

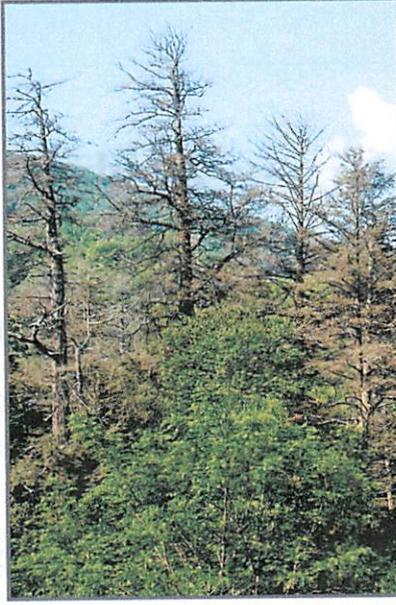


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The Use of Classical Biological Control to Preserve Forests in North America

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XXIX REDBAY AMBROSIA BEETLE

(*Xyleborus glabratus* Eichoff) (Coleoptera: Curculionidae)

J. L. Hanula¹ and A. E. Mayfield III²

¹USDA Forest Service, Southern Research Station, Georgia, USA

²USDA Forest Service, Southern Research Station, Asheville, North Carolina, USA

DESCRIPTION OF PEST

Taxonomy

The redbay ambrosia beetle, *Xyleborus glabratus* Eichoff, (Fig. 1) and its associated fungus *Raffaelea lauricola* T.C. Harr., Fraedrich & Aghayeva are exotic species, recently invasive to the United States. Together, they cause a vascular wilt disease that is highly destructive to some species in the Lauraceae (Fraedrich et al., 2008). *Xyleborus glabratus* is a member of the subtribe Xyleborina, within the subfamily Scolytinae. No synonyms are reported (Rabaglia et al., 2006).

Distribution

Xyleborus glabratus is native to Asia, recorded from Bangladesh, India, Myanmar (Burma), and Taiwan (Rabaglia et al., 2006). Harrington et al. (2011) reported capturing it in Japan. The first record in the United States

occurred at Port Wentworth near Savannah, Georgia, in 2002, followed by Hilton Head Island, South Carolina, in 2004. The current distribution of laurel wilt and the redbay ambrosia beetle is concentrated in parts of Florida, Georgia, and South Carolina (Fig. 2). Outlying sites in Mississippi, western Florida, and the northern part of South Carolina suggest that human movement of infested wood is also spreading the beetle.

Damage

Type This invasion has the potential to cause ecological and economic losses.

Ecological losses These can result through severe damage to native redbay (*Persea borbonia* [L.] Spreng.) and swampbay (*Persea palustris* [Raf.] Sarg.) trees. These aromatic, broadleaf evergreens are usually of small to medium size, although rare large individuals may reach diameters in excess of 100 cm. Some taxonomists do not consider redbay and swampbay to be distinct species;

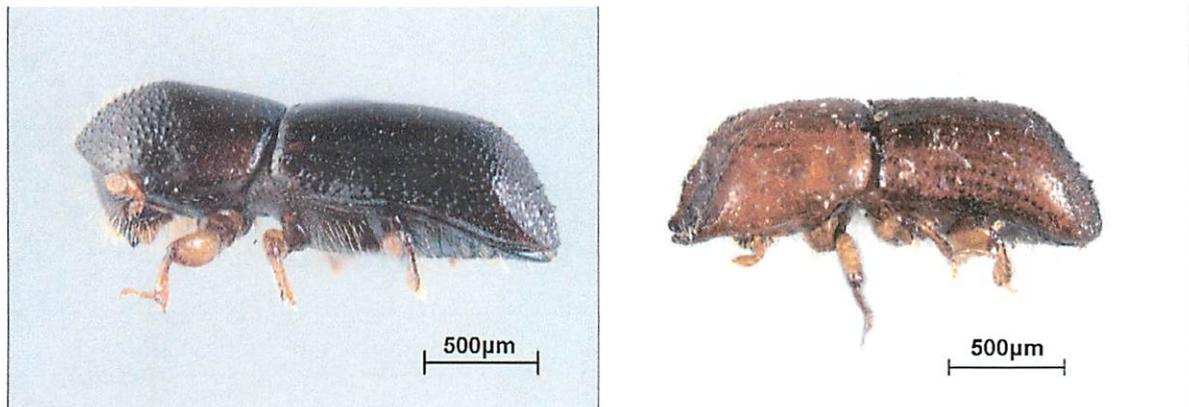


Figure 1 Female (left) and male redbay ambrosia beetle, *Xyleborus glabratus*. J. L. Hanula.

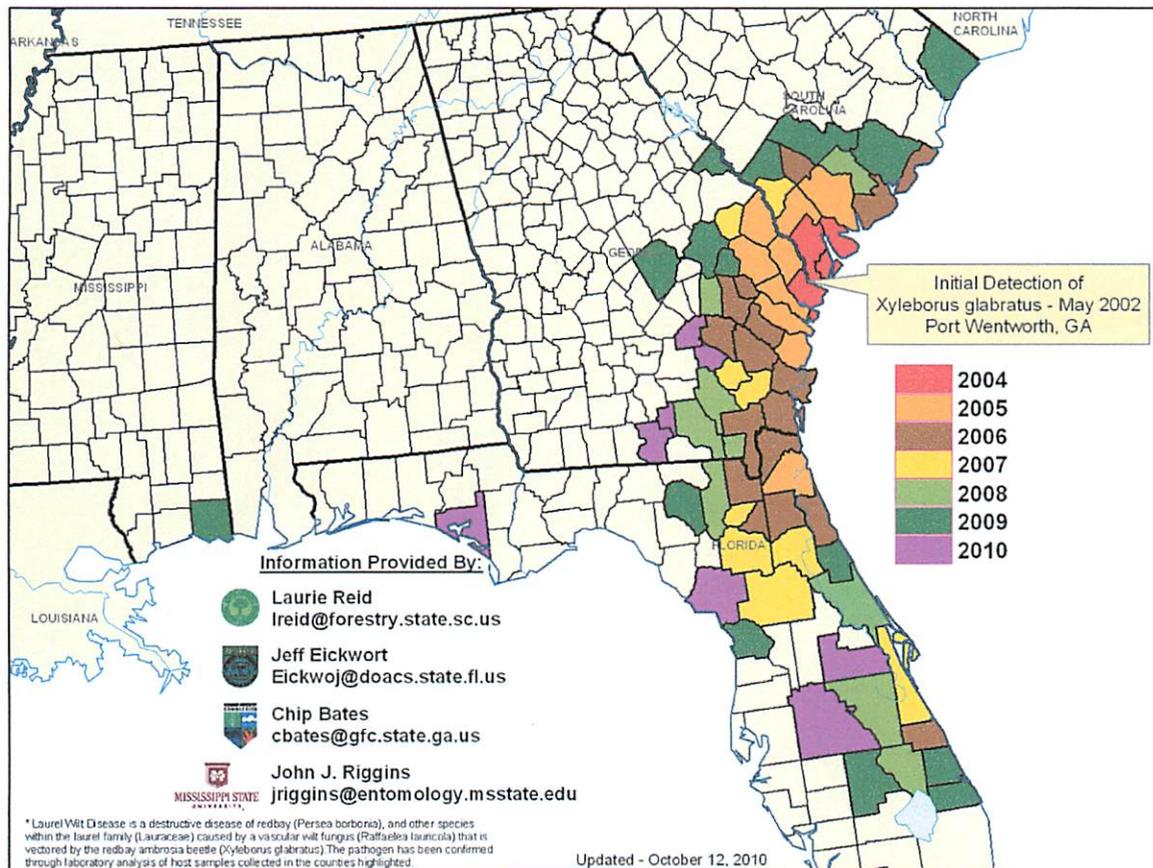


Figure 2 Distribution of redbay ambrosia beetle and laurel wilt by county over time.
http://www.fs.fed.us/r8/foresthealth/laurelwilt/dist_map.shtml.

these species, in combination with silkbay (*Persea borbonia* [L.] Spreng. var. *humilis* [Nash] L.E. Kopp), are sometimes collectively referred to as “redbay.” All appear to be equally susceptible to laurel wilt. Redbay (broadly defined) dies within a matter of weeks to a few months after attack by the redbay ambrosia beetle and infection with the laurel wilt fungus. The pathogen moves systemically in the xylem, causing dark vascular discoloration (Fig. 3) and eventual wilting. Within five years of initial infestation, almost all redbay and swampbay trees greater than 2.5 cm diameter die, although numerous seedlings and stump sprouts commonly survive in infested areas. Lower density populations of the beetle persist in areas where mature redbays have been eliminated (Hanula et al., 2008), so it is likely that as these seedlings and saplings mature they will also be attacked. However, redbay are abundant as small bushes or shrubs in pine forests that receive frequent prescribed burns. Due to the persistence of this class of smaller individuals, the extinction of redbay as a species

seems unlikely, although it is uncertain if it ever will reach tree status again.

Very little is known about the ecological role of redbay trees, although they are or were one of the most common trees on barrier islands and in the transitional zone between xeric upland and bottomland swamps or wetlands. According to Brendemuehl (1990), redbay are often associated with the rich, moist, mucky soils along swamp borders, but they also can grow in xeric sites, such as sandy soils associated with old dunes. Redbay is a major component of the Sweetbay-Swamp Tupelo-Redbay cover type (Society of American Foresters Type 104). It is also common in the loblolly pine-hardwood (Type 82), pond pine (Type 98), baldcypress-tupelo (Type 102), and water tupelo-swamp tupelo (Type 103) cover types, and is a minor component of several others (Brendemuehl, 1990). Its overall role in these forests is unknown, but it does serve as the primary host for the palamedes swallowtail (*Papilio palamedes* [Drury]), a common swallowtail butterfly on the

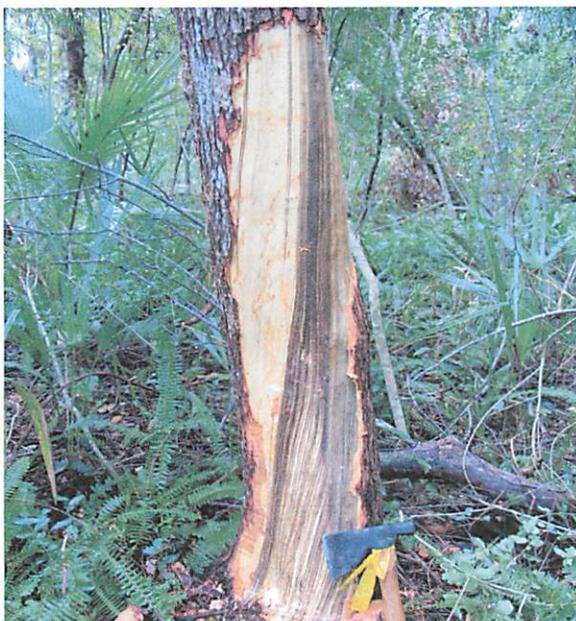


Figure 3 Dark discoloration in the outer sapwood of a redbay (*Persea borbonia*) affected by laurel wilt. Albert Mayfield, USDA Forest Service, Bugwood.org.

coastal plain (Minno et al., 2005). Because small seedlings, saplings, and stump sprouts can serve as host material for the larvae, the butterfly is not likely to disappear, although in many forests the amount of foliage available has been drastically reduced. The effect this will have on numbers of the palamedes swallowtail has not been studied. Redbay (broadly defined) is also the only known host of the gall-forming redbay psyllid (*Trioza magnoliae* [Ashmead]) (Hall, 1999). Galls of these psyllids are so ubiquitous on both immature and mature trees that they can aid in recognition of redbay (Nelson, 1994). The effect of losing mature redbay trees on populations of the psyllid is unknown: They will likely persist but perhaps at lower population levels. Redbay flowers are primarily pollinated by bees, so losing all mature redbay trees in forest tracts is likely to affect bee species that use redbay pollen. Redbay fruits are eaten by songbirds and wild turkey. These fruits are ranked fifteenth out of 63 fruits in dietary importance for these birds, on a volumetric basis (Brendemuehl, 1990).

In addition to redbay and swampbay, redbay ambrosia beetle and laurel wilt also kill sassafras (*Sassafras albidum* [Nutt.] Nees). Reports of sassafras mortality are increasing (C. Bates, pers. comm.) as the beetle reaches the edge of the range of redbay in Georgia, USA. There are questions regarding the attractiveness of sassafras to the beetle

(Hanula et al., 2008), and it is uncertain if sassafras will sustain beetle populations as large as those on redbay. One factor likely to influence the spread of *X. glabratus* in sassafras is this tree's more widely scattered distribution and smaller size in the Atlantic Coastal Plain and Piedmont, in contrast with higher densities and larger trees found in the southern Appalachian mountains and northward (Koch and Smith, 2008). A second factor that might influence the beetle's spread on sassafras is that sassafras wood appears to be relatively unattractive to *X. glabratus* (Hanula et al., 2008), and when beetles do attack it, brood production is lower than in redbay (Mayfield and Hanula, 2012). These attributes, combined with the lower densities of sassafras, could reduce the natural spread of *X. glabratus* into the Piedmont beyond the range of redbay. Very little is known about ecological role of sassafras, although it might be an important pioneer species aiding in restoration of depleted soils (Auten, 1945).

The laurel wilt fungus has been recovered from wilted pondspice (*Litsea aestivalis* [L.] Fern.) and southern spicebush (*Lindera mellisifolia* [Walt.] Blume), both of which are in the Lauraceae (Fraedrich et al., 2008). *Xyleborus glabratus* has been recovered from diseased pondspice (AEM unpublished data), but not from southern spicebush. Pondspice is a shrub that grows to 3 m in height. It is listed as endangered in Florida and Maryland and threatened in Georgia (USDA, Natural Resource Conservation Service, 2012). Southern spicebush is a low shrub rarely exceeding 2 m in height. It is on the federal list of endangered species. Although laurel wilt was recovered from wilted stems of both species in the field by Fraedrich et al. (2008), additional instances of infected pondberry occurring in areas of widespread redbay mortality have not been reported. Laurel wilt symptoms have subsequently been observed on pondspice stems at a number of locations in Florida, but pathogen confirmation was attempted at only one of these sites (Surdick and Jenkins, 2009, 2010).

Both the redbay ambrosia beetle and laurel wilt fungus have been recovered from avocado (*Persea americana* Mill.) trees in Florida (Mayfield et al., 2008ab), and avocado wood is as attractive to the beetles as redbay wood (Hanula et al., 2008). Avocado is native to Central America and Mexico (USDA GRIN, 2012) and is widely planted throughout tropical and subtropical regions of the world, including southern California and the Caribbean Islands. Although not native to Florida, avocado trees are widely planted as

ornamental fruit trees throughout much of the state and it is an economically important fruit crop in the southern tip of Florida (see below), the Caribbean islands, California, and Mexico. This beetle, should it spread westward to Mexico and into Central America, could have catastrophic consequences for this industry and could strongly affect subtropical species dependent on avocado.

Laurel wilt also has been recovered from camphor trees (*Cinnamomum camphora* [L.] Sieb.), an invasive species native to Asia (Smith et al., 2009a). Although Smith et al. (2009a) did not recover redbay ambrosia beetle from the trees, it is most likely the vector, because the camphor trees were in areas with extensive redbay mortality and high beetle populations. In this case, redbay ambrosia beetle and laurel wilt could have a positive ecological impact since camphor trees are considered invasive in Florida (Florida Exotic Pest Plant Council, 2009) and other areas. However, unlike redbay, camphor trees do not exhibit rapid decline and death but only localized wilt symptoms on one or a few branches (Smith et al., 2009a). Thus, its ability to rid forests of this invasive is probably going to be limited. Recent field trials have demonstrated that cut camphor wood is attractive to *X. glabratus* (Mayfield and Hanula, 2012); however, it is a poor host for brood production.

Camphor trees' ability to survive attack suggests some form of resistance or tolerance to the fungus, possibly derived through co-evolution in their native range. The ability of laurel wilt to infect and kill a wide variety of trees in the southeastern United States suggests that trees lacking a similar co-evolutionary history are likely to be equally susceptible. Thus, the ability of redbay ambrosia beetle and laurel wilt to cause harm to Lauraceae throughout the world should not be underestimated.

Economic losses These vary with the species of tree affected. Redbay beetle and laurel wilt kill redbay, sassafras, and avocado trees. Redbay trees have minor economic value. Larger trees mixed in with more economically important tree species are often cut during harvest and sold for pulpwood or cut up for lumber (for pallets, etc). Redbay wood is also used for cabinetry, but only on a very limited basis (Brendemuehl, 1990). Like redbay, sassafras trees are not widely used for pulp or lumber. For both species, the greatest economic impact may be through reduced property values for homeowners who have either species as ornamental plantings near their homes and incur the cost of removing dead trees. The latter is an additional

cost for parks, where redbay trees occur along trails or in campgrounds, or utility companies that may have trees fall across their lines.

The greatest potential economic impact of redbay ambrosia beetle and laurel wilt could be to the multimillion-dollar avocado industry in south Florida and, potentially, California. Homeowners with dooryard avocados could experience similar losses and costs as those with redbay trees. Evans et al. (2010) estimated that losses to the avocado industry due to redbay ambrosia beetle and laurel wilt could range from \$356 million if nothing is done to \$183 million if damage control is 50% effective. Even ignoring reduced property values and management costs associated with tree removal (a component of this estimate), the adverse impact on the regional economy from lost avocado production alone could range from \$54 million if nothing is done to \$27 million if treatments are 50% effective. However, these estimates are based on the assumption that all avocado varieties will prove to be completely susceptible to laurel wilt, which may not turn out to be the case. For example, Mayfield et al. (2008b) reported that only one of five cultivars in their test wilted and died after exposure to *X. glabratus* in a cage experiment, although *R. lauricola* was recovered from all five. In addition, avocado trees from Florida have been grown successfully in Taiwan since the early 1900s (Ling, 2003) in the presence of a local native population of *X. glabratus* carrying *R. lauricola* (Harrington, et al. 2011). There are no reports of a comparable wilt disease in avocados in Taiwan or elsewhere in Asia. Therefore, the situation may not be as dire as a total loss of the Florida crop. The discovery of dead and dying avocado trees in homeowner yards is cause for concern (Mayfield et al., 2008a) and, more recently, Ploetz et al. (2011) reported that avocado cultivars commonly used in Florida were moderately susceptible to laurel wilt. Thus, if the beetle can vector the fungus efficiently among avocado trees, avocado production in Florida may be harmed.

Extent of losses Three studies have examined the impact of redbay ambrosia beetle and laurel wilt on redbay trees in southeastern U. S. forests. Fraedrich et al. (2008) monitored 132 redbay trees ranging in size from 2.5 cm to >20 cm diameter at 1.4 m above ground (DBH) from July 2005 (when mortality was still relatively low) to January 2007. The largest trees died most rapidly, with 100% mortality of trees >20 cm by January 2006. Other size classes were infected and killed over a longer period of

time. Over 90% of trees >5 cm were dead by the end of the study, while 20% of trees in the 2.5–5 cm size class were still living.

Goldberg and Heine (2009) compared forest composition on a barrier island in northeastern Florida in 2008 to a previous study on the same island conducted in 1983 (Stalter and Dial, 1984). By 2008, there was a 32% decrease in mature redbay trees.

In another study, Hanula et al. (2008) estimated beetle and tree densities at seven locations, ranging from areas outside the known infestation to the areas where the beetle was first discovered. Live redbay trees >2.5 cm diameter densities were 4–9 trees/ha in the Savannah, Georgia area, where the beetle had been present the longest, compared to >460 tree/ha at the site outside the infested area. Numerous dead or dying trees in the other study plots indicated that the high number of trees at the un-infested site was probably consistent for areas of the lower coastal plain and barrier island forests, where redbay thrives. Therefore, based on these data we estimate that 95–98% of the trees have been killed in the Savannah area study sites. Koch and Smith (2008) provided tree density maps for redbay and sassafras based on USDA Forest Service, Forest Inventory and Analysis data. Although their results take into account all forest types within redbay's range, based on the extensive forested area likely to be affected by redbay ambrosia beetle and laurel wilt it is safe to say that 100 million or more redbay trees will be killed if the infestation spreads throughout the tree's range.

Biology of Pest

The redbay ambrosia beetle attacks and bores into living trees and inoculates the sapwood with *R. lauricola*, which causes a vascular wilt disease known as laurel wilt (Fraedrich et al., 2008). Laurel wilt is lethal to redbay and swampbay: it has killed thousands of these trees in Florida, Georgia, South Carolina, and Mississippi, and landscape avocado trees in Florida (Mayfield, et al. 2008a) and sassafras trees in Florida, Georgia, and South Carolina (Fraedrich et al., 2008; Smith et al., 2009b).

Xyleborus glabratus is a typical ambrosia beetle but has some unique characteristics. Like other ambrosia beetles, it bores into the xylem or wood of dead and dying trees and lays its eggs in the tunnels it creates. During excavation, the tunnels are inoculated with an ambrosia fungus from mycangia situated at the base of each mandible (Fraedrich

et al., 2008). The mycangia can contain up to four species of *Raffaelea* fungi at one time, and a total of six different species have been isolated from redbay ambrosia beetle mycangia (Harrington and Fraedrich, 2010). However, Harrington and Fraedrich (2010) note that it is unusual for ambrosia beetles to have so many fungi associated with them. *Raffaelea lauricola* was isolated from all but one of the beetles studied (Harrington and Fraedrich, 2010), which suggests it is the ambrosia fungus on which larvae feed. This is also the only known case where a mycangial fungus of an ambrosia beetle causes a lethal wilt disease (Fraedrich et al., 2008; Harrington et al., 2008; Harrington and Fraedrich, 2010).

Little information is available on the natural history of redbay ambrosia beetle from its native range. Rabaglia et al. (2006) (and references therein) list *Litsea elongata* (Nees) Benth. et Hook. f., *Lindera latifolia* Hook. f., *Shorea robusta* C. F. Gaertn., *Phoebe lanceolata* Wall. ex Nees) Nees, *Lithocarpus edulis* (Makino) Nakai, and *Leucaena glauca* (L.) Benth as hosts in Asia; however, it is unknown whether the beetle attacks these species while they are living or only after they die. There is no information to indicate that the fungus is lethal to these Asian hosts. The fact that so little is recorded about *X. glabratus* in Asia suggests that its mycangial fungi do not kill trees in its native range. The only life-history information available is based on studies in the southeastern United States, where adult beetles are active throughout the year, although peak flight occurs in late August and early September (Hanula et al., 2008, 2011). Very few beetles were caught from December through

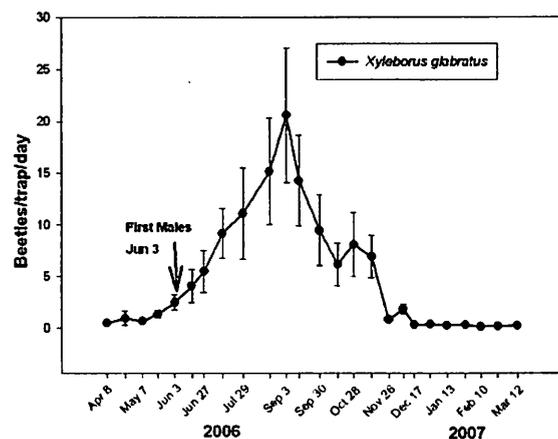


Figure 4 Seasonal arrival of redbay ambrosia beetles to trees infected with the laurel wilt fungus. (Hanula et al., 2008).

March, after which the adult abundance increased until it peaked in early September (Fig. 4, above).

Although adults are active all year, the low numbers in winter suggest that the adult stage may not be the primary overwintering form. Larvae are present in galleries in the winter (JLH, personal observation), but an infested tree cut in late October produced adult beetles in December and January in the laboratory so it is likely that development occurs as long as warm temperatures prevail. Thus, beetles flying in the winter may be newly emerged adults and not overwintering ones. Regardless, healthy trees wounded in late March were attacked and infested within one week (Hanula et al., 2008). Traps hung on trees to capture arriving beetles also caught males, and since males are flightless they most likely came from the trees on which the traps were hung. Based on these first males (Fig. 4), Hanula et al. (2008) suggested that brood development took approximately 56 days. More recently a preliminary effort to rear beetles from the galleries of individual females in logs resulted in initial adult brood emergence 56–63 days after the logs were exposed to attack (JLH, unpublished data), confirming the results from the previous study. This is consistent with other *Xyleborus* spp. (Hanula et al., 2008). Forty-five beetles were produced from one gallery (JLH, unpublished data). Most beetles fly within two meters of the ground, but a few were caught as high 15 meters (Hanula et al., 2011).

ANALYSIS OF RELATED NATIVE INSECTS IN THE UNITED STATES

Native Insects Related to the Pest (Nontarget Species)

The genus *Xyleborus* contains 20 species found in North America, twelve of which are native (Rabaglia et al., 2006); however, because native ambrosia beetles are rarely pests in North America north of Mexico, little is known about the majority of species. Bright (1968), Furniss and Carolin (1977), Drooz (1985) and Solomon (1995) provide generalized descriptions of the biology of Xyleborini ambrosia beetles, but little information about individual species. Of the species occurring in North America, the most detailed information is available on *Xyleborus dispar* (F.) (invasive) and *Xyleborus celsus* Eichhoff (native). *Xyleborus celsus* attacks dead or dying hickory trees (*Carya* spp.), but is not considered a pest.

Native Natural Enemies Affecting the Pest

No natural enemies of this species have been reported.

HISTORY OF BIOLOGICAL CONTROL EFFORTS

There have been some attempts at controlling insect vectors of plant pathogens, although most targeted species have biological and life-history traits very different from those of redbay ambrosia beetle. One of the earliest reports of a parasitoid apparently suppressing a vector population and subsequently the disease is that of the carrot-willow aphid, *Cavariella aegopodii* (Scopoll), from Europe, which was found vectoring carrot mottle virus in Australia (Stubbs, 1948). The braconid *Aphidius salicis* (Halliday) was introduced in 1962 and reportedly caused dramatic declines in aphid populations, based on aphid trapping data (Hughes et al., 1965). A corresponding decline in disease prevalence also was reported (Clausen, 1978). Waterhouse (1985) cited Stubbs et al. (1983) as stating that carrot mottle virus could no longer be found in Australia. However, Waterhouse's (1985) discovery of carrot red leaf virus in Australia, another virus vectored by *C. aegopodii*, brought into question previous claims of vector suppression by the parasitoid. The discovery of red leaf virus showed that the vector, *C. aegopodii*, was still present and an effective disease vector in Australia. The decline in dwarf mottle virus could not definitely be attributed to the parasitoid introduction, and indeed Büchen-Osmond (2010) suggest that the parasitoid's introduction in 1962 coincided with the use of more aphid resistant/repellent carrot cultivars, which may have caused the declines in aphids and disease prevalence.

In a second case, biological control of the beet leafhopper (*Circulifer tenellus* [Baker]), which vectors a curly top virus of a wide variety of crops (Bennett, 1971; Bayoun et al., 2008), was attempted. Nine egg parasitoids from Iran were imported to California where they were released from 1996 on (Bayoun et al., 2000). Bayoun et al. (2008) sampled beet leafhopper eggs at eight locations and determined that the most commonly recovered parasitoid was a native species. They found no evidence that it or the released species had any significant effect on beet leafhopper populations.

A recent, more successful example is that of glassy-winged sharpshooter, *Homalodisca vitripennis* (Germar), that was first discovered in California in 1989 (Sorensen and

Gill, 1996), where it vectored the bacterium *Xylella fastidiosa* (Wells) to many plant species, including many important crops (Purcell, 2010). Releases of the egg parasitoid *Gonatocerus triguttatus* Girault began in 2000 (Pilkington et al., 2005), followed by releases of *Gonatocerus ashmeadi* Girault, *Gonatocerus morilli* Howard, and *Anagrus epos* Girault. It was later determined that *G. ashmeadi* and *G. morilli* had already naturally invaded the area before these releases (Pilkington et al., 2005). Glassy-winged sharpshooter populations in the area were tracked in an organic lemon grove from 2002 to 2006 and found to decline 68% over this period (Hoddle, 2006), in the presence of ~20% egg parasitism each year (Hoddle, 2006). Grandgirard et al. (2009) reported that the parasitoid *G. ashmeadi* caused more than 95% reduction in the density of glassy-winged sharpshooter populations in the Society, Marquesas, and Austral archipelagos of French Polynesia, and that sharpshooter populations remained low in the year following population collapse.

Another important ongoing example of biological control of a vector concerns the Asian citrus psyllid, *Diaphorina citri* Kuwayama and citrus greening. Early biological control efforts against this pest are reviewed by Halbert and Manjunath (2004). On Réunion Island in the Indian Ocean, parasitism by the introduced parasitoid *Tamarixia radiata* (Waterston) was as high as 70% (Aubert, 1987), and was associated with improved citrus production (Aubert et al., 1996). In Florida, suppression of this vector has been less successful (Supriyanto and Whittle, 1991; Toorawa, 1998; McFarland and Hoy, 2001; Michaud, 2004), perhaps because of intraguild predation of mummies by coccinellids (Michaud, 2004). New parasitoid species have recently been imported to California from Pakistan, the native range of the vector. They have been established in the field and evaluations are underway.

Thus far, biological control programs aimed at controlling vectors of disease organisms have had mixed results. In all cases mentioned above, the targets were sucking insects, in which at least some life stages were relatively exposed. In two of those examples, parasitoids contributed to substantial reductions in vector populations, but both cases were on small islands (Aubert, 1987; Grandgirard et al., 2009).

The only biological control effort against an insect vector of a tree pathogen comparable to redbay ambrosia beetle is the case of the smaller European elm bark beetle, *Scolytus multistriatus* (Marsham), a vector of Dutch elm disease, which is caused by the fungi *Ophiostoma ulmi* (Buism.)

Nannf. (formerly called *Ceratocystis ulmi*) and *Ophiostoma novo-ulmi* Brasier. The elm bark beetle and Dutch elm disease are similar to redbay ambrosia beetle and laurel wilt, in that inoculation of a tree by a single beetle can result in tree death and the dead tree can then serve as host material for beetle brood development. *Scolytus multistriatus* was first reported in the United States in 1904 near Boston, and subsequently spread across the country. Because of its devastating effect on many city landscapes, a major effort was launched to develop control strategies, including biological control. The biological control of elm bark beetles has been reviewed elsewhere (Van Driesche et al., 1996; Bellows et al., 1998). One braconid parasitoid, *Dendrosoter protuberans* (Nees), was introduced from France (Kennedy, 1970) and became widely distributed throughout much of the United States (Hajek and Dahlsten, 1985). In addition to *D. protuberans*, *S. multistriatus* had a wide variety of other natural enemies (Van Driesche et al., 1996; Bellows et al., 1998), but their impacts on host populations are unknown. For example, Hajek and Dahlsten (1985) reported 67% mortality of elm bark beetle larvae, but attributed only 2% to parasitoids. Hanula (1981) reported 5–8% cumulative parasitism for two parasitoids, depending on height in the tree. Bellows et al. (1998) report that, despite extensive study, relatively little comparative information is available about the population dynamics of *S. multistriatus* in the United States and its native range.

Unlike phloem-feeding bark beetles, whose natural enemies include parasitoids that can oviposit into host larvae through the bark, ambrosia-beetle natural enemies must either eat their prey while they are on the bark surface or crawl into the galleries. Female ambrosia beetles excavate their galleries over extended periods of time so they are constantly pushing boring dust and frass through and out of them. It is unknown whether this behavior limits a parasitoid's or predator's ability to move into the galleries and find eggs or larvae, but it seems likely that it would. A third factor limiting biological control in the case of redbay ambrosia beetle is the limited information available about *X. glabratus* in its native range. Finally, any biological control project would need to consider the potential effects of exotic natural enemies on native ambrosia beetles (Hoddle, 2004), which are relatively rare compared to invasive species in the genus (Miller and Rabaglia, 2009).

Redbay ambrosia beetle and laurel wilt were first identified as damaging agents in 2004. Because of their recent discovery, rapid spread, the ability of a single beetle to inoculate and kill a tree, and the lack of successful

biological control for similar pest complexes (e.g., the smaller European elm bark beetle and Dutch elm disease), there has been little interest or hope for biological control of this insect. We are unaware of any attempted biological control programs for ambrosia beetle species.

One factor limiting interest in biological control of the ambrosia beetle may be the lack of information on its natural enemies in general. Our search for literature on insect natural enemies of ambrosia beetles (Table 1) found only a few studies that document or describe natural enemies from a small number of ambrosia beetle species, but even fewer (e.g., Novák, 1960; Darling and Roberts, 1999) that provide detailed biological information or comment on potential for these organisms to influence population dynamics of their hosts. About half of these reports are from ambrosia beetles in the Platypodinae, a different subfamily from that of *X. glabratus* (Scolytinae). As for insect enemies of other *Xyleborus* species, perhaps the most interesting reference is to that of the parasitoid wasp *Phymastichus xylebori* LaSalle (Hymenoptera: Eulophidae), which was recovered from *Xyleborus perforans* (Wollaston), a pest of macadamia trees in Hawaii (Chang, 1993; LaSalle,

1995). This parasitoid has apparently not been studied since the mid-1990s. It is uncertain whether the lack of study of natural enemies is due to an actual lack of natural enemy species, and/or lack of interest.

RECOMMENDATIONS FOR FURTHER WORK

Clearly, more work is needed on natural enemies of ambrosia beetles in general and on the natural enemies of *X. glabratus* in particular. Thus far, there is no evidence that any native parasitoids in North America have begun using *X. glabratus*, despite the pest's high numbers. In Asia, *X. glabratus* is poorly known and unstudied. Since there are no reports of it associated with tree mortality in Asia, it most likely acts like other ambrosia beetles, attacking dead or dying trees or branches. The lack of information from Asia on *X. glabratus* suggests it is not an abundant species, but the role of natural enemies in regulating populations there is unknown. Thus, more detailed studies of the biology of *X. glabratus* and exploration for natural enemies in its native range is warranted.

Table 1 Insect natural enemies of ambrosia beetles (Coleoptera: Curculionidae)

Enemy Species	Enemy Group	Host Species	Host Subfamily	Plant Species	Region	Reference
Parasitoids						
<i>Phymastichus xylebori</i> LaSalle	Hymenoptera: Eulophidae	<i>Xyleborus perforans</i> (Wollaston)	Scolytinae	<i>Macadamia integrifolia</i> Maiden & Betche	Hawai'i, USA	
<i>Perniphora robusta</i> Ruschka	Hymenoptera: Pteromalidae	<i>Trypodendron lineatum</i> (Olivier), <i>T. domesticum</i> (L.), <i>Xyleborus dispar</i> (F.)	Scolytinae	various	various	Chang, 1993; LaSalle, 1995
<i>Perniphora americana</i> Miller	Hymenoptera: Pteromalidae	Assoc. with <i>Trypodendron betulae</i> Swaine	Scolytinae	<i>Betula papyrifera</i> Marsh., <i>B. alleghaniensis</i> Britton	Maine, USA; New Brunswick, Canada	Novák, 1960; Kenis et al., 2004
<i>Cryptoxilos beaveri</i> Shaw and Berry	Hymenoptera: Braconidae	<i>Hypothenemus curtipennis</i> (Schedl), <i>H. dorsosignatus</i> (Schedl).	Scolytinae	<i>Commersonia bartramia</i> (L.) Merr.	Fiji	Miller, 1965

Table 1 Insect natural enemies of ambrosia beetles (Coleoptera: Curculionidae), *continued*.

Enemy Species	Enemy Group	Host Species	Host Subfamily	Plant Species	Region	Reference
<i>Cryptoxilos lymanthori</i> Deyrup	Hymenoptera: Braconidae	<i>H. dorsosignatus</i> (Schedl), <i>Lymanthor decipens</i> Wood & Bright	Scolytinae	<i>Acer saccharum</i> Marsh.	Indiana, USA	Shaw and Berry, 2005
<i>Eurytoma polygraphi</i> Ashmead	Hymenoptera: Eurytomidae	<i>T. lineatum</i> , <i>T. domesticum</i>	Scolytinae	Not specified	Not specified	Deyrup, 1981
<i>Monacon robertsi</i> Bouček	Hymenoptera: Perilampidae	<i>Crossotarsus barbatus</i> Chapuis	Platypodinae	<i>Xanthophyllum papuanum</i> Whitmore ex Meijden, <i>Ficus</i> sp.	Papua New Guinea; Indonesia	Darling and Roberts, 1999
<i>Monacon tricornis</i> Bouček	Hymenoptera: Perilampidae	<i>Crossotarsus kuntzeni</i> Schedl	Platypodinae	Not specified	Not specified	Darling and Roberts, 1999, citing Bouček, 1980
Predators						
<i>Sosylus</i> spp.	Coleoptera: Colydiidae	Various, Platypodinae	Platypodinae	various	Nigeria; Papua New Guinea	Roberts, 1969, 1980
<i>Ommadius</i> spp.	Coleoptera: Cleridae	Unspecified Platypodinae	Platypodinae	Not specified	Not specified	Darling and Roberts, 1999
<i>Cyphogogus splendens</i> Kleine	Coleoptera: Brentidae	<i>Crossotarsus biconcavus</i> Schedl; <i>C. barbatus</i> Chapuis; <i>Platypus selysi</i> Chapuis	Platypodinae	Not specified	Papua New Guinea	Thompson, 1996
<i>Cyphogogus modiglianii</i> Senna	Coleoptera: Brentidae	Unspecified Platypodinae	Platypodinae	Not specified	Papua New Guinea	Thompson, 1996
<i>Thanasimus dubius</i> (F.)	Coleoptera: Cleridae	<i>Platypus flavicornis</i> (F.)	Platypodinae	<i>Pinus</i> sp.	Texas, USA	Clarke and Menard, 2006
<i>Rhizophagus depressus</i> (F.) and <i>R. dispar</i> (Payk.)	Coleoptera: Rhizophagidae	<i>T. lineatum</i>	Scolytinae			Kenis et al., 2004, and references therein

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