller and Rabaglia 2009; Gandhi *et al.* 2010; Burbano *et al.* 2012). (-)- α -Pinene enhanced the response of *X. germanus* to ethanol during trapping studies conducted in 2003, but it had a negligible effect in subsequent trapping studies conducted in 2004 and 2008 (Ranger *et al.* 2011). A lure consisting of ethanol, (-)- α -pinene, (+)- α -pinene, (+)-camphene, (-)- β -pinene, (+)- β -pinene, myrcene, ρ -cymene, limonene, and eucalyptol was prepared based on ratios of the aforementioned compounds emitted from ethanol-injected *M. virginiana*, but it was not more attractive to *X. germanus* than ethanol alone (Ranger *et al.* 2012).

Ott (2007) identified volatiles emitted from flood-stressed oak trees, namely, 2-hexen-1-ol, 6-methyl-5-hepten-2-one, ethyl salicylate, nonanal, eugenol, guaiacol, and 1-hexanol. However, a lure composed of these compounds did not enhance the attraction of *X. crassiusculus* to ethanol alone, nor did they act as attractants when tested singly. Lures composed of eugenol plus ethanol and guaiacol plus ethanol generally caught more *X. crassiusculus* than ethanol alone, but the results were variable and not significant (Ott 2007). Eugenol or α -pinene alone also did not attract more *X. compactus* than a blank control (Burbano *et al.* 2012). Ethanol plus ginger oil, α -pinene, phoebe oil, or manuka oil also did not attract more *X. compactus* or *X. crassiusculus* than ethanol alone (Burbano *et al.* 2012).

Compared to ethanol, other stress-induced and host-derived compounds have generally exhibited negligible effects. A mixture of acetaldehyde, ethanol, and methanol was not more attractive to scolytines (not identified to species level) than ethanol alone was in field trapping studies (Montgomery and Wargo 1983). Acetaldehyde and acetone did not increase trap captures of scolytines when tested individually compared against an ethanol or water control (Montgomery and Wargo 1983). During field trapping studies, ethanol was highly attractive to *X. germanus*, methanol was slightly attractive, and acetaldehyde and acetone were inactive (Ranger *et al.* 2010).

Volatiles emitted from the fungal symbionts of *Xylosandrus* spp. ambrosia beetles are associated with behavioural activity. Hulcr *et al.* (2011) observed *X. crassiusculus* was attracted to volatiles emitted by its fungal symbiont, *Ambrosiella roeperi* (previously *Ambrosiella xylebori*), during olfactometer studies. Similarly, Egonyu and Torto (2018) observed that *X. compactus* was attracted to volatiles emitted from its fungal symbiont, *Fusarium solani* (Mart.) Sacc., during olfactometer studies. A variety of compounds were identified in volatile collections from *F. solani*, with ethanol, phenethyl alcohol, 3-methyl-1-butanol, and (ϵ)-caryophyllene being among the dominant components. Methyl isovalerate and 2,3-butanediol elicited antennal responses by *X. compactus* during gas chromatography–electroantennography experiments (Egonyu and Torto 2018), but unlike ethanol these compounds were only slightly attractive under field conditions.

There is currently no evidence that *X. compactus*, *X. crassiusculus*, *X. germanus*, or other xyleborines produce a long-range aggregation or sex pheromone that facilitates host-selection processes. Because males are flightless and females either mate before dispersing or produce males (through haplodiploidy) following invasion of the host, there should be little selection pressure for the evolution of a pheromone (Kirkendall *et al.* 1993; Peer and Taborsky 2005; Ott 2007; Ranger

et al. 2015b). Large clusters of *X. germanus* overwintering within a single gallery in a host tree have been documented (Weber and McPherson 1984). In one instance, 112 females and 42 males were present in a single gallery, which is more than 1 female could produce, suggesting that beetles probably immigrated from nearby galleries (Weber and McPherson 1984). Observations by Peer and Taborsky (2005) suggested that short-range chemical communication aids male *X. germanus* in locating female-occupied galleries.

Repellents

A repellent is a compound that causes directed, oriented movement away from the point source, and determining the extent to which a compound acts as a repellent, in the strict sense, is difficult to assess in field trials. Assessing the influence of a particular compound on baited trap captures or tree attacks does not directly measure the time course of behavioural responses of directed movements by an insect. As such, some compounds termed repellents by researchers and practitioners may have been shown only to inhibit attraction rather than direct movement away from the attractive source (Holighaus and Rohlf 2016). For the purposes of this review, this broader sense of repellent is used.

Several studies have assessed the inhibitory effects of selected compounds on *X. compactus*, *X. crassiusculus*, and *X. germanus*. Currently, the majority of studies have focused on verbenone, [4,6,6-trimethylbicyclo[3.1.1] hept-3-en-2-one], which was first identified from the hindgut of the southern pine beetle, *Dendroctonus frontalis* Zimmerman, and the western pine beetle, *Dendroctonus brevicomis* LeConte (Curculionidae) (Renwick 1967). Verbenone has also been isolated from coniferous (Cool and Zavarin 1992; Dallara *et al.* 2000) and deciduous plants (Buttery *et al.* 2000), is emitted by bark beetle fungal symbionts (Cale *et al.* 2019), and is also generated through the autoxidation that occurs when host-produced α -pinene is exposed to the air (Hunt *et al.* 1989).

Verbenone interrupts the attraction of several species of bark beetles to conspecific pheromones, host-derived volatiles, and trap trees (Bentz *et al.* 2005; Gillette *et al.* 2006). Based on this activity, the effects of verbenone have also been evaluated on ambrosia beetles. Dodds and Miller (2010) demonstrated that verbenone emitted from dispensers at a rate of 40 mg/day reduced the attraction of *X. germanus* to ethanol-baited traps by 67%. Similarly, verbenone emitted from dispensers at 2 mg/day reduced the attraction of *X. compactus* and *X. crassiusculus* to ethanol-baited traps (Burbano *et al.* 2012). At release rates of 2 and 50 mg/day, verbenone reduced the attraction of *X. germanus* to ethanol-baited traps by 98% and 97%, respectively (Ranger *et al.* 2013b, 2014). Traps releasing 32 mg/day verbenone also caught fewer *X. crassiusculus* and *X. germanus* than unbaited traps did (VanDerLaan and Ginzel 2013).

Verbenone reduces attraction and attacks on trap trees by *Xylosandrus* spp., but the results have been inconsistent. For example, a verbenone dispenser (40 mg/day) attached to herbicide-killed *Pinus resinosa* Aiton trap trees reduced the attraction of *X. germanus* but was not completely effective at preventing attacks (Dodds and Miller 2010). Similarly, a verbenone dispenser (50 mg/day) attached to ethanol-injected *M. virginiana* trap trees reduced ambrosia beetle attacks by 85% compared to trap trees without a verbenone dispenser, but it did not prevent attacks from occurring (Ranger *et al.* 2013b). In some instances, attacks on ethanol-injected *M. virginiana* trees also decreased with an increasing proximity to a verbenone emitter, but attacks still occurred on trap trees and the effect was inconsistent across locations and years. A verbenone (50 mg/day) dispenser attached to flood-stressed apple trees (*M. domestica*) also resulted in fewer ambrosia beetle galleries containing brood, but the effect was inconsistent and tree attacks still occurred (Agnello *et al.* 2017). In contrast, verbenone (50 mg/day) had no effect at reducing attacks on container-grown and flood-stressed *Cercis canadensis* L., *Cornus florida* L., and *Koelreuteria paniculata* Laxmann (Sapindaceae) trees deployed as part of multi-state trials (Werle *et al.* 2019). Altogether, these results demonstrate that verbenone can reduce ambrosia beetle attacks on vulnerable trees but has limited promise as a tree protectant.

The monoterpene (+)-limonene is one of the most common components of plant essential oils and is also emitted by a variety of microorganisms (Jongedijk *et al.* 2016). When released at a rate of 600 mg/day, (+)-limonene reduced the attraction of *X. crassiusculus* to ethanol-baited traps but was less effective than verbenone (Burbano *et al.* 2012). The monoterpene terpinolene released at 266 mg/day reduced captures of *X. germanus* in ethanol-baited traps by 65% (Ranger *et al.* 2014). A combination of verbenone and methyl salicylate was repellent to the redbay ambrosia beetle, *Xyleborus glabratus* Eichhoff (Curculionidae) (Hughes *et al.* 2017).

Volatiles produced by deleterious fungal competitors of the beetles' symbiont could be sources of promising repellent compounds against *Xylosandrus* spp. During olfactometer studies, *X. saxesenii* and *Xyleborus ferrugineus*, but not *X. crassiusculus*, were repelled by volatiles emitted from *Trichoderma* sp. (Hypocreaceae) mycelium growing on agar (Hulcr *et al.* 2011).

Applied chemical ecology

Knowledge about the host-selection behaviour and associated semiochemicals of *X. compactus*, *X. crassiusculus*, and *X. germanus* has helped to improve monitoring and management efforts. As discussed, ethanol is the most effective long-range attractant for detecting these *Xylosandrus* spp. Ethanol-baited traps are effective for monitoring purposes. However, supplementing traps with additional semiochemicals does not appear to offer a cost-effective improvement for the detection of *X. compactus*, *X. crassiusculus*, and *X. germanus*. To induce attacks on trees for monitoring purposes, trap trees can be created by irrigation or injections with ethanol, flood stressing or freeze stressing, or girdling using a combination of mechanical injury and herbicide treatment. Stem sections (*i.e.*, bolts) can also be used for monitoring attacks by soaking bolts in 10% ethanol for 24–48 hours or coring the centre of bolts and filling them with 95% ethanol (Reding and Ranger 2019).

Deploying repellent dispensers, such as verbenone, among vulnerable trees could be useful for establishing a push–pull management strategy (Pyke *et al.* 1987; Miller and Cowles 1990), whereby repellents push beetles away from vulnerable trees and attractants pull beetles into annihilative traps. A push–pull strategy has potential in horticultural production systems, but the strategy has not been widely adopted (Cook *et al.* 2007). Because wooded areas across the perimeter of neighbouring ornamental nurseries can serve as source populations of overwintering *Xylosandrus* spp. (Ranger *et al.* 2013b; Reding *et al.* 2015; Werle *et al.* 2015), migration of beetles could potentially be exploited in conjunction with their strong attraction to ethanol. For example, the strategic deployment of ethanol-baited traps or ethanol-infused bolts along the perimeter of production sites, especially sites adjacent to vulnerable trees, could intercept ambrosia beetles before their dispersal into ornamental nurseries.

To date, only a few studies have assessed behavioural manipulation strategies for reducing the pressure of *Xylosandrus* spp. on vulnerable trees. Werle *et al.* (2019) assessed the capability of verbenone dispensers as a “push” component and a perimeter of ethanol-baited traps as a “pull” component for reducing attacks on flood-stressed trees. Unexpectedly, verbenone dispensers emitting 50 mg/day and positioned among three to four flood-stressed trees failed to reduce ambrosia beetle attacks during trials conducted in Mississippi, Ohio, and Virginia. Traps baited with ethanol lures (65 mg/day) and positioned at 10 m intervals around the perimeter of the flooded trees intercepted enough ambrosia beetles to reduce attacks in some locations and years, but the effects were inconsistent and not sufficiently efficacious. Similarly, Adesso *et al.* (2019) evaluated interception strategies consisting of ethanol-injected trap trees and ethanol-baited traps. Ethanol-injected trap trees failed to reduce attacks on neighbouring, less attractive trees, and varying densities of perimeter traps baited with ethanol lures (65 mg/day) failed to protect ethanol-injected trap trees.

Ethanol-based interception strategies might be improved if lures with a release rate higher than the 65 mg/day tested by Werle *et al.* (2019) and Adesso *et al.* (2019) are used. A positive

correlation exists between ethanol release rate and trap captures or attacks by *Xylosandrus* spp. (Klimetzek *et al.* 1986; Ranger *et al.* 2012, 2015b), although this pattern was not evident for *X. germanus* when ethanol-soaked logs were used (Rassati *et al.* 2020). Additional studies are warranted because the optimal release rate of ethanol needs to be established for intercepting these *Xylosandrus* spp., and may vary depending on the species. For example, lures emitting 2 g/day attracted more scolytines than higher release rates did (Montgomery and Wargo 1983).

Maintaining host vigour to reduce the risk of stress-induced volatile emissions is currently the most reliable semiochemical-based management strategy for scolytine ambrosia beetles. Knowledge about the role of flood stress on host selection by *Xylosandrus* spp. ambrosia beetles has led to improved management tactics. Frank and Ranger (2016) demonstrated that a 50% media moisture level for container substrates is a threshold above which trees become vulnerable to attack. However, media moisture levels of container-grown trees in ornamental nurseries during spring months are often 70–90%, thereby increasing the risk for attacks by *X. crassiusculus*, *X. germanus*, and other ambrosia beetles.

Conclusions

A broad range of plant and tree species can be attacked by the three *Xylosandrus* spp. addressed in this review, whereas host-physiological status plays an important role during host selection, especially for *X. crassiusculus* and *X. germanus*. Thin-barked deciduous trees in the early stages of physiological stress can appear healthy and asymptomatic while emitting ethanol that functions as a long-range kairomone. Despite a broad host range, dispersing *Xylosandrus* adults exhibit an efficient capability of locating and preferentially attacking trees emitting ethanol, even within diverse horticultural landscapes.

There is no evidence that *X. crassiusculus* and *X. germanus* have generally switched to attacking and colonising healthy trees in nonnative habitats where the beetles have been introduced. Instead, stressed trees within horticultural production sites represent opportunistic hosts for dispersing females. Attacked trees can be spatially clustered within rows in horticultural production systems, a phenomenon that is often attributed to poor site conditions (*e.g.*, low-lying areas prone to flooding) or microclimate effects (*e.g.*, frost pockets). Neighbouring trees not emitting ethanol represent poor hosts for *X. crassiusculus* and *X. germanus* and are not typically attacked under experimental conditions. Indeed, foundresses prefer host tissues containing ethanol to initiate tunnelling as this substrate may represent a chemically favourable niche that promotes colonisation success.

Compared to what is known about *X. crassiusculus* and *X. germanus*, considerably less is known about the role of host quality during host selection by *X. compactus*. Nonetheless, dispersing *X. compactus* females are responsive to ethanol. Attacks by *X. compactus* have been reported on both apparently healthy and stressed trees, warranting controlled studies to assess the influence of experimentally imposed abiotic stressors on host selection and colonisation.

Similarly, the authors of this review are unaware of studies in the literature to assess the impact of biotic stressors, particularly tree pathogens, on host selection by all three of these *Xylosandrus* spp. Understanding these interactions is critical for sustainably managing these destructive insects in horticultural cropping systems.

This review's authors believe that certain semiochemicals may in future be used in xyleborine management if deployed in the context of a push–pull strategy. Verbenone inhibits the attraction of *Xylosandrus* spp. females to ethanol. However, verbenone alone has limited prospects for adoption as a management tool because growers generally have a low or zero tolerance for attacks. Applying a perimeter of ethanol-baited traps around vulnerable trees has shown some promise for intercepting dispersing ambrosia beetles, but additional studies are needed to increase trap captures. Nonetheless, the aggressiveness with which trees emitting ethanol are attacked,

particularly by *X. crassiusculus* and *X. germanus*, indicates the importance of maintaining host vigour as the first step in an integrated pest management programme for these insects.

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