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Profile

Biology, Ecology, and Management of Nonnative Ambrosia Beetles (Coleoptera: Curculionidae: Scolytinae) in Ornamental Plant Nurseries

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Abstract

Xylosandrus germanus (Blandford) and *Xylosandrus crassiusculus* (Motschulsky) (Coleoptera: Curculionidae: Scolytinae) are two of the most damaging nonnative ambrosia beetle pests in ornamental plant nurseries. Adult females tunnel into the stems and branches of host plants to create galleries with brood chambers. Hosts are infected with symbiotic *Ambrosiella* spp. fungi that serve as food for the larvae and adults. Plants can also become infected with secondary opportunistic pathogens, including *Fusarium* spp. Both *X. germanus* and *X. crassiusculus* have broad host ranges, and infestations can result in "toothpicks" of extruded chewed wood and sap flow associated with gallery entrances, canopy dieback, stem and trunk cankers, and plant death. Beetles efficiently locate and preferentially attack living, weakened plants, especially those physiologically stressed by flooding, inadequate drainage, frost injury, or winter injury and low temperature. Maintaining plant health is the foundation of a management plan. Vulnerable hosts can be partially protected with preventive pyrethroid applications in the spring before peak flight and attack, which are monitored using ethanol-based trapping tactics.

Key words: *Xylosandrus germanus*, *Xylosandrus crassiusculus*, integrated pest management, ambrosia beetle

Several species of nonnative ambrosia beetles (Coleoptera: Curculionidae: Scolytinae) in the tribe Xyleborini are established in North America including some destructive pests (Rabaglia et al. 2006, Hulcr and Dunn 2011, Ploetz et al. 2013). *Xylosandrus germanus* (Blandford) and the granulate ambrosia beetle, *Xylosandrus crassiusculus* (Motschulsky), are two of the most damaging species in ornamental plant nurseries (Fig. 1A–B; Oliver and Mannion 2001, Reding et al. 2010, LeBude et al. 2011, Fulcher et al. 2012, Frank et al. 2013, Ranger et al. 2015a). The black twig borer, *Xylosandrus compactus* (Eichhoff), is also an emerging pest in ornamental plant nurseries (Chong et al. 2009, Greco and Wright 2015), but the current review focuses on *X. germanus* and *X. crassiusculus*.

Xylosandrus germanus and *X. crassiusculus* are subtropical species native to southeastern Asia. *Xylosandrus germanus* was first reported in 1932 from greenhouse-grown grape vines in Long Island, NY (Felt 1932); *X. crassiusculus* was first reported in 1974 from peach trees in Summerville, SC (Anderson 1974). As of 2010, *X. germanus* and *X. crassiusculus* were found in 32 and 29 of 50 U.S. states, respectively (Haack et al. 2013). *Xylosandrus germanus* has become established in numerous states in the northeastern, mid-

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Fig. 1. Two nonnative and highly destructive ambrosia beetle pests in ornamental plant nurseries. (**A**) *Xylosandrus germanus*. (**B**) Granulate ambrosia beetle, *Xylosandrus crassiusculus*. Notice the head is hidden under a prominent pronotum. (Photo by B. Anderson.)

Atlantic, southeastern, southern, midwestern, and northwestern United States, along with the Canadian provinces British Columbia, Nova Scotia, Ontario, and Quebec (Rabaglia et al. 2006) and throughout much of Europe (Commonwealth Agricultural Bureaux International Invasive Species Compendium [CABI] 2008). *Xylosandrus crassiusculus* is established in many states in the northeastern, mid-Atlantic, southeastern, southern, and midwestern United States, along with Hawaii (Rabaglia et al. 2006). *Xylosandrus crassiusculus* currently has a narrower distribution in Europe but is established in Central America and the Caribbean, East and West Africa, and Oceania (CABI 2009). In the United States, *X. germanus* tends to be more abundant and problematic in the nurseries of the Midwest and the Northeast; *X. crassiusculus* dominates the mid-Atlantic and the South (Hudson and Mizell 1999; Oliver and Mannion 2001; Lightle et al. 2007; Gandhi et al. 2010; Thompson 2011; Reding et al. 2010, 2011; Ranger et al. 2013a; Werle et al. 2012, 2015).

A variety of factors make *X. germanus* and *X. crassiusculus* challenging to manage, including a broad host range, wood-boring habit, fungal symbionts that serve as their food source, and haplodiploid reproduction (Kirkendall et al. 1993, Normark et al. 1999, Dole et al. 2010, Ranger et al. 2015b). In many cases it is also difficult to detect or assess when plants are susceptible or attractive to attack. Studies conducted over the past decade have improved our understanding of these wood-boring pests and helped to identify biological weaknesses that can be exploited for management purposes. This article reviews important aspects related to the biology, ecology, and management of *X. germanus* and *X. crassiusculus* in relation to ornamental plant nurseries.

Description of Life Stages

Adult

Adult female *X. germanus* are dark brown to black, shiny, stout, almost cylindrical, rounded in front and rear, and with the head hidden under a prominent pronotum (Fig. 1A; Wood and Bright 1992, Solomon 1995, Rabaglia et al. 2006, CABI 2008). Adult females range 2.0–2.4 mm in length and are about 1.0 mm wide. The pronotum is about as long as wide with 8 to 10 low, blunt spines (=serrations). The elytra are shiny, 1.3 times longer than wide, and 1.4 times as long as the pronotum. A steep downward slope (i.e., elytral declivity) forms just beyond the middle of the elytra. The widely separated procoxae distinguish the genus *Xylosandrus* from other Xyleborini (Rabaglia et al. 2006).

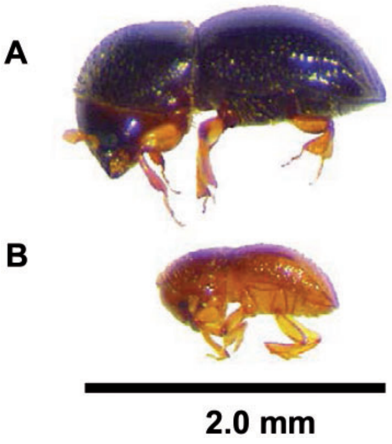

Fig. 2. Adult *X. germanus*. (**A**) Female. (**B**) Male. Unlike females, males are flightless. (Photo by B. Anderson.)

The pronotum of adult female *X. crassiusculus* tends to be more reddish-brown than *X. germanus*, but the distal half of the elytra is dark brown (Fig. 1B). The females are stout and squat, cylindrical, rounded in front and rear from a dorsal view, and with the head largely hidden under a prominent pronotum (Wood 1982, Kovach and Gorsuch 1985, Solomon 1995, Pennacchio et al. 2003, Rabaglia et al. 2006, CABI 2009). Females range 2.1–2.9 mm in length and are about 1.2 mm wide (Fig. 1B). The pronotum is as long as it is wide and the anterior margin has several blunt serrations. The elytra are slightly longer than wide and somewhat larger than the pronotum, and the elytral declivity is steep, convex, and densely covered with small granules arranged uniformly on the entire surface that result in a dull appearance.

Like other xyleborine ambrosia beetles, male *X. germanus* and *X. crassiusculus* are much smaller than the females, flightless, and rarely seen outside the gallery. Males generally resemble females, but are light brown, weakly sclerotized, and spheroid (Fig. 2A–B; Wood and Bright 1992; Solomon 1995; Rabaglia et al. 2006; CABI 2008, 2009). For both species, the elytra are 1.5 times as long as wide and the downward slope is less convex than for females.

Egg

The egg of *X. germanus* is white, translucent, shiny, ellipsoidal, about 0.67 mm long, and 0.38 mm wide (Fig. 3A; Hoffman 1941, CABI 2008). The egg of *X. crassiusculus* is similar in appearance to that of *X. germanus* but has not been formally described.

Larva

Neonates of *X. germanus* and *X. crassiusculus* are white, legless, elongate, and rather flat but become robust and slightly curved, developing a distinct light-brown head capsule with maturity (Fig. 3B–C; Hoffman 1941; Weber and McPherson 1983a; CABI 2008, 2009). Both species have three larval instars (Weber and McPherson 1983a).

Pupa

The pupa of *X. germanus* is white and has legs and wings that are free from the body and a moveable abdomen, averaging 2.53 mm long and

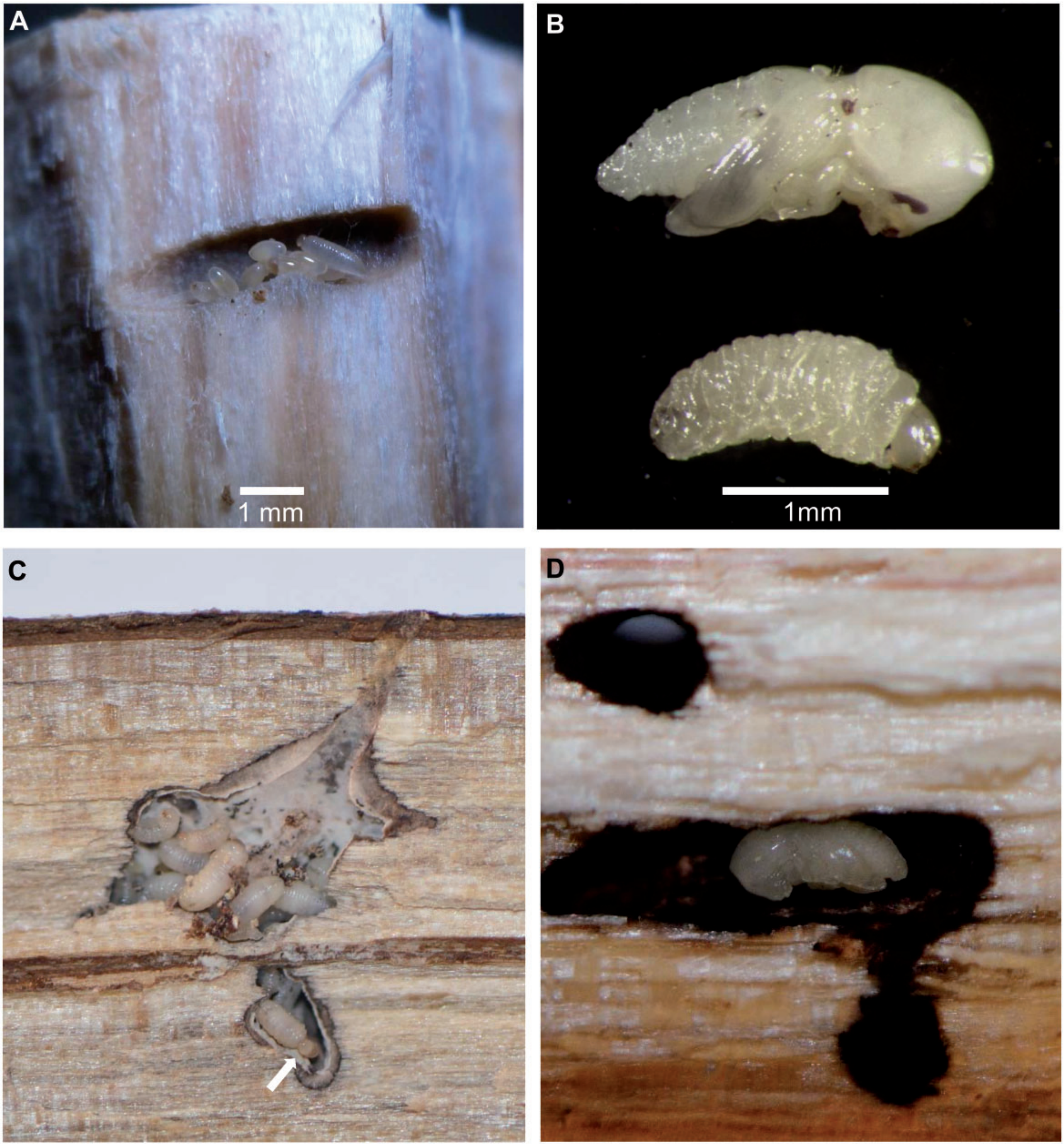

Fig. 3. Life stages of *X. germanus*. (**A**) White, translucent, and shiny eggs and a larva within a gallery created in fragrant snowbell, *Styrax obassia* S. et Z. (**B**) Larva and pupa of *X. germanus*. (**C**) Larva and (**D**) pupa of *X. germanus* within a host gallery created in honeylocust. White arrow indicates eggs. (Photo 3A by E. Barekzi; 3B–D by C. Ranger.)

1.09 mm wide for females and 1.78 mm long and 0.95 mm wide for males (Fig. 3B, D; Hoffman 1941, Weber and McPherson 1983a, Solomon 1995). The pupa of X. *crassiusculus* has not been formally described but is generally similar in appearance to that of X. *germanus*.

Gallery Formation

Adult female X. *germanus* and X. *crassiusculus* tunnel horizontally into the xylem of stems or trunks and sometimes branches and exposed roots. Gallery entrances are about 1 mm in diameter (Fig. 4A–D). Tunnels widen into brood chambers and additional tunnels may extend vertically with and across the grain of the wood (Fig. 3C and Fig. 5A–D; Hoffman 1941, Kaneko et al. 1965, Weber and McPherson 1983a). In smaller diameter stems and branches, the tunnel and brood chamber may extend horizontally into the pith (Fig. 5A, C, D). In larger diameter stems, the tunnels may branch once or twice in association with a horizontal brood chamber (Fig. 5B; Hoffman 1941, Kaneko et al. 1965, Weber and McPherson 1983a). Depth of tunneling and gallery architecture can vary considerably depending on host species (Hoffman 1941, Groschke 1953, Schneider and Farrier 1969).

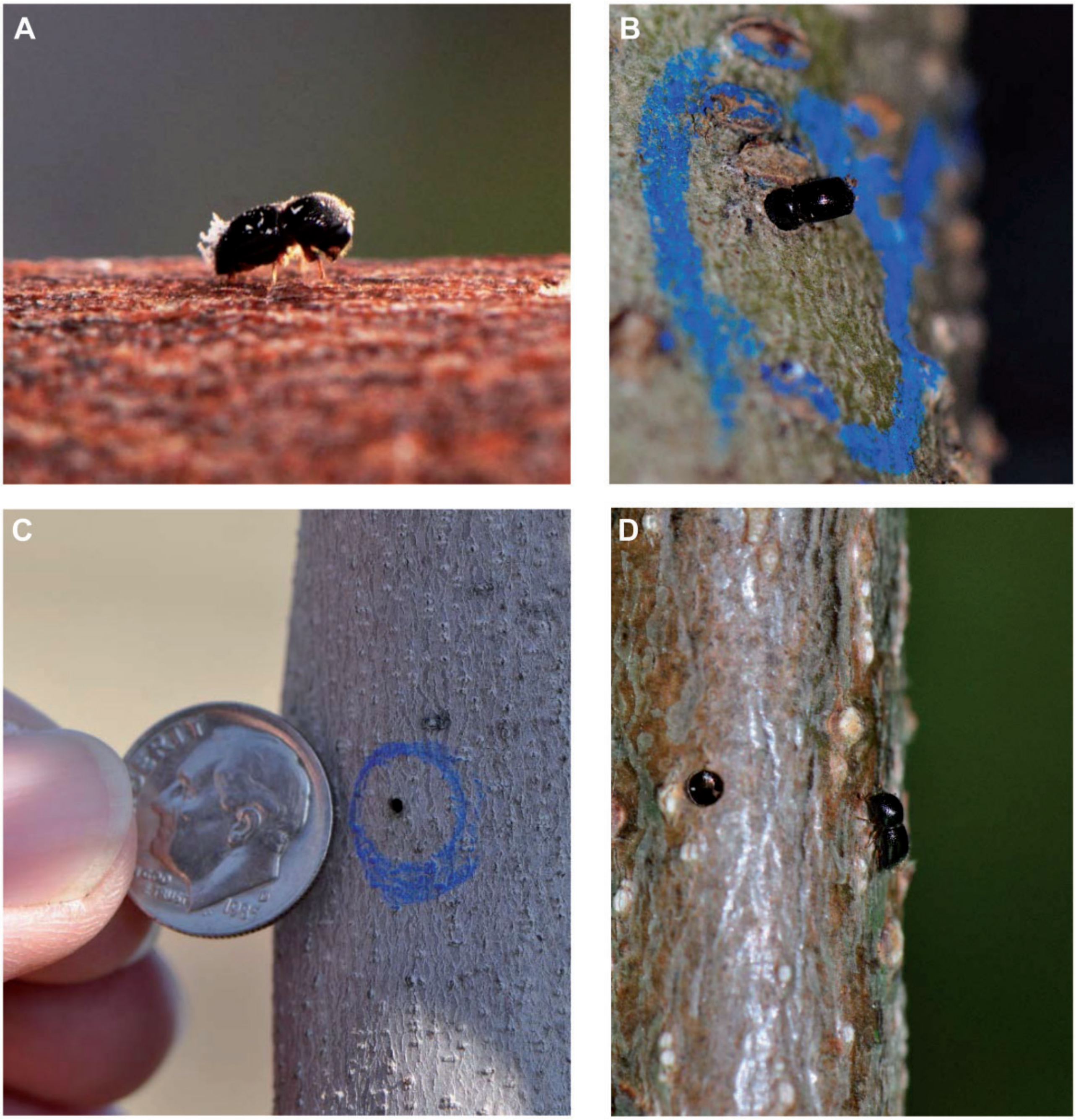

Fig. 4. (**A**) Adult female *X. germanus* on the stem surface of Japanese snowbell, *S. japonicus*. (**B**) Adult female *X. germanus* in the early stages of tunneling into the stem of a host. (**C**) The gallery entrance created by *X. germanus* is about 1 mm in diameter. (**D**) Adult *X. germanus* and a gallery entrance created in sweetbay magnolia (Photos by C. Ranger.)

Symbiotic and Auxiliary Fungi

Adult females carry spores within an invaginated, membranous, and pouch-like structure called a mycangium, located between the pro- and mesothorax (Fig. 6A; Francke-Grosmann 1956, Batra 1963, Hulcr and Cognato 2010). Spores of the symbiotic fungi are transferred from the beetles into their host tunnels during excavation (Fig. 6B; Batra 1985), but the mechanism of discharge is not known. Notably, adult female *X. germanus* and *X. crassiusculus* initiate oviposition only after their symbiotic fungus is established within the gallery (French and Roeper 1972, Weber and McPherson 1983a), which thereby represents a biological weak point that potentially could be exploited to disrupt their colonization success for management purposes.

Ambrosiella grosmanniae C. Mayers, McNew & T.C. Harr. was identified as the mycangial symbiont of *X. germanus* based on specimens collected in the United States and three European countries (Mayers et al. 2015), and *Ambrosiella roeperi* T.C. Harr. & McNew was identified as the mycangial symbiont of *X. crassiusculus* from specimens collected in the United States and Taiwan (Harrington et al. 2014, Mayers et al. 2015). The thoracic mycangia of *X. germanus* and *X. crassiusculus* are dominated by their

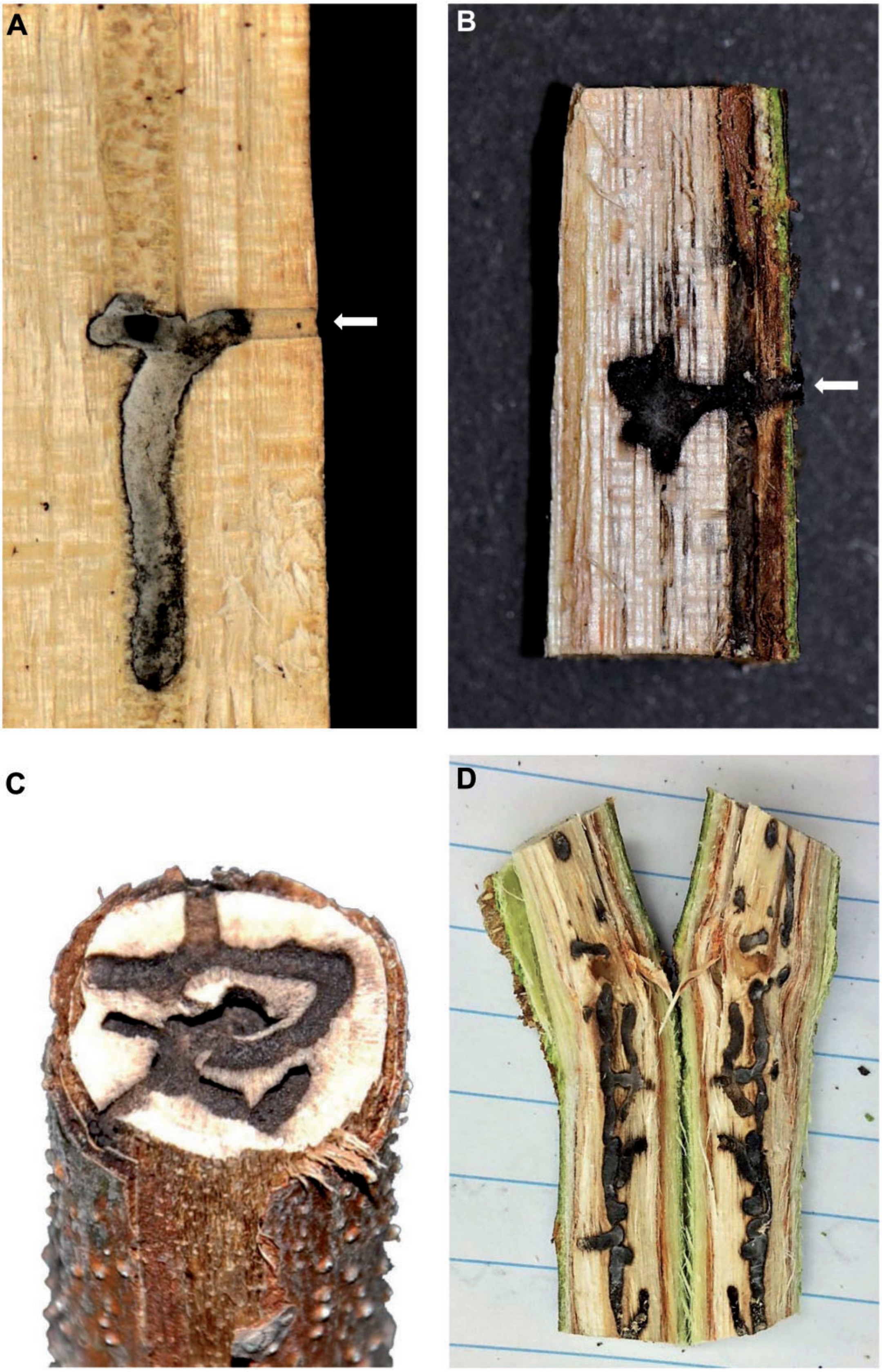

Fig. 5. Gallery architecture created by *X. germanus* and *X. crassiusculus* can vary depending on the host species and stem diameter. (**A**) Gallery created by *X. germanus* within the pith of sweetbay magnolia. (**B**) Tunneling with the grain of the wood just underneath the bark surface of honeylocust and a brood chamber for rearing the larvae. (**C**) Tunnels and a brood chamber within the heartwood and sapwood of sweetbay magnolia. (**D**) Tunnels and brood chambers within a stem of honeylocust. Arrows denote the gallery entrance. (Photos by C. Ranger.)

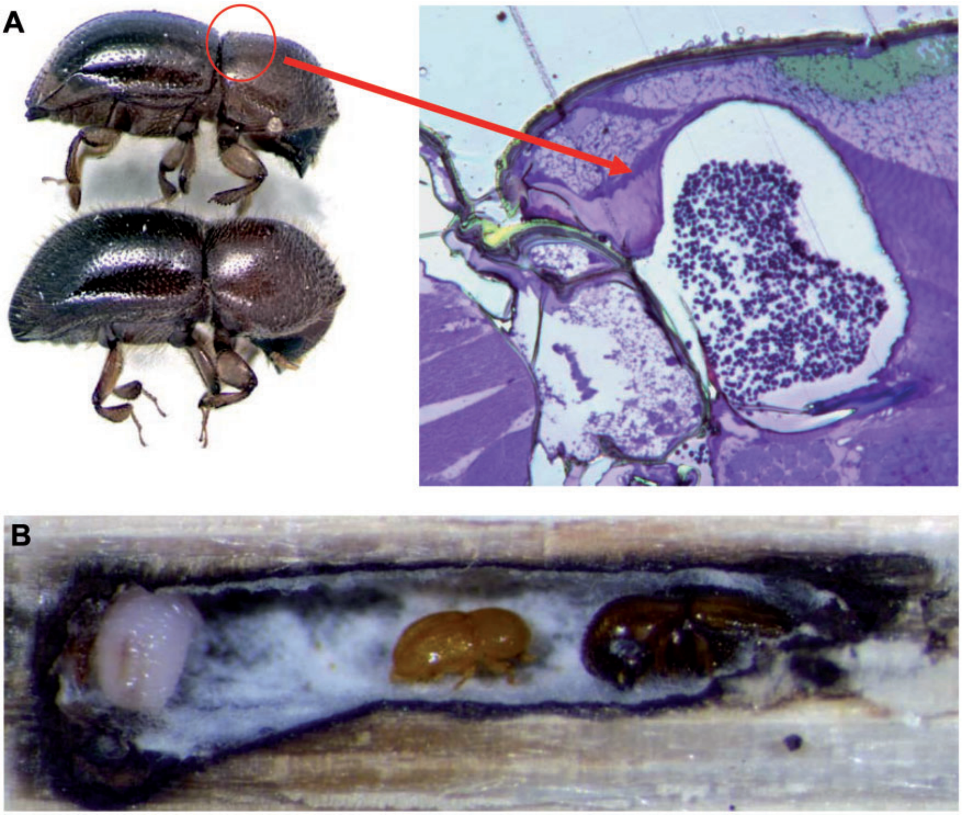

Fig. 6. Adult female *X. germanus* and *X. crassiusculus* carry their symbiotic fungus within an invaginated pouch-like structure called a mycangium. (**A**) Spores of the symbiotic fungus are contained within the mycangium located between the pro- and mesothorax. (**B**) White ambrosial form of *X. germanus*' symbiotic fungus growing within a gallery containing an immature, adult male, and adult female. (Photo 6 A by B. Anderson; 6B by C. Ranger.)

Ambrosiella symbionts (Kostovcik et al. 2015, Mayers et al. 2015). Spores of nonspecific fungi also may be present, but their growth and proliferation appear to be restricted, presumably by glandular secretions within the mycangium (Kostovcik et al. 2015).

The majority of *Ambrosiella* spp. biomass is in the xylem, but two growth forms can be observed within the galleries: a dark mycelial form that can grow in the beetles' absence (Fig. 5B–D) and can be consumed and a white ambrosial form consisting of conidia and sprout cells that is only produced in association with the beetles (Fig. 6B) and is required for proper development of the larvae and pupae (French and Roeper 1972, Kinuura 1995, Dute et al. 2002). Old galleries contain the mycelial form of the fungus and not the white ambrosial form (Hoffman 1941).

A diverse set of auxiliary microorganisms, including bacteria, yeasts, and filamentous fungi, have been isolated from the galleries of *X. germanus* and *X. crassiusculus* (Dute et al. 2002, Hulcr et al. 2012). *Ophiostoma novo-ulmi* Brasier, *Fusarium lateritium* Nees, *Fusarium solani* (Mart.), and *Fusarium oxysporum* Schlechter ex Fries have been isolated from galleries of *X. germanus* (Kessler 1974; Anderson and Hoffard 1978; Weber and McPherson 1984a, 1985; Kovach 1986; Ploetz et al. 2013). *Aspergillus niger* Tiegh., *Candida* spp., *F. lateritium*, *F. oxysporum*, *F. solani*, *Nectria cinnabarina* Tode ex Fr., *Penicillium* spp., *Pestalotia* spp, *Phomopsis* spp., *Pichia* spp., and *Saccharomycopsis* spp. have been isolated from galleries of *X. crassiusculus* (Kinuura 1995, Dute et al. 2002). Some species, particularly those in the genera *Ophiostoma*, *Fusarium*, and *Phomopsis*, can be plant pathogenic (Kessler 1974, Anderson and Hoffard 1978, Weber and McPherson 1984a, Kovach 1986, Kinuura 1995, Dute et al. 2002, Ploetz et al. 2013). Carrillo et al. (2014) also detected the pathogen responsible for laurel wilt disease, *Raffaelea lauricola* sp. nov. (T.C. Harr., Fraedrich & Aghayeva), from specimens of *X. crassiusculus* reared on laurel wilt-infected bolts of swampbay, *Persea palustris* (Raf.) Sarg. Furthermore, *X. crassiusculus* transmitted *R. lauricola* to redbay, *Persea borbonia* [L.] Spreng., and avocado, *Persea americana* Mill., under controlled infestations (Carrillo et al. 2014).

Life History

Adult *X. germanus* and *X. crassiusculus* disperse from their overwintering galleries as mated females. Eggs are deposited loosely in the distal parts of the brood chamber, where substantial fungal growth is present (Hoffman 1941). *Xylosandrus germanus* laid an average of 1 egg per day and a total of 18 eggs per female when reared on an artificial diet (Weber and McPherson 1983a); *X. crassiusculus* laid 1 to 6 eggs per day over a prolonged period (Wu et al. 1978). Incubation period for *X. germanus* eggs ranged from 2 to 6 d depending on substrate (i.e., artificial diet vs. natural host) and temperature (Hoffman 1941, Kaneko 1965, Kaneko et al. 1965, Weber and McPherson 1983a).

Neonates move slowly in an undulating fashion and begin feeding on the ambrosial fungus within the gallery (Hoffman 1941). Average developmental time of *X. germanus* from egg to adult was 15 to 18 d on tea roots at 23 to 24°C (Kaneko 1965, Kaneko et al. 1965), but required 24.9 d on artificial diet at 24°C (Weber and McPherson 1983a). Developmental times for *X. crassiusculus* have not been reported.

Adult progeny of *X. germanus* emerged from infested stems held under laboratory conditions about 60 d after gallery initiation (Buchanan 1941), whereas *X. crassiusculus* adults emerged after 48–62 d (Kovach 1986). Similarly, under field conditions in Tennessee, progeny of *X. crassiusculus* and *X. germanus* emerged 55–60 d after gallery initiation (Oliver and Mannion 2001). The observed discrepancy between developmental time from egg to adult and subsequent emergence times of adult progeny from galleries is likely due to delayed dispersal of ambrosia beetle progeny from their natal galleries (Biedermann and Taborsky 2011, Keller et al. 2011). Adult progeny of some Scolytinae species delay dispersal from their natal galleries during which time they aid in the care of younger siblings (Peer and Taborsky 2007, Kirkendall et al. 2015).

Large variability has been documented in the number of adult *X. germanus* and *X. crassiusculus* progeny emerging per gallery. For instance, total progeny per gallery of *X. germanus* ranged from 1 to 53 when reared on black walnut (Weber and McPherson 1983a), 20 to 50 progeny when reared on tea plants (Kaneko 1965), 2 to 54 progeny when reared on elm (Hoffman 1941), and up to 18 progeny on chestnut (Oliver and Mannion 2001). Similarly, an average of 8 *X. crassiusculus* adult females emerged per gallery in peach trees (Kovach 1986), up to 27 progeny emerged per gallery from Bradford pear and Kwanzan cherry (Mizell et al. 1994), and up to 59 progeny per gallery for chestnut (Oliver and Mannion 2001). While brood sizes up to 65 and 100 progeny were reported for *X. crassiusculus* from the Congo and Ghana, respectively, 10–40 progeny are more likely in regions where year-round reproduction does not occur as in the tropics (Schedl 1963; Beaver 1976, 1988). The basis for variable progeny sizes is unknown, but might be related to growth of their symbionts within the host gallery.

Like other xyleborine ambrosia beetles, *X. germanus* and *X. crassiusculus* demonstrate haplodiploid sex determination; males arise from unfertilized eggs and possess eight chromosomes while females arise from fertilized eggs and have 16 chromosomes (Takagi and Kaneko 1966, Normark et al. 1999, Hulcr et al. 2007). Offspring sex ratios are strongly biased toward females and ratios of 9:1 and 10:1 have been documented for *X. germanus* and *X. crassiusculus*, respectively (Kaneko 1965, Kaneko et al. 1965, Takagi and Kaneko 1966, Weber and McPherson 1983a, Kinuura 1993). However, the number of males in *X. germanus* families increases with brood size and females adjust their offspring sex ratio depending on colony density within the host (Peer and Taborsky 2004, Keller et al. 2011).

Xyleborini ambrosia beetles, including *X. germanus* and *X. crassiusculus*, show high levels of inbreeding among siblings within the gallery system (Kirkendall et al. 1993; Peer and Taborsky 2004, 2005). Males traditionally have been thought to never (or rarely) leave their maternal galleries after sib-mating (Hoffman 1941, Bright 1968, Weber and McPherson 1984b), but *X. crassiusculus* and *X. germanus* males were found to occasionally leave their galleries presumably in search of mating opportunities with females in neighboring galleries (Oliver and Mannion 2001, Peer and Taborsky 2004).

Phenology and Flight Activity

Xylosandrus germanus and *X. crassiusculus* overwinter as adults, primarily females, within their galleries (Hoffman 1941, Gauss 1960, Weber and McPherson 1983a). Both species may have an obligatory diapause (Kovach 1986). Relatively large clusters of overwintering adults from different broods have been recovered from single galleries. Hoffman (1941) reported 200 *X. germanus* within an irregular gallery in elm. Weber and McPherson (1983a) reported 112 females and 42 males in a single gallery in black walnut. Females from nearby galleries presumably gather together in the individual gallery since a single female does not produce such a large brood (Weber and McPherson 1983a).

Data from *X. germanus* trap collections suggest two generations per year in Illinois, North Carolina, Ohio, and Tennessee (Hoffman 1941; Weber and McPherson 1983a, 1991; Oliver and Mannion 2001; Gandhi et al. 2010). One to two generations per year for *X. germanus* also have been reported from Japan and Europe (Kaneko et al. 1965, Bruge 1995, Faccoli 2000, Henin and Versteirt 2004). However, the number of generations per year is at least partly dependent on ambient temperatures, and *X. germanus* and *X. crassiusculus* may have up to three generations per year within warmer US climates (Hoffman 1941, Gandhi et al. 2010). Up to four generations per year of *X. crassiusculus* were reported in Taiwan (Wu et al. 1978).

Since *X. germanus* and *X. crassiusculus* overwinter as adults, they do not require a minimum heat accumulation (i.e., degree-days) in order to complete their development. However, flight and attack activity in Ohio are influenced by spring temperatures; no attacks or trap captures occurred prior to one to two days of at least 20°C maximum daily temperatures (Reding et al. 2013a). First flight of overwintering *X. crassiusculus* was initiated in February to March with adult flights continuing into October in South Carolina, Mississippi, and Florida (Kovach 1986, Atkinson et al. 2000, Werle et al. 2012). First flight of *X. germanus* and *X. crassiusculus* occurred in March to April with adult flights continuing into at least September in Illinois, Missouri, North Carolina, Ohio, Tennessee, and Virginia (Weber and McPherson 1983a, 1991; Oliver and Mannion 2001; Reding et al. 2010, 2013a; Reed and Muzika 2010).

Peak diurnal flight activity by *X. germanus* and *X. crassiusculus* occurs in late afternoon into night (Wu et al. 1978, Weber and McPherson 1991, Zach et al. 2001) and *X. germanus* and *X. crassiusculus* generally fly low to the ground. Weber and McPherson (1991) captured the majority of *X. germanus* specimens at a 1 m trap height, and Reding et al. (2010) determined traps at 0.5 m were more effective than 1.7 or 3.0 m. Similarly, traps positioned at 0.5 and 1.7 m above ground were more effective than 3.0 m for *X. crassiusculus* (Reding et al. 2010).

Hosts

Xylosandrus germanus and *X. crassiusculus* attack a wide variety of woody species. Over 200 species in 51 families were included by Weber and McPherson (1983b) in a world list of hosts for *X. germanus*. Similarly, over 120 species were listed for *X. crassiusculus* (Schedl 1963). While deciduous and coniferous species are attacked, reports from ornamental plant nurseries (Ranger et al. 2015a) and tree fruit orchards (Agnello et al. 2015) generally involve thin-barked deciduous species. Main hosts for *X. germanus* and *X. crassiusculus* cannot be distinguished due to their broad host range and preference for living but weakened individuals; hosts can also vary across growing regions. However, some genera or species that have been attacked in ornamental plant nurseries within different regions include dogwood (*Cornus* spp.), honeylocust (*Gleditsia triacanthos* L.), Japanese snowbell (*Styrax japonicus* S. et Z.), magnolia (*Magnolia* spp.), maple (*Acer* spp.), oak (*Quercus* spp.), and redbud (*Cercis* spp.) (Reding et al. 2010; Ranger et al. 2015a; Frank, Gill, Ranger, Schultz, Werle, personal observation). Examples of attacked

Fig. 7. Infestations of *X. germanus* and *X. crassiusculus* on ornamental nursery trees can sometimes be difficult to detect. Tunnels created in (**A**) dogwood, (**B**) eastern redbud, (**C**) and honeylocust. White arrows indicate gallery entrances. (Photos by C. Ranger.)

plant species have also been compiled (Schedl 1963; Weber and McPherson 1983b; Mizell et al. 1994; Solomon 1995; CABI 2008, 2009) and documented (Ranger et al. 2015a).

Stems and trunks are preferred over branches for both *X. germanus* and *X. crassiusculus* (Oliver and Mannion 2001; Reding et al. 2010; Ranger et al. 2013b, 2015b). Stems <10 cm and 7.5 cm in diameter are preferred by *X. germanus* and *X. crassiusculus*, respectively, but as neither species are strongly size-selective they will also attack recently cut stumps and logs stored in millyards (Wood 1982, Weber and McPherson 1984b, Braza 1995, Solomon 1995, Soné et al. 1998, Atkinson et al. 2000, Zach et al. 2001, Henin and Versteirt 2004, Coyle et al. 2015). Plants of varying sizes and species growing in ornamental nurseries, orchards, plantations, and landscapes can be targeted for attack. The broad range of plants attacked by *X. germanus* and *X. crassiusculus*, coupled with the large diversity of trees commonly grown within ornamental nurseries, poses considerable challenges from a management perspective.

Symptoms and Damage

Mass attacks by *X. germanus*, *X. crassiusculus*, and other opportunistic generalist ambrosia beetles can quickly result in extensive losses within ornamental nurseries. Plants can exhibit rapid dieback following attacks by *X. germanus* and *X. crassiusculus*, especially during spring months. The physiological and pathological basis for dieback is not well understood or established, but dieback may in part be attributed to a host hypersensitive response to symbiotic and opportunistic microorganisms associated with *X. germanus* and *X. crassiusculus*. Attacks do not always result in plant death, but growth, aesthetic, and economic value of ornamental nursery plants can be negatively affected. Since tunneling by ambrosia beetles can kill small-diameter plants or make them unmarketable (detection in shipment can result in rejection by state horticulture inspectors), ornamental producers generally have very little to no tolerance for ambrosia beetle attacks.

Attacks can sometimes be difficult to detect due to the small diameter of the gallery entrance (Figs. 4C and 7A–C). Yet, toothpick-like extrusions of chewed wood material projecting up to 3–4 cm out from the stems are a characteristic symptom of attacks by *X. germanus*, *X. crassiusculus*, and other ambrosia beetles (Fig. 8A–D), but these are not always apparent especially during windy, dry, or wet conditions. Since the adult females do not feed on the host plant, the “toothpicks” are not frass but instead compacted chewed wood material excavated during the tunneling process. Sap stains on bark is also a key symptom associated with ambrosia beetle attacks and is most frequently observed in spring, but sometimes in late summer or early fall, particularly on honeylocust (Fig. 9A–F; Ranger, personal observation). Wilting foliage and branch dieback are also symptomatic of ambrosia beetle attacks and commonly observed in spring; profuse basal sprouting can (later) occur in response to dieback (Fig. 10A–D).

Tissue discoloration is also common in tissues adjacent to the galleries, which may be attributed to symbiotic fungi, secondary pathogens, host defense responses, and infusion of oxygen into the tissues (Fig. 11A–E; Koch 2008). *Ambrosiella* spp. nutritional symbionts are not fungi commonly associated with wilt diseases and are not known to be pathogenic (Mayers et al. 2015). Still, a hypersensitive overreaction to the symbiotic fungi or secondary microorganisms leading to walling-out (i.e., compartmentalization) in the vascular tissues (Merrill 1992) or pathogenicity of opportunistic microbes (e.g., *Fusarium* spp.; Fig. 12A–B) coupled with weakened host vigor may induce dieback and hasten plant death. Rather than acting as direct vectors of *Fusarium* spp., *X. germanus* and *X. crassiusculus* may facilitate the introduction of secondary pathogens that subsequently enhance their colonization success (Mayers et al. 2015). Attacks by *X. germanus* on black walnut were suggested to provide an infection site for *Fusarium* spp., and *X. germanus*

Fig. 8. Sawdust "toothpicks" projecting from the stems and branches of trees are a distinct symptom of attacks by *X. germanus*, *X. crassiusculus*, and other ambrosia beetles. Toothpick projecting out of a stem of (**A**) sweetbay magnolia and a (**B**) *Magnolia* sp. Numerous toothpicks associated with (**C**) flowering dogwood and (**D**) eastern redbud trees under attack. (Photos by C. Ranger.)

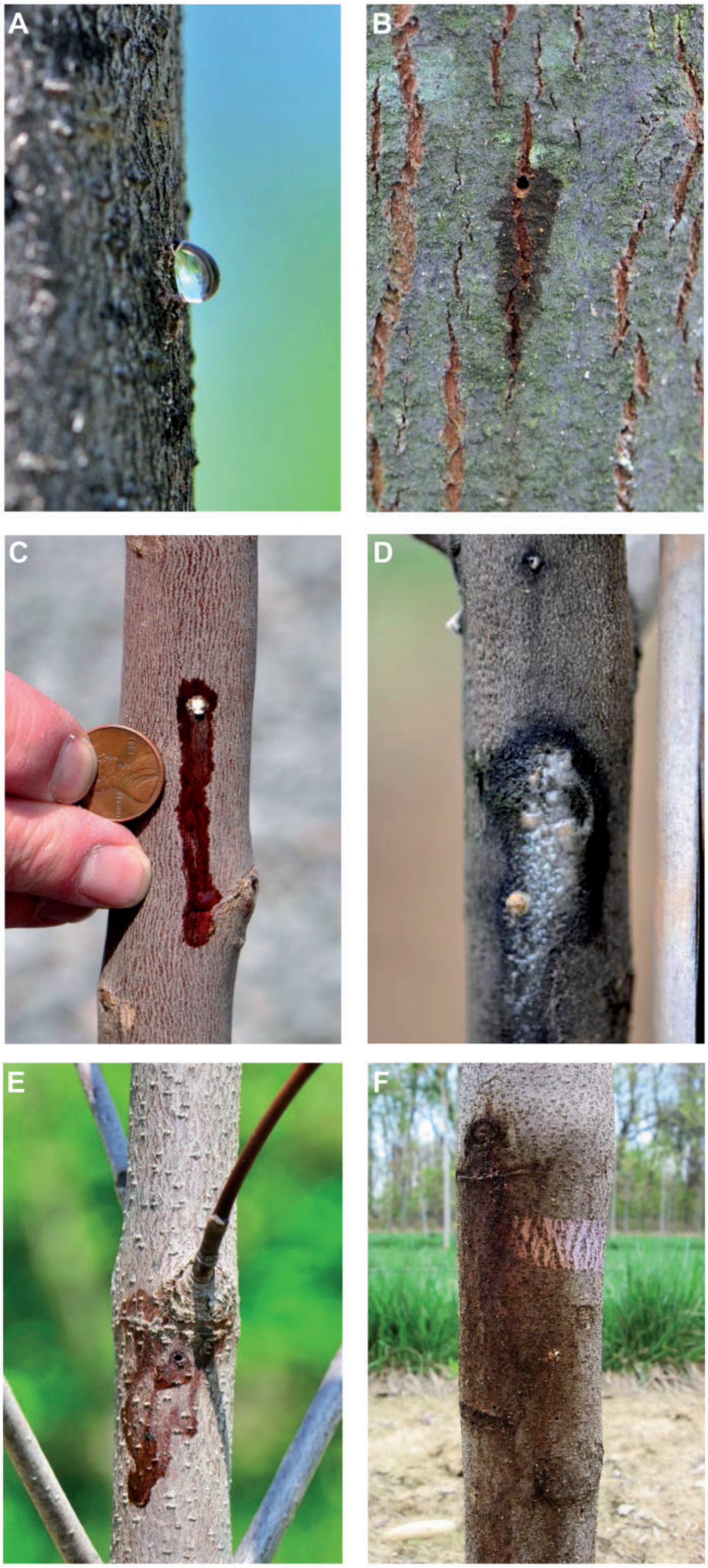

Fig. 9. Varying amounts of defensive sap production are associated with attacks by *X. germanus, X. crassiusculus*, and other ambrosia beetles on trees in ornamental nurseries. (**A**) Initial droplet of sap produced from a tunnel entrance. (**B**) Sap associated with a tunnel created in eastern redbud. (**C–D**) Sap produced by Japanese snowbell and (**E–F**) staining and discoloration on the bark of flowering dogwood. (Photos by C. Ranger.)

Fig. 10. Wilting foliage is most commonly observed during spring months. Wilted foliage on (**A**) sweetbay magnolia and (**B**) flowering dogwood attacked by ambrosia beetles. Branch dieback and profuse basal sprouts on (**C**) sweetbay magnolia and dieback on (**D**) Chinese fringe tree, *C. retusus*, held overwinter in a hoop house. (Photos by C. Ranger.)

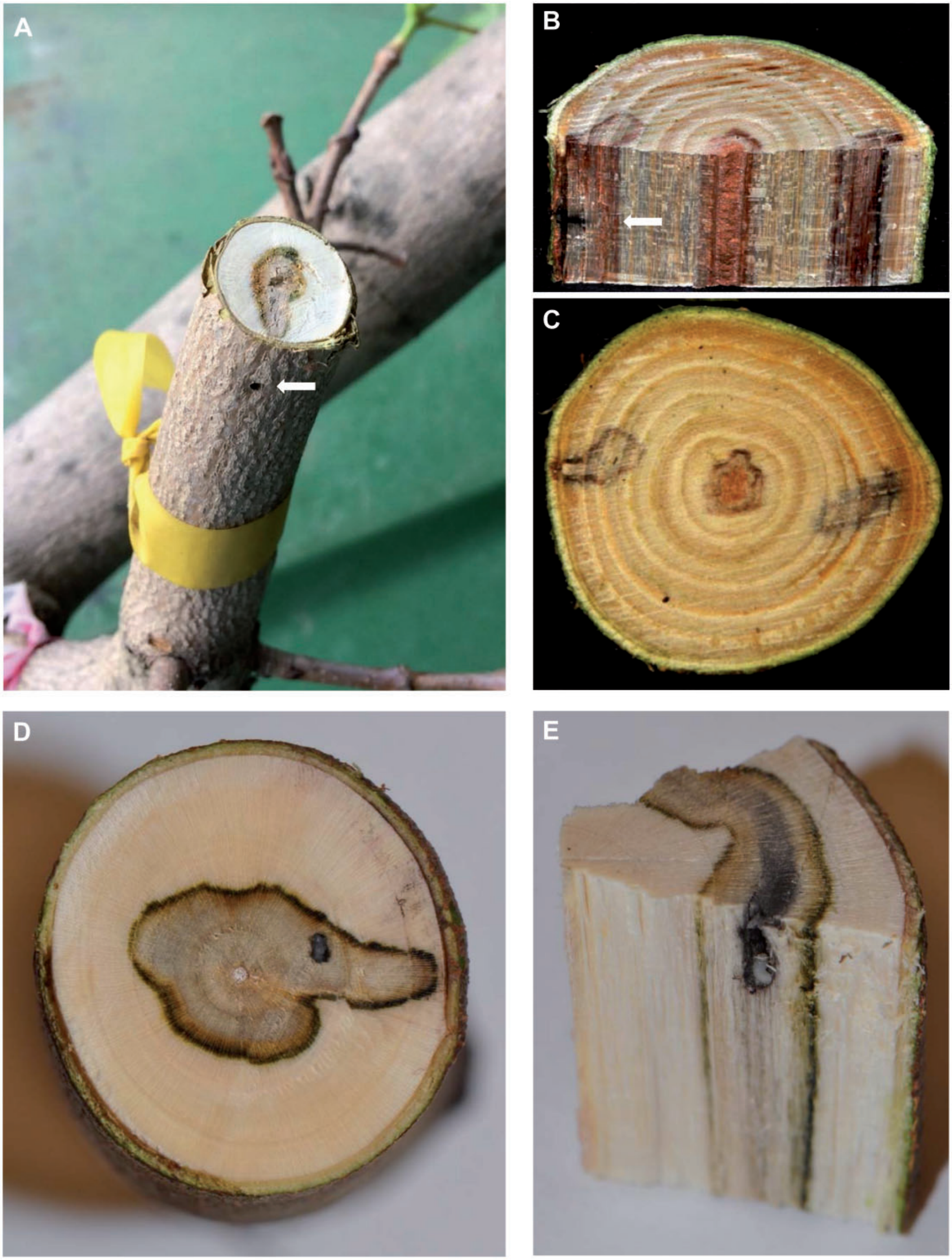

Fig. 11. Tissue discoloration occurs adjacent to galleries created by *X. germanus* and *X. crassiusculus*. (**A**) Staining of tissue above a gallery created in the branch of an unknown tree species. Discolored tissue adjacent to attacks created in (**B–C**) honeylocust and (**D–E**) flowering dogwood. White arrows indicate gallery entrances. (Photos by C. Ranger.)

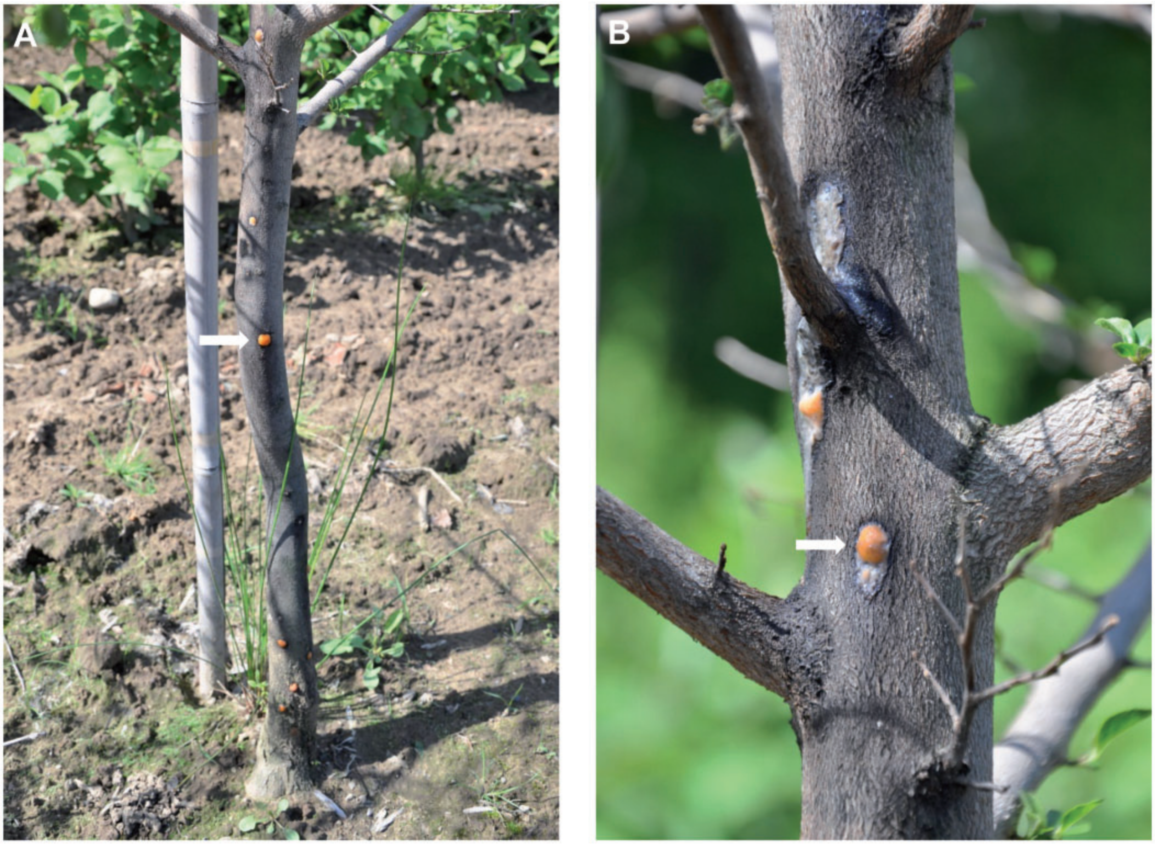

Fig. 12. Opportunistic pathogens can infect defensive sap secretions associated with gallery entrances. (**A–B**) *Fusarium* sp. infecting the site of ambrosia beetle attacks on Japanese snowbell (Photos by C. Ranger.)

consistently was associated with cankers caused by *F. solani* on yellow poplar in a plantation (Kessler 1974, Anderson and Hoffard 1978). *Fusarium* spp. infections have been observed growing from the tunnel entrances and within the associated sap (Ranger and Werle, personal observation; Fig. 12A–B). Mechanical damage associated with tunneling is not responsible for wilting and dieback, but blockage of the transpiration stream by fungi or a mucilaginous material may be responsible (Kovach 1986, Dute et al. 2002).

Impact of Physiological Stressors on Host Preference

Xylosandrus germanus and *X. crassiusculus* traditionally have been viewed as pests of stressed, diseased, or dying plants, but attacks have also been reported on "apparently healthy" plants showing no visible symptoms of chronic (e.g., dieback, stunted, or poor growth) or acute (e.g., wilting) stress. However, it should be cautioned that plants subjected to physiological stress may visually appear healthy, but still emit stress-related volatiles that signal their weakened state to opportunistic ambrosia beetles like *X. germanus* and *X. crassiusculus* (Ranger et al. 2010, 2015a,b). In some cases, visible symptoms resulting from physiological stress can take several years to become fully evident (Schoeneweiss 1978, Wargo 1996). Plants considered apparently healthy while under attack by *X. germanus*, *X. crassiusculus*, and other opportunistic ambrosia beetles are likely to be experiencing or have a history of physiologically stress at the time of attack (Ranger et al. 2010, 2015a,b). For instance, plantation-grown black walnut (*Juglans nigra* L.) trees initially characterized as apparently healthy at the time of attack by *X. germanus* exhibited slower growth rates in the year before attack compared to nonattacked trees (Weber and McPherson 1984b). Similarly, European beech trees, *Fagus sylvatica* L., growing in Western Europe that were considered apparently healthy at the time of attack by *X. germanus* and other opportunistic ambrosia beetles may have first been injured by extreme frost events (Nageleisen 1994, Grégoire et al. 2001, Henin and Versteirt 2004, La Spina et al. 2013). Visually assessing plant health may therefore not be particularly effective for distinguishing individuals that are at risk for attack by *X. germanus*, *X. crassiusculus*, and other ambrosia beetles. Furthermore, at times it can be challenging to determine what physiological stressor(s) predisposed plants to attack, particularly if the attacks were initiated at a low level and went undetected. Efforts are currently underway to assess portable devices for aiding arborists and pest management professionals in evaluating plant health by detecting the emission of ethanol from plants that visually appear apparently healthy (Ranger and Schultz, unpublished data).

Ethanol, a chemical indicator of plant stress, is a host-derived volatile highly attractive to *X. germanus*, *X. crassiusculus*, and numerous other opportunistic ambrosia beetles (Kelsey 2001; Ranger et al. 2010, 2012, 2013a,b, 2015a,b). Both *X. germanus* and *X. crassiusculus* exhibit an efficient capability to locate and preferentially attack trees emitting ethanol while rarely landing on or attacking neighboring trees not emitting ethanol (Ranger et al. 2015a). No evidence yet indicates *X. germanus* or *X. crassiusculus* produce an aggregation pheromone. Instead, their ability to locate vulnerable plants and the decision to attack is strongly influenced by ethanol and potentially other attractants emitted from vulnerable hosts. Low amounts of ethanol can be found in the vascular tissue of

Fig. 13. (**A–B**) Flooding and poor drainage in ornamental nurseries can predispose intolerant trees to attack by ambrosia beetles. (**C**) A crop of dogwood, *C. florida* and *C. kousa* × *florida*, trees growing at an ornamental nursery in northeastern Ohio subjected to flooding and poor drainage in spring 2011 subsequently were attacked by ambrosia beetles. (**D**) Excessive planting depth may have exacerbated the effects of flooding and poor drainage. (**E**) Necrotic tissue moving upwards from the roots was observed on trees that exhibited dieback but no ambrosia beetle attacks, which further supports the trees were physiologically stressed at the time of attack. White arrows denote necrotic transition zone. (Photos by C. Ranger.)

healthy plants, but dramatically higher amounts of ethanol are emitted by trees subjected to a variety of physiological stressors, including flood and drought stress, frost injury, girdling, impaired root function, root and crown disturbance, pollutants, and pathogens (Kimmerer and Kozlowski 1982; Kimmerer and MacDonald 1987; Kelsey and Joseph 2001; Ranger et al. 2013b, 2015b).

Instances of flooding and poor drainage are not uncommon in ornamental plant nurseries (Fig. 13A–E). For example, field observations from commercial nurseries in northeastern Ohio during 2011 indicated record-breaking spring precipitation, poor drainage, and perhaps excessive planting depth predisposed dogwood trees, *Cornus florida* and *Cornus kousa* × *florida*, to attack (Fig. 13C–E; Ranger et al. 2013b). In one case more than 200 dogwoods were lost to attack by ambrosia beetles, mainly *X. germanus*. The grower initially concluded the trees were healthy at the time of attack with no history of infestation, but closer examination demonstrated ambrosia beetles acted as bio-indicators of tree stress. Notably, out of 166 randomly selected trees examined, 165 or 99% exhibited extensive branch dieback, but only 117 or 70.5% of the trees were attacked by ambrosia beetles (Ranger, personal observation). A region of necrotic tissue was observed moving up the stem from the roots on both nonattacked trees and attacked trees (Fig. 13C–E). Experiments conducted under controlled conditions have supported anecdotal field observations that *X. germanus* and *X. crassiusculus* preferentially attack flood-stressed trees but rarely attack neighboring nonflooded trees (Ott 2007; Ranger et al. 2013b, 2015b; Reed et al. 2015). *Xylosandrus germanus* and *X. crassiusculus* also can distinguish among tree species varying in their tolerance of flood-stress and preferentially select intolerant over more tolerant species corresponding to ethanol emissions (Ranger et al. 2015b). Both *X. germanus* and *X. crassiusculus* also colonized flood-stressed *C. florida*, but failed to introduce their symbiotic fungus or produce offspring within galleries created in nonflooded trees.

Drought stress also induces ethanol production by plants (Kelsey and Joseph 2001), but the presumed unsuitability of drought-stressed stems for growing their symbiotic fungi may minimize the impact of this particular stressor on predisposing plants to colonization. Under free choice conditions, *X. germanus* and *X. crassiusculus* preferentially attacked flood-stressed over drought-stressed *C. florida* trees (Frank, Ranger, and Schultz, unpublished data). Thus, factors other than just ethanol emission probably play a role in the decision-making process during host acceptance by *X. germanus* and *X. crassiusculus*, such as host tissue moisture levels.

In addition to water-related stressors, field observations from ornamental plant nurseries suggest that frost injury predisposes intolerant trees to attack (Fig. 14A–E; Ranger et al. 2015a). For instance, trees growing within ornamental nurseries in northeastern Ohio were subjected to a mild winter in 2011–2012 and a record-breaking warm March resulting in trees budding up to one month earlier than normal (Timlin et al. 2012). Vulnerable root and vegetative tissues were then exposed to successive freezing events that occurred in April 2012. Ambrosia beetle attacks subsequently were documented on trees intolerant of late frost, namely, eastern redbud (*Cercis canadensis* L.), Japanese maple (*Acer palmatum* Thunb.), Japanese snowbell (*S. japonicus*), Japanese zelkova (*Zelkova serrata* (Thunb.) Makino), and Kentucky yellowwood (*Cladrastis kentukea* (Dum.-Cours.) Rudd) (Ranger et al. 2015a). Ambrosia beetle attacks were also observed on tulip poplar (*Liriodendron tulipifera* L.) following an early spring freeze in Ohio and Tennessee (Ranger and Oliver, personal observation). Similarly, Heidenreich (1960) reported that young oak (*Quercus rubra* L.) and sycamore (*Acer pseudoplatanus* L.) trees damaged by frost were subsequently attacked by *X. germanus*. Extreme frost events also preceded attacks by *X. germanus* and other ambrosia beetles in large stands of European beech trees, *F. sylvatica*, in Western Europe (Grégoire et al. 2001, La Spina et al. 2013). Bark tissue on *F. sylvatica* trees experimentally injured by freezing was more attractive to *X. germanus* and other ambrosia beetles than noninjured tissue (La Spina et al. 2013). Experimentally frost-injured *S. japonica* were also preferentially attacked by *X. germanus* and *X. crassiusculus* (Ranger and Schultz, personal observation).

Field observations and reports from ornamental nurseries and tree fruit orchards throughout the midwestern, eastern, and southeastern United States also indicated low temperature stress during the winter months of 2013–2014 and again in 2014–2015 appear to have predisposed trees to attack (Fig. 15A–D). In particular, tree species in an ornamental nursery in Ohio exhibiting varying degrees of bark splitting were attacked by ambrosia beetles in 2014 and 2015, namely, Chinese elm (*Ulmus parvifolia* Jacq.), Chinese fringetree (*Chionanthus retusus* Lindl. & Paxt.), common hackberry (*Celtis occidentalis* L.), hardy rubber tree (*Eucommia ulmoides* Oliv.), eastern redbud, hawthorn (*Crataegus punctata* Jacq.), linden (*Tilia sp.*), oak (*Quercus* spp.), sweetgum (*Liquidambar styraciflua* L.), and sugar maple (*Acer saccharum* Marsh.) (Fig. 15A–D; Ranger pers. obs.). Low temperature stress also may have predisposed kwanzan cherry (*Prunus serrulata* L.) to attacks in Virginia (Schultz, personal observation), and striped maple (*Acer pensylvanicum* L.), hornbeam (*Carpinus betulus* L.), paperbark maples (*Acer griseum* Pax.), red beech (*Nothofagus fusca* (Hook. f.) Oerst.), Japanese snowbell, and yellowwood (*Cladrastis* sp.) in Maryland in 2014 and 2015 (Gill personal observation).

Monitoring Tactics

Ethanol is the standard attractant used in traps for monitoring *X. germanus*, *X. crassiusculus*, and a variety of other ambrosia beetles. Ethanol lures can be easily made by filling a plastic container with 70–95% ethanol (i.e., ethyl alcohol) and inserting a wick through the lid. Denatured ethanol can be used, but not isopropyl or other commercially available alcohols. However, commercial lures eliminate the need for frequent refilling due to rapid evaporation of the ethanol (Oliver et al. 2004). Unscented ethanol-based hand sanitizers can also be used as a lure (Steininger et al. 2015). Attraction of *X. germanus* and *X. crassiusculus* to ethanol can be enhanced by addition of conophthorin and α-pinene, but the effect is not always consistent and the additional lure costs do not provide an added benefit (Miller and Rabaglia 2009; Dodds and Miller 2010; Gandhi et al. 2010; Ranger et al. 2011a, 2014; Van DerLaan and Ginzel 2013; Miller et al. 2015).

A variety of ethanol-based traps (Fig. 16A–H) can be purchased commercially or homemade. Oliver et al. (2004) evaluated a variety of homemade and commercial traps and found that a simple Baker-type trap made from a 2-liter soft drink bottle was inexpensive and effective (Fig. 16A). Similarly, Steininger et al. (2015) determined a simple, one-window bottle trap was comparable to bottle traps with multiple windows for capturing *X. crassiusculus* and other Scolytinae. Lures should ideally be suspended within the trap to maximize ambrosia beetle attraction. Soapy water or low-toxicity antifreeze (i.e., propylene glycol) diluted with an equal part of water should be used as a killing agent and preservative in the traps. Fumigant strips in the collection vessel were less effective than propylene glycol (Oliver et al. 2004).

Fig. 14. Frost injury has preceded attacks by ambrosia beetles within ornamental nurseries. (**A**) Japanese snowbell trees growing in an ornamental nursery in Ohio were frost injured in spring 2009 and subsequently attacked once ambrosia beetles began their spring flight. (**B**) Eastern redbud trees growing in an ornamental nursery in northeastern Ohio were frost injured following a mild winter in 2011–2012 and subsequently attacked by ambrosia beetles. (**C–D**) Tip dieback on Kentucky yellowwood tree growing at a residence in northeastern Ohio resulting from frost injury in spring 2012. Ambrosia beetle attacks were initiated after the tree was frost injured on at least two occasions. (**E**) Defense sap production as indicated by white arrows on the trunk of a relatively large (30 cm diam.) yellowwood tree injured by frost and subsequently attacked by ambrosia beetles. (Photos by C. Ranger.)

Fig. 15. Low temperature stress and winter injury imposed during the winter months of 2013–2014 and 2014–2015 in northeastern Ohio preceded extensive attacks by ambrosia beetles in ornamental nurseries. (**A**) Low temperature stress and winter injury preceded attacks by ambrosia beetles on sugar maple trees. Attacked trees often occur in clusters within nurseries as indicated by white arrows. (**B**) Ambrosia beetle attacks circled in blue on the stem of a sugar maple tree exhibiting bark splitting in spring 2014. (**C**) Ambrosia beetle attacks on an eastern redbud tree growing at an ornamental nursery in northeastern Ohio exhibiting bark splitting in spring 2014. (**D**) Ambrosia beetle attack on a tree growing at an ornamental nursery in northeastern Ohio exhibiting bark splitting in spring 2015. (Photos by C. Ranger.)

Fig. 16. A variety of ethanol-based tactics for monitoring ambrosia beetle flight activity can be homemade or purchased from vendors. Traps are best positioned low to the ground and within or along the edge of a wooded area adjacent to an ornamental nursery. (**A**) A simple Baker-type trap made from a two-liter soft drink bottle. Ethanol lures should be suspended within the upper portion of the trap. Soapy water or low toxicity antifreeze diluted with equal parts water should be used as a killing agent and preservative. (**B**) A modified Baker-type trap that uses a Tornado Tube (Steve Spangler Science, Colorado) to connect the mouths of two bottles, permitting easier recovery of trap contents. (**C–D**) A Lindgren trap can be purchased from a vendor and the number of funnels adjusted. (**E**) Stems can be cored out, filled with 95% ethanol, and plugged with a rubber stopper to induce ambrosia beetle attacks for monitoring purposes. Stems also can be soaked in 95% ethanol for 24 h to induce attacks. (**F**) A pressurized system can be used to inject ethanol into trees for inducing ambrosia beetle attacks on specific trees to monitor attack activity or ensure beetle pressure for evaluating insecticide efficacy. (**G**) Chewed wood ejected from ambrosia beetle tunnels in sweetbay magnolia injected with ethanol. (**H**) Trees intolerant of flooding, including dogwood, can be flood-stressed for use as trap trees using a pot-in-pot system and lining the outer pot with a plastic bag to prevent drainage and induce attacks on specific trees. (Photos 16A–C, 16E–F by C. Ranger; photos 16D and 16G by P. Schultz.).

As an alternative to wick-type or sachet lures, woody stems can be cored, filled with 95% ethanol, and plugged with a rubber stopper or soaked for 24 h in 95% ethanol then placed in traps (Fig. 16E). Traps baited with ethanol-infused stem sections were five times more attractive to *X. germanus* than traps baited with a pouch-style ethanol lure (Ranger et al. 2012). Baiting, irrigating, or injecting trees with ethanol also induces attacks on specific trees, and can provide insight into seasonal attack activity and be useful for screening insecticides (Fig. 16F–G; Ranger et al. 2010, 2012, 2013a, 2015a; Frank and Sadof 2011; Reding et al. 2013b). Trees intolerant of flooding, such as *C. florida*, can be flood-stressed using a plastic bag and pot-in-pot system to prevent drainage and induce attacks for monitoring purposes or evaluating insecticides (Fig. 16H; Ranger et al. 2013a, 2015b).

Ethanol-baited traps or ethanol-infused bolts should be suspended just above ground level (Weber and McPherson 1991, Reding et al. 2010). To intercept beetles, traps should also be placed near wooded areas, which are the source of beetles dispersing into ornamental nurseries (Ranger et al. 2013a, Reding et al. 2015, Werle et al. 2015).

Management and Control Options

Cultural Control

Maintaining plant health is the foundation of an integrated pest management program for ambrosia beetles in ornamental plant nurseries, particularly since insecticides are difficult to time accurately and do not completely prevent attacks on stressed plants. Both *X. germanus* and *X. crassiusculus* are poor colonizers of vigorous plants (Ranger et al. 2015b). The significance of physiological stressors in predisposing plants to attack should not be overlooked. Risk factors should be considered and addressed as part of an effective management program. Appreciating that many have noted plants were "apparently healthy" prior to attack, growers would benefit from an awareness of factors that predispose plants to attack (such as flooding) and tools that can detect when they are in a susceptible state, when such factors are not otherwise apparent. Their capability to rapidly locate plants in the early stages of physiological stress makes *X. germanus* and *X. crassiusculus* challenging to manage. Despite a broad host range, beetles can distinguish among slight differences in host condition and only target certain species and cultivars within a given year and location based on host vigor (Weber and McPherson 1984b, Ranger et al. 2015a). Both *X. germanus* and *X. crassiusculus* are poor colonizers of healthy plants, which is likely due to an inability to establish their symbiotic fungus in such hosts; as previously noted, oviposition does not begin until the symbiotic fungus is established.

Controlled experiments and anecdotal field observations indicate poor drainage and plant unsuitability for a particular growing site resulting in susceptibility to frost injury and low temperature stress can contribute to plants being predisposed to attack. Predictions for increasing frequency and severity of extreme climatic events suggest we may expect increasing attacks by nonnative ambrosia beetles on intolerant plants. Plant species or cultivars tolerant of abiotic stressors should be incorporated into production practices, but the tolerance levels of contemporary ornamental plant cultivars are not always thoroughly understood.

Trap plants can be used to attract additional beetles for two to three weeks after attacks are initiated, but should be burned or chipped before new adults emerge. Since plants can occasionally recover from attacks, ornamental plant producers may choose to avoid culling plants with a relatively low level of attacks. Neighboring healthy plants are poor hosts for *X. germanus* and *X. crassiusculus* and unlikely to be attacked or colonized (Ranger et al. 2015b). Dying plants and brush piles within ornamental nurseries also should be burned or chipped annually to minimize breeding sites.

Biological/Microbial Control

No parasitoids have been found associated with *X. germanus* (Weber and McPherson 1983a, Kenis et al. 2004), although a wasp (Hymenoptera: Eulophidae) was found in a gallery of *X. germanus* in Germany (Gauss 1960). A variety of opportunistic predatory insects such as clerid beetles are known to feed on bark and ambrosia beetles (Kenis et al. 2004), but almost no specific examples exist in the literature pertaining to *X. germanus* or *X. crassiusculus*.

Some entomopathogenic fungi have exhibited promising efficacy against *X. germanus* and its symbiotic fungi. Castrillo et al. (2011) demonstrated commercial strains of *Beauveria bassiana* (Bals.) Vuill. strain ATCC 7040 (Naturalis-L, Troy BioSciences, Phoenix, AZ) and *Metarhizium anisopliae* strain F52 (Met52, Novozyme Biologicals, Bagsvaerd, Denmark) were associated with comparatively high mortality of adult female *X. germanus*. Inoculation of adult females also reduced the number of beetles forming galleries and producing brood. Brood sizes of inoculated *X. germanus* females also were smaller and some had up to 100% of the progeny infected across all life stages.

Chemical Control

Nursery growers rely on properly timed preventive trunk sprays of insecticides to protect plants from attack by *X. germanus* and *X. crassiusculus*. No insecticide treatments provide 100% protection. Furthermore, no rescue treatments exist for ambrosia beetles once they have tunneled into a host plant, so timing insecticides prior to attack based upon adult flight activity is currently the best strategy. Oliver and Mannion (2001) noted that insecticide applications are most effective when closely timed with flight activity, applied repeatedly, or have long residual activity. Reding et al. (2013a) demonstrated preventive insecticide treatments should be applied in the spring after 56 degree-days (10°C base temperature) have been reached and before temperatures of $\geq$20°C are forecasted. Current management recommendations are trunk applications every two weeks during spring flight activity, which could encompass 12–16 wk in southern regions (Frank and Sadof 2011).

Some pyrethroid insecticides have been found to be more effective than other materials, if somewhat inconsistent. Cypermethrin and bifenthrin provided the best efficacy against attacks by *X. crassiusculus* on attractive bolts, while permethrin, chlorpyrifos, and esfenvalerate provided a lower level of efficacy (Mizell and Riddle 2004). Acephate, cyfluthrin, endosulfan, fenpropathrin, imidacloprid, and thiamethoxam were ineffective as sprays. Frank and Bambara (2009) also indicated chlorpyrifos was ineffective. Permethrin was associated with the fewest attacks on ethanol-injected trees, while substrate drenches and trunk sprays of systemic insecticides including chlorantraniliprole, cyantraniliprole, tolfenpyrad, and dinotefuran were not effective (Reding et al. 2013b). Permethrin also minimized attacks on ethanol-injected trees (Frank and Sadof 2011) and has been recommended for ambrosia beetle control, but repeated treatments may be required during peak ambrosia beetle flight. In addition to active ingredient, insecticide formulation can influence efficacy and residual activity of trunk sprays for bark beetles and other wood-boring insects, with emulsifiable concentrates (EC) generally being more effective than wettable powders (WP) (Fettig et al. 2013; Herms, personal observation). Preventive treatments with fungicides have not exhibited efficacy (Ranger and Schultz, personal observation).

Trunk sprays of some botanical formulations, especially products containing allyl isothiocyanate, also show some efficacy against reducing ambrosia beetle attacks (Ranger et al. 2011b). However, the higher costs often associated with botanical insecticides could hamper their incorporation into a management program. Botanical insecticides would be of interest to organic producers.

Since the majority of attacks by *X. germanus* and *X. crassiusculus* occur on the main trunk (Oliver and Mannion 2001; Reding et al. 2010; Ranger et al. 2013b, 2015a), thorough coverage of this region is important. Restricting permethrin applications to the trunks of trees using a precision sprayer provided protection against ambrosia beetle attacks equal to airblast applications (Frank and Sadof 2011). Broadcast applications of insecticides to trees for ambrosia beetle control results in excessive nontarget deposits, is prone to drift, disrupts natural enemy abundance, and leads to outbreaks of secondary pests, particularly spider mites (Frank and Sadof 2011).

Push–Pull Strategy

Ambrosia beetles, including *X. germanus* and *X. crassiusculus*, overwinter within their host plants, and recent studies have confirmed that wooded areas serve as source populations for beetles moving into neighboring ornamental nurseries (Ranger et al. 2013a, Reding et al. 2015, Werle et al. 2015). Behavioral manipulation as part of a push–pull management strategy (Pyke et al. 1987, Miller and Cowles 1990) may be effective for managing ambrosia beetles in ornamental nurseries, using repellents to push beetles away from vulnerable nursery stock and attractants to pull beetles into annihilative traps.

Verbenone, a bark beetle antiaggregation pheromone, is a promising push component for strategic deployment in ornamental nurseries. At a release rate of 50 mg/d, verbenone reduced attraction of *X. germanus* to ethanol-baited traps by 96.9% (Ranger et al. 2013a). Verbenone also reduced attraction of *X. germanus* to ethanol-baited traps at a release rate of 2 mg/d (Ranger et al. 2014). Orientation by *X. crassiusculus*, *X. compactus*, and *X. saxesenii* also were disrupted by verbenone (Dudley et al. 2006, Van DerLaan and Ginzel 2013). A verbenone dispenser attached to ethanol-injected *Magnolia virginiana* L. trap trees deployed in Ohio reduced ambrosia beetle attacks by 85% compared to trap trees without a verbenone dispenser (Ranger et al. 2013a). In some instances, attacks on ethanol-injected trees also decreased with an increasing proximity to a verbenone emitter. Similarly, verbenone reduced the attraction of *X. germanus* and *Gnathotrichus materiarius* (Fitch) to red pine, *Pinus resinosa* Ait., trap trees, which were created by stem injections of the herbicide dicamba (3,6-dichloro-*o*-anisic acid; Dodds and Miller 2010). The capability of verbenone to interrupt ambrosia beetle orientation and reduce attacks suggests deployment of verbenone emitters could be a push component for deflecting beetles before their dispersal into ornamental nurseries. The effectiveness of repellents under field conditions also can improve by incorporating attractive host-plant odors (i.e., ethanol-baited traps) and host-masking repellents.

The strategic deployment of an ethanol-based trapping tactic, such as ethanol-baited traps or ethanol-infused stems, along the perimeter of growing areas adjacent to woodlots is a promising pull component that could be used to intercept ambrosia beetles before their dispersal into ornamental nurseries, given the positive concentration response to ethanol exhibited by *X. germanus* and *X. crassiusculus* (Klimetzek et al. 1986, Reding et al. 2011, Ranger et al. 2012). However, additional studies are required to determine the optimal combination of repellent push components and attractive pull components along the perimeter of ornamental nurseries.

Concluding Remarks

Ambrosia beetles, particularly *X. germanus* and *X. crassiusculus*, are among the most destructive and challenging insect pests of crops in ornamental plant nurseries. There is still much critical knowledge to learn about ambrosia beetle biology, behavior, and ecology, especially as more invasive bark and ambrosia beetles are introduced into N. America. For example, the nonnative ambrosia beetle *Anisandrus maiche* Stark has recently become established in Ohio, Pennsylvania, and West Virginia and been documented to attack ornamental nursery trees (Rabaglia et al. 2009, Ranger et al. 2015b). Although this publication focused on *X. germanus* and *X. crassiusculus*, understanding the biology, ecology, and pathology of their primary and auxiliary fungi are also important components necessary for developing effective management plans. Although rapid wilting and dieback are commonly observed following ambrosia beetle attacks, the fundamental causes for the symptoms are not well understood. Further studies are needed to optimize a push–pull strategy for managing ambrosia beetles in ornamental plant nurseries.

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