Effect of Tree Species and End Seal on Attractiveness and Utility of Cut Bolts to the Redbay Ambrosia Beetle and Granulate Ambrosia Beetle (Coleoptera: Curculionidae: Scolytinae)

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ABSTRACT The redbay ambrosia beetle, *Xyleborus glabratus* Eichhoff, is a non-native invasive pest and vector of the fungus that causes laurel wilt disease in certain trees of the family Lauraceae. This study assessed the relative attractiveness and suitability of cut bolts of several tree species to *X. glabratus*. In 2009, female *X. glabratus* were equally attracted to traps baited with swampbay (*Persea palustris* (Rafinesque) Sargent) and camphortree (*Cinnamomum camphora* (L.) J. Presl), which were more attractive than avocado (*Persea americana* Miller), lancewood (*Ocotea coriacea* (Swartz) Britton), and sweetbay (*Magnolia virginiana* L.). These species were more attractive than loblolly bay (*Gordonia lasianthus* (L.) J. Ellis). *X. glabratus* entrance hole density and emergence from caged bolts were highest on swampbay and camphortree. In 2010, swampbay was significantly more attractive to *X. glabratus* than sassafras (*Sassafras albidum* (Nuttall) Nees), yellow poplar (*Liriodendron tulipifera* L.), and eastern redbud (*Cercis canadensis* L.). Sassafras bolts end sealed with a liquid wax-and-water emulsion were more attractive to *X. glabratus* than end-sealed bolts of yellow poplar and redbud. Relative to unsealed bolts, end seal decreased *X. glabratus* entrance hole density on swampbay and decreased granulate ambrosia beetle (*Xylosandrus crassiusculus* (Motschulsky)) trap catch, entrance hole density, and adult emergence from swampbay. *X. crassiusculus* was not attracted to sassafras, yellow poplar, and redbud and was not more attracted to manuka oil than to unbaited traps. Sassafras was more attractive to *X. glabratus* than previously reported and supported reproducing populations of the insect. End sealing bolts with a wax-and-water emulsion may not be optimal for attracting and rearing ambrosia beetles in small logs.

KEY WORDS Scolytinae, exotic species, attraction, emergence, laurel wilt

The redbay ambrosia beetle (*Xyleborus glabratus* Eichhoff) is a non-native invasive pest in the southeastern United States. Native to Asia, it was first detected near Savannah, GA, in 2002 (Rabaglia et al. 2006) and has since been discovered in South Carolina, North Carolina, Florida, Mississippi, and Alabama (USDA Forest Service 2011). The beetle carries several species of symbiont fungi in its mycangia, one of which (*Raffaelea lauricola* Harrington, Fraedrich and Aghayeva) causes a vascular disease called laurel wilt in certain trees in the family Lauraceae (Harrington et al. 2008, 2010). The disease occurs when female *X. glabratus* initiate attack on live host trees and inoculate the xylem with *R. lauricola*, which moves systemically in the sapwood and causes the tree to wilt (Fraedrich et al. 2008). Laurel wilt has caused widespread mortality of redbay (*Persea borbonia* (L.) Sprengel) and swampbay (*Persea palustris* (Rafinesque) Sargent), which are common, shade tolerant, broad-leaved evergreen trees of various forested habitats and residential areas of the southeastern Atlantic Coastal Plain region (Fraedrich et al. 2008). Laurel wilt commonly kills nearly all tree-sized individuals of redbay and swampbay in an area within 3–5 yr after *X. glabratus* becomes established and detected (Mayfield et al. 2009).

Reproduction in Xyleborine ambrosia beetles such as *X. glabratus* is characterized by a high degree of inbreeding and sibling mating, and females greatly outnumber flightless haploid males (Wood 1982). Peak flight of female *X. glabratus* in South Carolina and Georgia occurs in late summer to early fall, but beetles can be collected in flight traps year round (Hanula et al. 2008, 2011). Development from egg to adult takes ≈45 d (J.L.H., unpublished data) and there are multiple generations per year. Based on observations of redbay trees in various stages of laurel wilt development and *X. glabratus* colonization, Fraedrich et al. (2008) hypothesized that trees initially become diseased when female *X. glabratus* initiate attack on healthy trees, deposit spores of *R. lauricola* into the xylem, and then abort tunnels before oviposition. After the pathogen has moved systemically through the

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trees, *X. glabratus* colonizes the weakened or dead host for brood production (Fraedrich et al. 2008). Hanula and Sullivan (2008) found that females are attracted to volatiles from redbay wood, manuka oil (extract of *Leptospermum scoparium* Forster and Forster, family Myrtaceae) and phoebe oil (extract of *Phoebe porosa* (Nees and Martius) Mez, family Lauraceae) and suggested that α-copaene may be a primary, host-produced attractant. Cut bolts of a nonlauraceous plant, lychee (*Litchi chinensis* Sonnerat, family Sapindaceae) were recently shown to be attractive to *X. glabratus* as well (Kendra et al. 2011).

In addition to the highly vulnerable redbay and swampbay, several other woody plant species in the family Lauraceae have been reported as susceptible hosts of laurel wilt in the field. Avocado (*Persea americana* Miller), a major commercial fruit-producing species, has been killed by laurel wilt in residential landscapes and experimental plantings (Mayfield et al. 2008a). Cut avocado bolts are attractive to *X. glabratus* (Hanula et al. 2008, Kendra et al. 2011) and females will bore into young avocado plants (Mayfield et al. 2008b). Sassafras (*Sassafras albidum* (Nuttall) Nees) has been killed by laurel wilt in geographic isolation from other diseased host species, both as individual trees and as thickets of multiple ramets (Smith et al. 2009a). Incidence of laurel wilt in sassafras has thus far remained in the Atlantic Coastal Plain region, and Hanula et al. (2008) found cut bolts of sassafras to be relatively unattractive to *X. glabratus.* Nonetheless, sassafras is distributed throughout the eastern United States and could serve as a means by which *X. glabratus* and *R. lauricola* could greatly expand their nonnative range. Pondberry (*Lindera melissifolia* (Walter) Blume) is a federally listed endangered species from which *R. lauricola* has been recovered (Fraedrich et al. 2008), but known populations of this species are few and the impact of laurel wilt on pondberry is uncertain. Several instances of laurel wilt in pondspice (*Litsea aestivalis* (L.) Fernald), a state-listed endangered species, have been reported including recovery of both *X. glabratus* and *R. lauricola* from wilted trees (Hughes et al. 2011). In addition, laurel wilt has occurred in camphortree (*Cinnamomum camphora* (L.) J. Presl) a non-native species of Asian origin, but widespread mortality in camphortree has not been observed (Smith et al. 2009b).

In areas where redbay populations have been drastically reduced by laurel wilt, *X. glabratus* populations drop dramatically based on attacks on redbay bolts but persist at very low densities, despite the apparent absence of redbay host material (Hanula et al. 2008). This raises the question of whether *X. glabratus* may be attracted to and use other species in the landscape (including dead, dying, or injured trees) that do not develop laurel wilt disease symptoms, but nonetheless serve as brood material, particularly in the absence of redbay. Although detection of laurel wilt has been limited to trees in the Lauraceae to date, the reported native host range of *X. glabratus* in Asia includes species in the Lauraceae (*Lindera latifolia* Hooker f., *Litsea elongate* (Nees) Bentham et Hooker f., *Phoebe lanceolata* (Nees) Nees), Dipterocarpaceae (*Shorea robusta* C. F. Gaertner), Fagaceae (*Lithocarpus edulis* (Makino) Nakai), and Fabaceae (*Leucaena glauca* (L.) Bentham) (Rabaglia et al. 2006). These reports of nonlauraceous hosts in the beetle's native range and the attraction of *X. glabratus* to at least one nonlauraceous species cultivated here in the United States (Kendra et al. 2011) suggests that the host range for *X. glabratus* in North America may not be limited to the Lauraceae. As the non-native geographic distribution of the laurel wilt complex steadily expands (USDA Forest Service 2011), there is a need to identify and evaluate potential hosts of *X. glabratus* to make informed management decisions and anticipate potential impacts of laurel wilt in new areas. Identification of attractive host material may reveal likely suscepts to laurel wilt, or species that might serve as refuges for *X. glabratus* populations in the absence of redbay or other preferred hosts.

Many studies designed to attract bark or wood-boring beetles, or to rear them from cut host material, have sealed the ends of the cut bolts with wax for the purpose of retaining moisture (Smith et al. 2002, Liu et al. 2010, Ulyshen et al. 2010). Studies that specifically evaluate the effect of end-seal on attractiveness and subsequent success of rearing wood-inhabiting beetles from cut bolts, however, are lacking. Ambrosia beetles and other wood-inhabiting insects are some of the most frequently intercepted non-native pests at ports of entry in the United States, and some of the most serious North American forests pests are members of this group (Haack 2006). Knowing whether to end seal logs to optimize attraction and rearing of ambrosia beetles would be of value to scientists conducting research on these insects.

Studies were conducted in 2009 and 2010 to determine the relative attractiveness of cut bolts of a variety of tree species to *X. glabratus* and to evaluate the potential of these species to serve as brood material. In 2010, we included evaluation of the granulate ambrosia beetle, *Xylosandrus crassiusculus* (Motschulsky), a non-native species with a relatively broad host range that is naturalized in the southeastern United States and readily attacks dying *Persea* spp. (Horn and Horn 2006, Hanula et al. 2008). In addition, in 2010 we evaluated the effect of sealing the ends of bolts with a wax-and-water emulsion on beetle response.

Materials and Methods

2009 Study

In 2009, bolts of swampbay, camphortree, avocado (unknown cultivar), lancewood (*Ocotea coriacea* (Swartz) Britton), loblolly bay (*Gordonia lasianthus* (L.) J. Ellis), and sweetbay (*Magnolia virginiana* L.) were evaluated for attractiveness and host suitability to *X. glabratus.* These species were chosen because swampbay, avocado, camphortree, and lancewood are in the Lauraceae, and laurel wilt disease has been documented in all of these except lancewood, a native evergreen understory shrub restricted to eastern and southern Florida (Nelson 1994). Sweetbay and loblolly bay are common nonlauraceous associates of swampbay in flatwoods, floodplain, or other moist sites and represent possible alternative host material for *X. glabratus* by virtue of spatial proximity. Furthermore, sweetbay (family Magnoliaceae) is in the Magnoliales, a plant order closely related the Laurales (that includes the Lauraceae) (Soltis et al. 2005).

Sixteen bolts of each species, 30 cm long and 5–10 cm in diameter, were cut from trees in the following Florida counties: Baker (camphortree), Miami-Dade (avocado), Broward (lancewood), and Alachua (swampbay, loblolly bay, sweetbay). A metal hook was screwed into one cut end of each bolt. Bolt traps were deployed on 30 June 2009 in a 21-yr-old, previously thinned slash pine (*Pinus elliottii* Engelm.) plantation on a moist flatwoods site in Alachua County, FL (29.59760 N, −82.17688 W). The stand contained naturally occurring swampbay trees killed by laurel wilt scattered throughout the midstory, as well as natural mixtures of laurel oak (*Quercus laurifolia* Michaux), water oak (*Quercus nigra* L.), red maple (*Acer rubrum* L.), baldcypress (*Taxodium distichum* (L.)Richard), and sweetbay. Each trap consisted of two conspecific bolts bound together with wire and hung vertically from a rope suspended between two trees, 1.2–1.8 m above the ground. Two white sticky cards (23 × 28 cm, wing-style trap bottoms, Scentry Biologicals, Inc., Billings, MT), facing out in opposite directions, were stapled to the bottom 2 cm of each hanging bolt pair. No trap was hung within 3 m of a swampbay tree. Bolts were arranged in a randomized complete block design with eight replicate blocks of seven traps (treatments), with each trap representing one of the six species listed above or an unbaited control trap (sticky cards only, no bolt). Within blocks, traps were assigned randomly to the treatments and spaced at least 10 m apart. Blocks were spaced at least 20 m apart. Sticky cards were collected and replaced every 8–10 d for 36 d, at which time bolts were removed from the field. Numbers of adult female *X. glabratus* captured on the cards for each trap were counted and expressed as numbers of beetles per trap per day.

Upon removal from the field on 5 August 2009, each pair of bolts from six of the eight replicates (randomly selected) was placed in a rearing container made from a 19 liters plastic bucket with a 2.5 cm hole drilled in the bottom, leading into a clear 500 ml polycarbonate jar (Thermo Fisher Inc., Waltham, MA). The screw cap of the jar was fastened to the bucket bottom. Rearing buckets were stored on a wooden rack at the Florida Department of Agriculture and Consumer Services, Division of Plant Industry, Insect Rearing Laboratory at 24–27°C and 60–70% RH with a light source continually illuminating the collection jars. Every 1–2 wk, all adult bark and ambrosia beetles (Coleoptera: Curculionidae: Scolytinae) in the jars were collected, identified and counted by species. After 110 d, all bolts were removed from the buckets and one-fourth of the surface of each bolt (a section half the length of the bolt by half its circumference) was debarked with a knife and all ambrosia beetle entrance holes on the surface of the sapwood were counted. Distinction was made between holes of the size typically made by *X. glabratus* (roughly equal to the diameter of a No. 1 size paper clip, 0.8 mm diameter) and those made by larger ambrosia beetles such as *X. crassiusculus.* Number of emerged ambrosia beetles and number of ambrosia beetle entrance holes were expressed per 100 cm^2 of bolt surface area.

2010 Study

In 2010, bolts of swampbay, sassafras, yellow poplar (*Liriodendron tulipifera* L.), and eastern redbud (*Cercis canadensis* L.) were evaluated for attractiveness and host suitability to *X. glabratus.* Swampbay and sassafras are members of the Lauraceae known to be infected by laurel wilt. Yellow poplar is in the Magnoliales (closely related to Laurales) as is sweetbay tested in 2009, and has a broad geographic and site distribution in the eastern United States. Redbud is a commonly planted ornamental in the Fabaceae, a reported *X. glabratus* host plant family in the beetle's native range (Rabaglia et al. 2006).

Fourteen bolts of each species, 30 cm long and 9–14 cm in diameter, were cut on 21 and 22 June 2010. Sassafras and yellow poplar bolts were cut from the Coweeta Hydrologic Laboratory (NC), redbud bolts were cut from the Oconee National Forest (GA), and swampbay bolts were cut from the Francis Marion National Forest (SC). Immediately after cutting, a liquid wax-and-water emulsion log end sealant (Bailey's Seal II, Bailey's, Laytonville, CA) was brushed onto both ends of seven of the 14 bolts per tree species and allowed to air dry. A metal screw hook was inserted into one cut end of each bolt. Seven 30 cm sections of pressure treated landscape timber (controls) were also cut and supplied with a hook but were not end sealed.

Bolt traps were deployed on 23 June 2010 in a floodplain stand of mixed deciduous and pine species that paralleled the headwaters of Alligator Creek on the Francis Marion National Forest near Cordesville, SC (33.16707 N, −79.87013 W). Common tree species included swamp tupelo (*Nyssa sylvatica* variety *biflora* (Walter) Sargent), swampbay, red maple, sweetgum (*Liquidambar styraciflua* L.), baldcypress, laurel oak, loblolly pine (*Pinus taeda* L.), and longleaf pine (*P. palustris* Miller). Each trap consisted of one bolt hanging from a hook on a rope suspended between two trees, 1.2–1.8 m above the ground. Two white sticky cards (23 × 28 cm, wing-style trap bottoms; Scentry Biologicals), facing out in opposite directions, were stapled to the bottom 2 cm of the hanging bolt. No bolt was hung within 3 m of a swampbay tree. Bolts were arranged in seven replicate blocks of nine traps. Each block included one end-sealed bolt and one unsealed bolt of each of the four test species, and one landscape timber bolt as a control. Within blocks, bolt traps were assigned randomly to the treatments and spaced at least 10 m apart. Blocks were spaced at least 20 m apart and were arranged in a linear pattern to stay within the mixed floodplain forest that was bounded by pine stands on either side. Sticky cards were collected and replaced after 16 d and collected again after 33 d when bolts were removed from the field. Numbers of adult female *X. glabratus* and *X. crassiusculus* captured on the cards were counted and expressed as numbers of beetles per trap per day.

After removing bolts from the field on 26 July 2010, each bolt was placed in a rearing container made from a 19 liters plastic bucket with two 10 cm ventilation holes cut in opposite sides that were covered with fine (200 micron) mesh screen (Dynamesh, West Chicago, IL) using hot melt glue. The bolt was suspended within the bucket by its hook fitted through an eyebolt in the inside center of the bucket lid. The bottom of the bucket was cut out and fitted with a 23-cm diameter (1 liter) plastic funnel (LUBEQ Corporation, Elgin, IL), which led into a 250 ml Nalgene polypropylene straight-sided jar with screw cap (Thermo Fisher Inc., Waltham, MA). The collection jar was filled with a small amount of propylene glycol antifreeze to kill and preserve insects entering the jar. Buckets were suspended by their handles on wooden racks and kept at room temperature. An LED light was positioned directly beneath each collection jar and left on continuously in an otherwise dark room. Approximately every 2 wk, all adult beetles in the jars were collected and preserved and all *X. glabratus* and *X. crassiusculus* were counted. Pressure treated timber bolts were not placed in rearing containers because they were not attractive to ambrosia beetles in the field and were impervious to wood boring insects. After 8 mo, bolts were removed from rearing containers, all bark was removed with a draw knife, and ambrosia beetle entrance holes on the surface of the sapwood were counted. As in 2009, distinction was made between holes of the size made by *X. glabratus* and those made by *X. crassiusculus.* Emergence of ambrosia beetles other than, but of similar size to, *X. glabratus* or *X. crassiusculus* was rare and represented one percent or less of the total beetles emerged each year. Number of emerged ambrosia beetles and number of ambrosia beetle entrance holes were expressed per 100 cm^2 of bolt surface area.

Because end-seal effects were detected in 2010, a hanging bolt trap experiment to evaluate a potential repellent effect of the end seal was initiated on 13 July 2011 at the Cordesville, SC, site described above. Each trap bolt consisted of a pressure-treated pine landscape timber 30 cm long, hanging from a hook on a rope suspended between two trees as described above. Two halves of a white sticky card (wing-style trap bottoms; Scentry Biologicals), facing out in opposite directions, were stapled to the bottom 2 cm of the hanging bolt. No trap was hung within 3 m of a swampbay tree. Bolts were arranged in six replicate blocks of four traps. Each trap within a block was randomly assigned to one of four treatments: 1) landscape timber only (control), 2) landscape timber with ends treated with end seal (Bailey's Seal II), 3) landscape timber with a half-size manuka oil lure (Synergy Semiochemical Corp., Burnaby, BC, Canada), and 4) landscape timber with end seal and a manuka oil lure. Traps were spaced at least 10 m apart and blocks were spaced at least 50 m apart. Traps were deployed on 13 July 2011 and collected after 21 d. Numbers of adult female *X. glabratus* and *X. crassiusculus* captured on the cards were counted and recorded.

Data Analysis

In 2009, one-way analysis of variance (ANOVA) was used to test the null hypothesis of no significant difference between treatment means for the following variables: 1) number of *X. glabratus* caught per trap per day, 2) number of entrance holes per 100 cm^2 of bolt surface, and 3) number of *X. glabratus* emerged per 100 cm^2 of bolt surface. In 2010, two-factor ANOVA was used to evaluate the effects of bolt species, end seal (sealed vs. unsealed), and species × end seal interaction, on means of the same variables analyzed in 2009, for both *X. glabratus* and *X. crassiusculus.* Because the control treatment in 2010 included only unsealed bolts and the mean and variance of beetles caught was nearly zero, it was excluded from ANOVA to maintain a balanced two-factor design. When testing for a repellent effect of the end seal applied to baited and unbaited pressured-treated pine bolts, a one-way ANOVA was used to test the null hypothesis of no significant difference between total number of *X. glabratus* and *X. crassiusculus* trapped over a 21 d period. In all tests, response variables were log-transformed ($\log_{10}[x+1]$) to reduce heteroscedasticity but actual means are reported in figures and tables. Means were considered significant if $P < 0.05$ and mean comparisons were made using Tukey's Honestly Significant Difference (HSD). Data were analyzed using Statistica v. 9.1 (StafSoft, Inc., Tulsa, OK).

Results

2009 Study

Attraction to Bolts. In 2009, the mean number of *X. glabratus* captured per trap per day differed significantly by tree species (Table 1). Swampbay and camphortree were equally attractive to female *X. glabratus* and caught more beetles than other species in this trial (Fig. 1). Sweetbay, avocado, and lancewood did not differ significantly in attractiveness and caught more *X. glabratus* than the unbaited control. Loblolly bay was not attractive and did not differ from the unbaited control (Fig. 1).

Entrance Holes and Beetle Emergence. In 2009, tree species had a significant effect on *X. glabratus* entrance hole density and the number of beetles emerging from caged bolts (Table 1). Entrance hole density on camphortree was higher than on avocado, lancewood, sweetbay, and loblolly bay, but not significantly different from attack density on swampbay (Fig. 2). Adult emergence of *X. glabratus* from camphortree was low and did not differ significantly from emergence from other species (Fig. 2). Although swampbay gave rise to the highest mean number of *X. glabratus* (1.6 beetles per 100 cm^2), emergence among

Table 1. Summary of ANOVA results for the effects of tree species and end seal on trap catch, entrance hole density, and adult emergence of *X. glabratus* and *X. crassiusculus* in hanging bolt trap studies in 2009 (Hawthorne, FL) and 2010 (Cordesville, SC)

Year	Response variable[a]	Treatment effect	*F*	df	*P*
2009	*X. glabratus* trap catch[b]	Tree species	32.4	6, 49	<0.001
	X. glabratus entrance holes[c]	Tree species	12.0	5, 42	<0.001
	X. glabratus emergence[d]	Tree species	3.7	5, 30	0.011
2010	*X. glabratus* trap catch	Tree species	61.1	3, 48	<0.001
		End seal[e]	1.8	1, 48	0.183
		Tree species × end seal	1.3	3, 48	0.287
	X. glabratus entrance holes	Tree species	95.5	3, 48	<0.001
		End seal	22.8	1, 48	<0.001
		Tree species × end seal	8.2	3, 48	<0.001
	X. glabratus emergence	Tree species	89.3	3, 48	<0.001
		End seal	4.6	1, 48	0.037
		Tree species × end seal	1.7	3, 48	0.173
	X. crassiusculus trap catch	Tree species	92.3	3, 48	<0.001
		End seal	7.6	1, 48	0.008
		Tree species × end seal	3.8	3, 48	0.016
	X. crassiusculus entrance holes	Tree species	204.2	3, 48	<0.001
		End seal	31.9	1, 48	<0.001
		Tree species × end seal	33.0	3, 48	<0.001
	X. crassiusculus emergence	Tree species	31.2	3, 48	<0.001
		End seal	7.1	1, 48	0.010
		Tree species × end seal	7.1	3, 48	<0.001

[a] All response variables were log transformed ($\log_{10}[x+1]$).

[b] Trap catch = no. beetles captured on sticky cards per trap per day.

[c] Entrance holes = no. entrance holes per 100 cm^2 of bolt surface.

[d] Emergence = no. beetles per 100 cm^2 of bolt surface that emerged from caged bolts after field deployment.

[e] End sealed bolts were coated with a wax-and-water emulsion on the cut ends before field deployment.

replicates was highly variable and the mean was markedly lower than emergence from this same species in 2010 (Fig. 2).

2010 Study

Attraction to Bolts. In 2010, the mean number of *X. glabratus* captured per trap per day differed significantly by tree species but not by end seal treatment (Table 1). Swampbay was significantly more attractive to *X. glabratus* than sassafras, yellow poplar, and redbud (Fig. 3). End-sealed swampbay bolts caught fewer *X. glabratus* than unsealed bolts, but the difference was not significant (Fig. 3). End-sealed sassafras caught more *X. glabratus* than end-sealed bolts of tulip poplar and redbud, whereas mean trap catch on unsealed bolts of these species did not differ (Fig. 4). Mean trap catch of *X. glabratus* on yellow poplar and redbud was fewer than 0.2 beetles per trap per day, similar to catches on pressure treated pine control bolts (Fig. 4).

Trap catches of *X. crassiusculus* in 2010 were significantly affected by tree species, end seal application and by their interaction (Table 1). Swampbay caught significantly more *X. crassiusculus* than sassafras, yellow poplar, or redbud; the latter three species were unattractive, regardless of end seal treatment (Fig. 3).

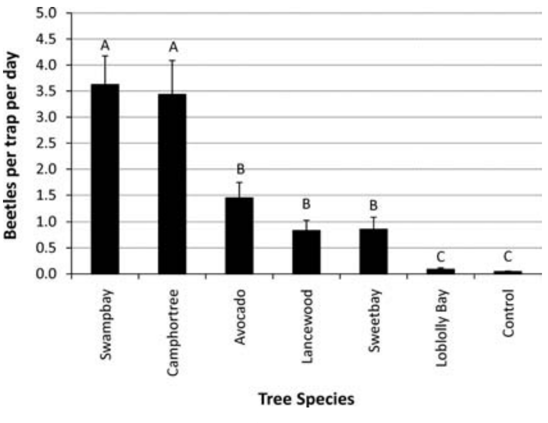

Fig. 1. Mean ± SE number of *X. glabratus* captured per trap per day on bolt traps of various species near Hawthorne, FL, in 2009. Bars labeled with the same letter are not significantly different at the $P = 0.05$ level.

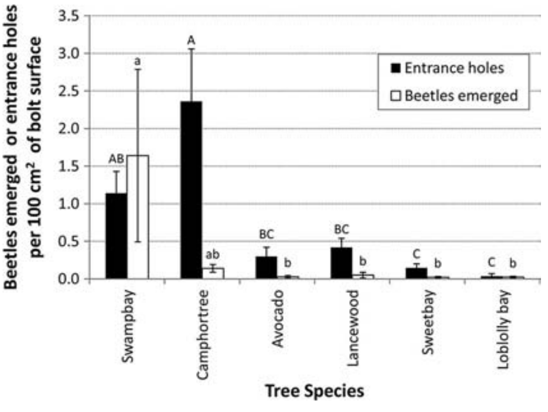

Fig. 2. Mean ± SE number of *X. glabratus* entrance holes and beetles emerged per 100 cm^2 of bolt surface area for various species deployed near Hawthorne, FL, in 2009. Bars labeled with the same letter and case are not significantly different at the $P = 0.05$ level.

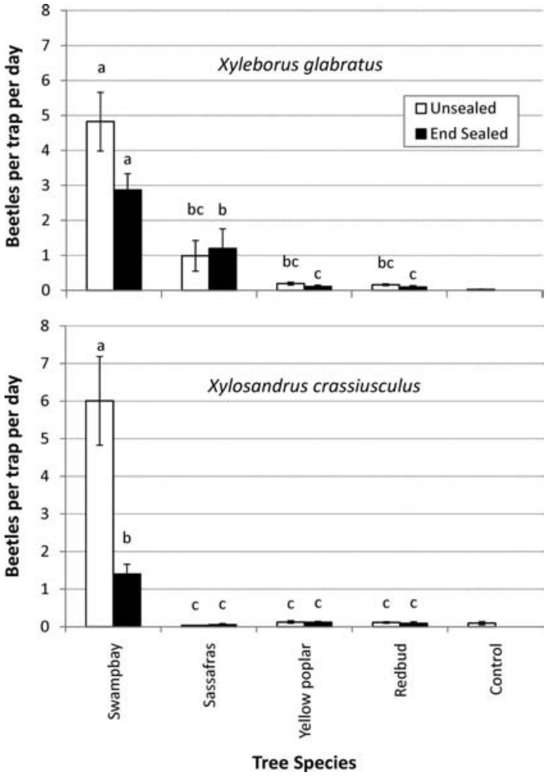

Fig. 3. Mean ± SE number of *X. glabratus* (top) and *X. crassiusculus* (bottom) captured per trap per day on bolt traps of various tree species near Cordesville, SC, in 2010. End sealed bolts were coated with a wax-and-water-emulsion on the cut ends, whereas unsealed bolts received no end treatment. For each insect species, bars labeled with the same letter are not significantly different at the $P = 0.05$ level. The control treatment was excluded from ANOVA.

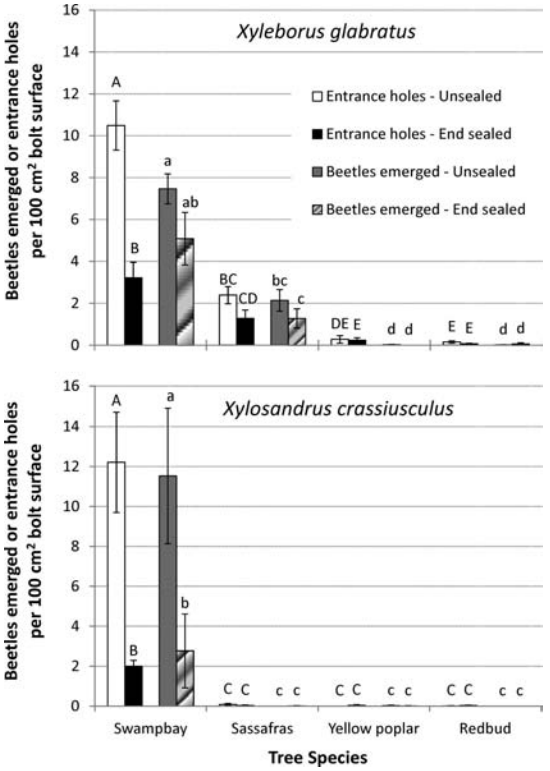

Fig. 4. Mean ± SE number of *X. glabratus* (top) and *X. crassiusculus* (bottom) entrance holes and beetles emerged per 100 cm^2 of bolt surface area for various species hung near Cordesville, SC, in 2010. End sealed bolts were coated with a wax-and-water-emulsion on the cut ends, whereas unsealed bolts received no end treatment. Bars labeled with the same letter and case are not significantly different at the $P = 0.05$ level.

End-sealed swampbay bolts caught significantly fewer *X. crassiusculus* than unsealed bolts (Fig. 3).

Entrance Holes and Beetle Emergence. In 2010, tree species, end seal, and their interaction had a significant effect on *X. glabratus* entrance hole density (Table 1). Among bolts receiving the same end treatment, swampbay bolts had more entrance holes than sassafras, which had more entrance holes than yellow poplar or redbud (Fig. 4). End sealing significantly decreased the number of *X. glabratus* entrance holes on swampbay compared with unsealed bolts, but it had no effect when applied to other species (Fig. 4).

Among bolts receiving the same end treatment, more *X. glabratus* emerged from swampbay bolts than from sassafras, which produced more emerging beetles than yellow poplar or redbud (Fig. 4). Flightless males emerged from swampbay and sassafras, indicating brood production within the bolts of these species. Only two adult female *X. glabratus* (one from each of two bolts) emerged from yellow poplar, and only seven female beetles (from three bolts) emerged from redbud. *X. glabratus* emerged from swampbay bolts for >160 d postcollection, with peak emergence between 40 and 70 d (Fig. 5). Emergence of *X. glabratus* from sassafras bolts peaked between 30 and 40 d postcollection; emergence continued in end sealed sassafras bolts for >70 d and in unsealed bolts for ≈100 d (Fig. 5).

Tree species, end seal, and their interaction had significant effects on *X. crassiusculus* entrance hole density and emergence in 2010 (Table 1). End sealing decreased the number of *X. crassiusculus* entrance holes and emerging adults on swampbay (Fig. 4). Very few to no *X. crassiusculus* entered or emerged from sassafras, yellow poplar, or redbud (Fig. 4). Emergence of *X. crassiusculus* in rearing containers peaked ≈40 d postcollection and continued for ≈70 d in end sealed bolts and 100 d in unsealed bolts (Fig. 5).

Test for Deterrent Effect of End Seal. Pressure-treated pine bolts baited with manuka oil caught significantly more *X. glabratus* (log-transformed) over 21 d than control bolts or bolts treated only with end seal ($F = 54.0$; df = 3,20; $P < 0.001$) (Fig. 6). Bolts treated with manuka oil plus end seal did not differ in attraction to *X. glabratus* from those treated with manuka oil only (Fig. 6). Manuka oil was relatively unattractive to *X. crassiusculus* and

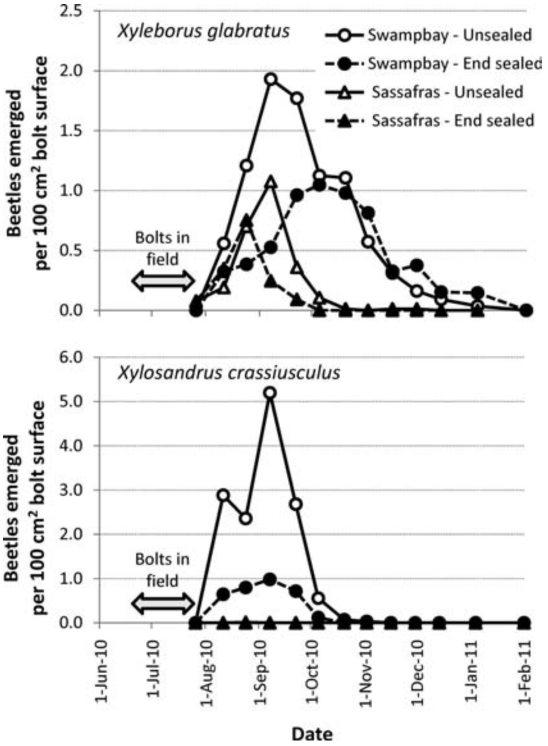

Fig. 5. Emergence of *X. glabratus* (top) and *X. crassiusculus* (bottom) from swampbay (*P. palustris*) and sassafras (*S. albidum*) bolts after 33 d in the field near Cordesville, SC, in 2010. Rearing containers were monitored for 190 d post-collection.

none of the manuka oil or end seal treatments differed significantly from the control ($F = 1.1$; df = 3, 20; $P = 0.366$).

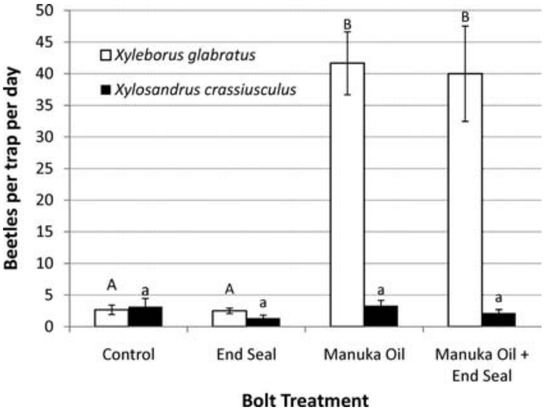

Fig. 6. Mean ± SE number of *X. glabratus* (white bars) and *X. crassiusculus* (black bars) captured on pressure treated bolt traps near Cordesville, SC, during a 21 d period (13 July through 3 August) in 2011. For each insect species, bars labeled with the same letter are not significantly different at the $P = 0.05$ level.

Discussion

Swampbay and redbay are very similar species with only minor phenotypic differences and some taxonomists consider swampbay a subspecies of redbay (Coder 2006). Mean (SE) trap catch on swampbay bolts in this study ranged from 2.9 (0.5) to 4.8 (0.8) beetles per trap per day. These values are similar to mean trap catches reported in Hanula et al. (2008) and Hanula and Sullivan (2008) using wounded redbay trees or cut redbay bolts. Hanula et al. (2008) reported on multiple redbay trapping trials conducted at different sites, during different years, and with different kinds of traps, all of which may be sources of variance in beetle trap catch density. Although simultaneous comparisons of swampbay and redbay at the same site have not been made to our knowledge, we suspect these two species are similar in attractiveness to *X. glabratus* as suggested by similar trap catch densities across studies and similar susceptibility to laurel wilt in the field. Large percentages of both species are killed by laurel wilt and both are readily colonized by *X. glabratus* (Mayfield et al. 2009).

In this study, camphortree was very attractive to *X. glabratus* and did not differ from swampbay in mean trap catch, entrance hole density, or beetle emergence. Camphortree is native to eastern Asia where it is valued for timber and camphor oil. It was introduced into Florida in 1875 and is now either cultivated or naturalized throughout the southeastern United States from the Carolinas west to Texas, and in southern California (Langeland et al. 2008). In Florida it is considered an invasive species that alters native plant communities (Florida Exotic Plant Pest Council 2009), but it is not on the Federal Noxious Weed list (USDA-APHIS 2010) and is commonly sold in ornamental trade (Langeland et al. 2008). The laurel wilt fungus, *R. lauricola*, has been isolated from wilting camphortrees in Georgia and Florida, but these trees did not exhibit rapid wilting of the entire crown as is observed in redbay and swampbay (Smith et al. 2009b). Our results suggest that camphortree is likely to be attacked by *X. glabratus* when encountered in the landscape. As an Asian species, however, camphortree may have a level of coevolved resistance to the laurel wilt pathogen that allows it to tolerate infection, meaning the disease may not kill and create numerous brood trees for *X. glabratus* as occurs with redbay and swampbay. Still, weakened, dead, or cut camphortree material in the landscape may serve as suitable *X. glabratus* host material for limited brood production.

Despite high entrance hole densities on camphortree, the mean number of *X. glabratus* emerging from camphortree was low, as was emergence from all other tree species in 2009. This may have been because of high humidity and water condensation in the rearing containers, possibly creating suboptimal conditions for brood development. Ventilation holes were added to the container design in 2010 and excessive water condensation was not observed. Nearly five times as many *X. glabratus* emerged from unsealed swampbay in 2010 as compared with 2009, despite similar numbers of beetles trapped in the field.

In 2009, avocado was significantly less attractive than swampbay and camphortree (attracting less than half as many beetles), but it attracted significantly more *X. glabratus* than loblolly bay and unbaited control traps. Very few entrance holes and emerging beetles were observed in avocado. In a previous trial comparing bolt traps baited with swampbay, avocado, and red maple, Hanula et al. (2008) found no difference between avocado and swampbay in total *X. glabratus* trap catch, but found significantly fewer entrance holes on avocado. Ploetz et al. (2011) speculated that avocado may be a relatively poor host for *X. glabratus,* noting that *X. glabratus* constituted a very small (<1%) percentage of 1,000 scolytids emerging from avocado bolts cut from trees killed by laurel wilt in Florida. Kendra et al. (2011) found bolts of three avocado cultivars to be more attractive to *X. glabratus* than unbaited controls, and observed females boring into bolts in choice and no-choice bioassays. Mayfield et al. (2008a) reported *X. glabratus* boring into small live avocado plants when caged onto the stems of five different cultivars, but observed wilt symptoms and mortality in only one cultivar. Mortality of landscape avocados because of laurel wilt has been observed along the Florida peninsula from Jacksonville south to Broward County (Ploetz et al. 2011). Overall, these observations suggest that *X. glabratus* finds avocado sufficiently attractive to initiate attacks that result in pathogen transmission, but may not attack at sufficient densities or reproduce well enough to build large populations in avocado wood.

Lancewood and sweetbay were four times less attractive to *X. glabratus* than swampbay, but they did not differ from avocado in attractiveness and caught 10 times as many beetles as loblolly bay. Lancewood (family Lauraceae) has not yet been reported as a laurel wilt host, but it is much less common in the landscape than redbay or swampbay and the extent to which it has been impacted by laurel wilt in Florida has not been closely evaluated. Sweetbay, a member of the Magnoliaceae, is an unlikely host of laurel wilt disease, which to date has only been reported from members of the Lauraceae. Our trapping data suggest, however, that cut sweetbay bolts emit one or more volatile compounds that are attractive to *X. glabratus.* Hanula and Sullivan (2008) suggested that the sesquiterpene α-copaene may be the primary host attractant in redbay and manuka oil, but other compounds may contribute to attraction as well. Kendra et al. (2011) identified three sesquiterpenes (α-copaene, β-caryophyllene, and α-humulene) present in lychee, various avocado cultivars, and essential oil lures that were positively correlated with *X. glabratus* trap catches. Evaluation of the sesquiterpene content of sweetbay and possibly other *Magnolia* spp. may yield additional information about the olfactory stimuli used by *X. glabratus* for host location.

In 2010, sassafras bolts exhibited lower *X. glabratus* trap catch, entrance hole density, and adult emergence than swampbay. These trap catch results are consistent with previous trials that found sassafras bolts to be less attractive than redbay bolts (Hanula et al. 2008). Notably, emergence of *X. glabratus* from sassafras bolts exposed in the field for 33 d peaked ≈30–40 d after placement in rearing containers, and then quickly declined. In contrast, emergence of *X. glabratus* from swampbay bolts continued much longer (Fig. 5), probably because one or more additional generations of beetles were being produced in swampbay inside the container. Our results indicate that sassafras, although less attractive and yielding fewer beetles than swampbay, is a suitable host for *X. glabratus.* This is consistent with reports of laurel wilt in sassafras in geographic isolation from redbay or other known hosts (Smith et al. 2009a, Cameron et al. 2010). Cameron et al. (2010) observed rapid progression of sassafras mortality because of laurel wilt in several monitoring plots established in Georgia, as well as the emergence of numerous callow *X. glabratus* adults from diseased sassafras trees. Whether sassafras populations will be a pathway for the spread of *X. glabratus* and laurel wilt into the Piedmont, Appalachians, or other geographic regions of the eastern United States remains to be seen. Koch and Smith (2008) used climate matching to predict the potential geographic limits of *X. glabratus* and suggested that climatic conditions (particularly rainfall) may limit the beetle to the southeastern coastal plain of the United States. More research on the epidemiology of laurel wilt in sassafras and the biology of *X. glabratus* and *R. lauricola* under various temperature and moisture regimes seems warranted.

Bolts of the nonlauraceous trees loblolly bay (Theaceae), yellow poplar (Magnoliaceae), and redbud (Fabaceae) were unattractive to *X. glabratus* and yielded very few emerging adults. The few beetles that did emerge from these species (n = 2, 2, and 7 from loblolly bay, yellow poplar, and redbud, respectively) may have been adults that attacked the bolts in the field and then exited in the rearing container. None of these species appears likely to be suitable for *X. glabratus* brood production in the field.

The granulate ambrosia beetle, *X. crassiusculus,* was readily attracted to and used swampbay, but was not attracted to sassafras, yellow poplar, or redbud. *X. crassiusculus* is reported to attack >120 woody plant species in >40 families worldwide and >20 different taxa in the United States (Solomon 1995, Cote 2008, Atkinson et al. 1988). Although yellow poplar and redbud are reported as hosts in Indiana (Cote 2008), attack and emergence of *X. crassiusculus* from these species in this study were negligible.

Adding end seal to swampbay bolts decreased *X. glabratus* attack density and greatly reduced *X. crassiusculus* trap catch, attack density, and emergence (Figs. 3–5). One possible explanation for these results is that the end seal treatment reduced volatilization of attractive compounds from the cut ends of the bolts, making them less attractive to flying beetles. Release rates of manuka oil (an effective *X. glabratus* lure) from 5 to 200 mg/d had no effect on the number of *X. glabratus* captured (Hanula and Sullivan 2008, Hanula et al. 2011). If *X. glabratus* responds to the same compounds in redbay as in manuka oil (e.g., α-copaene), it is unclear why a decrease in volatile concentrations from swampbay bolts via end-sealing would affect *X. glabratus* attraction, when changing the concentration of manuka oil does not. If end sealing decreases concentrations of volatile attractants released, it may be that there are additional attractants in swampbay that are not present or abundant in manuka oil, or that reductions in release rates lower than 5 mg/d reduce *X. glabratus* attraction.

Another possible explanation for the observed end-seal effect is that the sealant contained some kind of volatile compound that acted as a repellent to *X. glabratus* and *X. crassiusculus.* The product used in this study is a chemically stable, relatively odorless, wax-and-water emulsion that is used to prevent moisture loss and end-splitting in commercial sawlogs (http://www.baileysonline.com/PDF/Baileys_End_Seal_Flyer.pdf). We did not detect a repellent effect of the end seal on *X. glabratus* (Fig. 6), but no assessment of a repellent effect on *X. crassiusculus* could be made in our trial, as it was not attracted to manuka oil lures. Like several other species of ambrosia beetles, *X. crassiusculus* is readily attracted to ethanol-baited traps (Oliver and Mannion 2001) and likely responds to the release of ethanol from cut bolts. Studies comparing the volatile profiles from aerations of end sealed and unsealed bolts of preferred host species would help to explain the effects of end seal on the ambrosia beetles observed in this study.

The wax-and-water emulsion used in this study was easy to apply with a paintbrush. For application in the field, this has practical advantages over dipping logs into a container of melted paraffin wax over a portable heat source. However, because the wax-and-water emulsion resulted in lower attack densities (*X. glabratus*), trap catches and numbers of beetles emerged (*X. crassiusculus*), brushing a wax-and-water emulsion onto the cut ends of bolts is not recommended for studies where the objective is to trap and rear ambrosia beetles. Using a different kind of end seal (e.g., melted paraffin wax) or application of end seal to logs after field deployment but before placement in rearing containers may yield different results.

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