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Ambrosia Beetle (Coleoptera: Scolytidae) Species Attacking Chestnut and Captured in Ethanol-Baited Traps in Middle Tennessee

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ABSTRACT Ambrosia beetles can be important pests of nursery production. The beetles are difficult to control with insecticides, requiring that pesticides be closely timed before tree attack, applied repeatedly, or have long residual activity. The goal of this project was to improve management decisions for ambrosia beetle control in nurseries. This study used ethanol-baited traps, field observations of tree attacks, and emergence cages over beetle galleries to determine the following: (1) composition of ambrosia beetle fauna in middle Tennessee, (2) species responsible for attacks on chestnut (*Castanea mollissima* Blume), a susceptible tree species, (3) timing of tree attacks and progeny emergence, and (4) the relationship between tree attacks, progeny emergence, and beetle collections in ethanol-baited traps. Ambrosia beetles were surveyed using ethanol-baited Lindgren traps at the Tennessee State University Nursery Crop Research Station in McMinnville, TN, and at two commercial nurseries near Dibrell and Tarlton, TN, during 1998 and 1999. At the Nursery Station, species composition of ambrosia beetles attacking chestnut trees was determined in 1999. *Xyleborinus saxeseni* Ratzeburg, *Xylosandrus crassiusculus* Motschulsky, and *Monarthrum fasciatum* Say were the dominant ambrosia beetle species collected in traps. *Xyleborinus saxeseni* was the dominant species at all three locations when both 1998 and 1999 collections were totaled. Other commonly trapped species included *Monarthrum mali* Fitch, *Xyleborus atratus* Eichhoff, and *Xyleborus pelliculosus* Eichhoff. Tree attacks began on 2 April before trees broke dormancy. The majority of chestnut attacks occurred in April and May. Progeny emerged from 48% of the caged galleries, including 35.9, 10.3, 3.3, and 1.1% *X. germanus*, *X. crassiusculus*, *Hypothenemus* spp., and *X. saxeseni*, respectively. Beetles exhibited several unusual behaviors during this study, including emergence of female *X. germanus* from trees the following spring, emergence of live male *X. germanus* and *X. crassiusculus*, a staggered chronology of progeny emergence, and presence of multiple beetle species emerging from the same gallery. *Xylosandrus crassiusculus* and *X. germanus* were the dominant species attacking chestnut, but total trap collections of *X. germanus* were small ($\leq 1.7\%$). Several findings from this study have significance to the nursery industry. The timing of peak trap collections during April (particularly collections of *X. crassiusculus* and *X. saxeseni*) coincided with peak tree attacks. The factors responsible for chestnut susceptibility to attack were not measured in this study, but since the majority of trees were attacked before dormancy break, tree phenological state probably is an important determinant of tree vulnerability. The collection of some species like *X. germanus* in trap collections may be a more important indicator of tree attack than abundance in the trap. Progeny emergence from chestnut trees during June and July did not coincide with increased trap collections or renewed attacks on chestnut. Therefore, traps may not always indicate ambrosia beetle abundance. Several new state records were collected during this study, including *X. crassiusculus*, a species capable of serious economic damage to nursery stock.

KEY WORDS *Xylosandrus crassiusculus*, *Xylosandrus germanus*, *Xyleborinus saxeseni*, Scolytidae, insect-plant interactions, flight patterns

AMBROSIA BEETLES (SCOLYTIDAE: Coleoptera) can be important pests of nursery production. Adult beetles bore into trees, excavate a gallery that may consist of one to several tunnels and a brood chamber, and then introduce a symbiotic fungus (i.e., ambrosia), which serves as food for adults and larvae (Baker and Norris 1968; Weber and McPherson 1984; Roeper 1996). During entry into trees, ambrosia beetles often inoculate

trees with additional pathogenic fungi (Kessler 1974; Anderson and Hoffard 1978) or bacteria (Hall et al. 1982). For example, under controlled conditions, *Xylosandrus germanus* Blandford was capable of Dutch elm disease pathogen transmission (Buchanan 1941). Beetle larvae complete their development in the tree, and female progeny exit the tree to begin a new gallery (Weber and McPherson 1983).

Due to the cryptic nature of scolytids, ambrosia and bark beetles often are transported from one region to another in trees or wood products. Many of the ambrosia beetle species that currently occur in the

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United States are foreign introductions (Bright 1968; Wood 1977; Atkinson et al. 1990). Three species in the genus *Xylosandrus*, including *X. germanus*, *X. compactus* (Eichhoff), and *X. crassiusculus* (Motschulsky) have all caused considerable economic damage since their domestic introductions in 1932, 1952, and 1974, respectively (Felt 1932; Anderson 1974; Ngoan et al. 1976; Wood 1977; Anderson and Hoffard 1978; Weber 1982; Mizell et al. 1994). In one study, attacks by introduced ambrosia beetles were not associated with obvious stress factors (Kovach 1986). *Xylosandrus crassiusculus* and *X. germanus* are both polyphagous and will attack "apparently" healthy trees (Weber 1978; Atkinson et al. 1988b). Although attacks by *X. germanus* do not always result in tree mortality, tree growth may be seriously reduced (Weber 1982). Control of *X. crassiusculus* with insecticides has had limited success (Hudson and Mizell 1999). To effectively protect trees with chemicals, pesticides must either be closely timed with beetle attack, applied repeatedly, or have long residual activity. Pesticide management that is closely timed with beetle attack periods will provide the most efficacious, economical, and environmentally sound pest control (Hudson and Mizell 1999). The timing of tree attacks likely varies among regions, due to differences in scolytid fauna, timing of beetle flight, and phenological variation in susceptibility of different tree hosts (Roling and Kearby 1975; Turnbow and Franklin 1980; Atkinson et al. 1988a). Middle Tennessee is the primary nursery-growing region in the state. Therefore, the goal of this research was to improve management decisions for ambrosia beetle control in nurseries of middle Tennessee by addressing the following objectives: 1) to determine which ambrosia beetle species are present in the middle Tennessee region, 2) to determine which species are responsible for attacks on a susceptible tree species, 3) to determine timing of tree attacks and progeny emergence, and 4) to determine if tree attacks and progeny emergence coincide with adult beetle collections in ethanol-baited traps.

Materials and Methods

Ambrosia Beetle Trapping. Ambrosia beetles were surveyed at the Tennessee State University Nursery Crop Research Station (Nursery Station) at McMinnville Tennessee beginning on 5 March 1998. Periodic trap collections also were made during 1997. Lindgren funnel traps (eight funnels/trap) initially were baited on 5 March 1998 with a 5.3-ml vial filled with 70% ethanol and wired to the outer support strut on the trap (Lindgren 1983). The 5.3-ml vial was replaced with a 25 ml vial on 29 March 1998 to lengthen ethanol output. The ethanol was refilled or replaced during each trap examination. On 24 April 1998, ethanol vials were replaced with UHR ethanol lures (95% ethanol and 5% water with an average release rate of 1 g ethanol/d at 22°C) supplied by Phero Tech Incorporated (7572 Progress Way, Delta, B. C., Canada V4 g 1E9). Lures were changed at ≈ 50 d intervals during midsummer months and at 100 ± 11 d intervals during

the remainder of the year. A strip (≈ 2 cm long) of Hercon VaporTape II (10% 2,2-dichlorovinyl dimethyl phosphate) periodically was placed in the collection container of the trap to kill captured beetles. The area beneath traps was mowed and treated with glyphosate (Roundup PRO [240 ml/11.4 liter]), oryzalin (Surflan A.S. [70 ml/11.4 liter]), and isoxaben (Gallery 75 DF [15 ml/11.4 liter]) as needed to prevent weed growth from obscuring traps. Traps were suspended from a tree branch, near the edge of a mixed pine-hardwood forest on the northern and southern end of the research station. Traps were placed with the base ≈ 60 cm from the ground and were emptied at 2–5 d intervals depending on the season and beetle collection rate. In addition, a Lindgren funnel trap was placed in two commercial nurseries in northern Grundy County near Tarlton, TN, and in northern Warren County near Dibrell, TN. Traps at Dibrell and Tarlton were checked at ≈ 14 - to 28-d intervals, depending on the season and beetle collection rate. Beetle collections also were occasionally received from traps operated in Franklin and Davidson Counties during 1998 and 1999. Beetle samples were separated to species for each sample date and location.

Timing of Tree Attack. The seasonal incidence of tree attack by ambrosia beetles was determined by examining chestnut trees, *Castanea mollissima* Blume, for new entry holes (galleries). Five trees (1.0- to 1.9-cm caliper at 15.2 cm high) were transplanted at four locations on the Nursery Station on 8 February 1999. Each plot was ≈ 2 m from the edge of a deciduous forest, and trees were planted at a 3-m spacing. Plots were maintained with mowing, and trees were irrigated as needed. On 9 February, a 35-ml volume of Osmocote 8 mo slow release fertilizer (18–6–12; N-P-K) was broadcast around the base of each tree. Trees were examined approximately three times per week from February to late July by thoroughly examining the trunk and branches for new ambrosia beetle galleries. After July, trees were examined weekly until 15 May 2000. For each new gallery, information recorded included the date of first observance, the height from the soil surface, the caliper of the limb at the bore location, and the compass direction of the bore entrance. The height, cardinal direction, and caliper of the stem at the entrance site of each gallery was compared between major species of ambrosia beetles using analysis of variance (ANOVA) for a randomized complete block design on $\log_{10}(X + 0.0001)$ transformed data, and means separated by least significant difference (LSD) Test ($\alpha = 0.05$) (SAS Institute 1997). Other characteristics recorded for some galleries included unusual location (e.g., bud, leaf scar) or excrement nature (e.g., toothpick strands). The number of new tree attacks was contrasted with the number of trap captures for the dominant species.

Progeny Species Composition, Date of Emergence, and Related Data. To determine the beetle fauna attacking chestnut and the number of progeny emerging from individual galleries, a maximum of 10 new galleries were caged on each sample date by randomly

Table 1. Species of Scolytidae captured in ethanol-baited Lindgren traps at three middle Tennessee sites during 1998 and 1999

Species	1998				1999				Grand Total	First report in Tennessee ^a
	NCRS	DIB	TAR	Total	NCRS	DIB	TAR	Total		
<i>Ambrosiodmus rubricollis</i> Eichhoff	15	0	8	23	48	2	9	59	82	No
<i>Ambrosiodmus tachygraphus</i> Zimmermann	45	0	2	47	47	5	11	63	110	Yes
<i>Corthylus columbianus</i> Hopkins	5	0	1	6	3	2	0	5	11	No
<i>Dryoxylon onoharaensum</i> (Murayama) ^b	6	1	1	8	5	3	0	8	16	Yes
<i>Gnathotrichus materiarius</i> Fitch	0	0	0	0	1	0	0	1	1	Yes
<i>Hypothenemus</i> sp. 1	4	0	1	5	4	0	1	5	10	?
<i>Hypothenemus</i> sp. 2	2	1	0	3	2	0	0	2	5	?
<i>Hypothenemus</i> sp. 3	0	1	0	1	1	0	0	1	2	?
<i>Monarthrum fasciatum</i> Say	500	3	11	514	50	25	11	86	600	No
<i>Monarthrum mali</i> Fitch	65	0	43	108	24	11	135	170	278	No
<i>Pityophthorus</i> sp. 1	1	0	0	1	0	0	0	0	1	?
<i>Pityophthorus</i> sp. 2	1	0	0	1	0	0	0	0	1	?
<i>Pityophthorus liquidambarus</i> Blackman	0	0	3	3	0	0	0	0	3	Yes
<i>Xyleborinus saxeseni</i> Ratzeburg	430	101	261	792	822	447	329	1,598	2,390	No
<i>Xyleborus affinis</i> Eichhoff	0	0	0	0	1	1	0	2	2	Yes
<i>Xyleborus atratus</i> Eichhoff	74	1	3	78	31	10	17	58	136	No
<i>Xyleborus californicus</i> Wood	1	0	0	1	1	7	0	8	9	Yes
<i>Xyleborus ferrugineus</i> Fabricius	2	0	2	4	3	0	1	4	8	No
<i>Xyleborus pelliculosus</i> Eichhoff	140	0	0	140	51	3	3	57	197	Yes
<i>Xyleborus sayi</i> Hopkins	0	0	8	8	0	0	6	6	14	No
<i>Xylosandrus crassiusculus</i> (Motschulsky)	116	9	106	231	96	109	412	617	848	Yes
<i>Xylosandrus germanus</i> Blandford	56	0	17	73	3	2	5	10	83	No
<i>Xyloterinus politus</i> Say	1	0	2	3	0	0	0	0	3	No
Total	1,464	117	469	2,050	1,193	627	940	2,760	4,810	

None of the beetles in this table had previously been reported in the USDA CAPS Database. NCRS = Tennessee State University Nursery Crop Research Station, McMinnville, TN (Total of 2 Lindgren traps combined). DIB and TAR = Commercial nurseries near Dibrell and Tarlton, TN, respectively (1 Lindgren trap per site).

^a Information from the USDA Cooperative Agricultural Pest Survey (CAPS) Database, Atkinson and Peck (1994), Bright (1968), Vandenberg et al. (2000), Wood (1977), Wood and Bright (1992).

^b Recently redescribed from *Xyleborus onoharaensis* Murayama (Bright and Rabaglia 1999).

selecting two to three bores in each plot. Cages consisted of plastic cylinders (1 cm long by 1 cm diameter). A 2-mm hole was drilled through both sides of the cylinder near the middle. On one end of the cylinder, a 1-mm semicircular indentation was formed on each side (using a rotating 2-mm drill bit). Two GB natural white nylon cable ties (10 cm long by 1.5 mm wide) were inserted through the central holes from the exterior (one with the receptacle entrance up and the other down) and the cable portion of each tie pulled into the cylinder and out the bottom. The semicircular indentation at the base of the cylinder formed a slot for the exiting cable tie, thus permitting the cylinder to rest flat against the tree. The cables were wrapped around the tree, and inserted into the receiving receptacle of the opposite tie. The cylinder was then lined up over the gallery entrance, and the ties pulled tight. Gaps between the cylinder and the tree were filled with GE silicone II household glue (Waterford, NY).

Each cage had a removable cover that consisted of a tygon tube (≈3 cm long by 8 mm diameter with 1.5-mm walls) that had a screened (0.3-mm² mesh) and an open end. The open-end of the cover was then inserted over the outside of the cylinder already permanently attached to the tree. The tygon tube was easy to remove when checking for emerged beetles, but prevented beetle escape by forming a tight seal with the inner plastic cylinder. The screened-end of the tygon tube allowed condensation to escape, which reduced mold growth in the cage. The screen also

functioned to permit volatile compounds from either the damaged tree or the insect to exit the cage. Cages were checked for progeny and cleared of sawdust and feces at the same time trees were examined for new galleries. Major species of ambrosia beetles were compared for differences in progeny emergence using ANOVA for a randomized complete block design on log₁₀ (X + 0.0001) transformed data, and means separated by LSD test (α = 0.05). Voucher specimens for all species have been deposited in the Insect Collection of the Tennessee State University Nursery Crop Research Station, McMinnville, TN.

Results

Ambrosia Beetle Trapping. In total, 21, 15, and 16 different species of scolytid beetles were collected at the Nursery Station, Dibrell, and Tarlton sites in 1998 and 1999, respectively (Table 1). Eight of these species are new state records for Tennessee. *Xyleborinus saxeseni* Ratzeburg was the most abundant species trapped at all sites when 1998 and 1999 trap totals were combined. *Xylosandrus crassiusculus* Motschulsky or *Monarthrum fasciatum* Say were the dominant species at some sites/yr. Other common species at the three sites included *Monarthrum mali* Fitch, *Xyleborus atratus* Eichhoff, and *Xyleborus pelliculosus* Eichhoff. *Xyleborus affinis* Eichhoff and *Xyleborus californicus* Wood only occurred at the Nursery Station and Dibrell sites (Table 1). *Xyleborus ferrugineus* Fabricius and *Xyloterinus politus* Say only occurred at the Nurs-

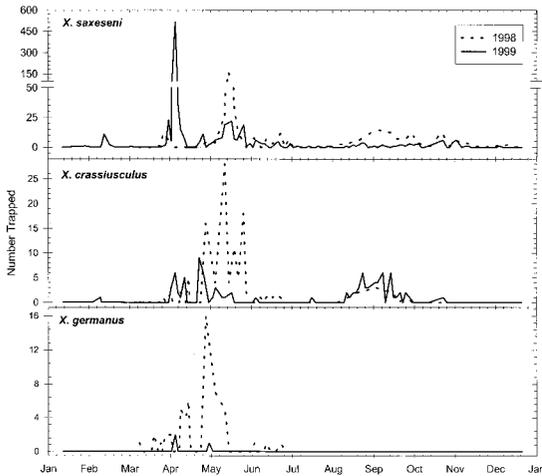


Fig. 1. Total number of *Xyleborinus saxeseni*, *Xylosandrus crassiusculus*, and *Xylosandrus germanus* collected in two ethanol-baited Lindgren traps at the Nursery Crop Research Station, McMinnville, TN, during 1998 and 1999.

ery Station and Tarlton sites (Table 1). Species only collected during 1997 pretrapping at the Nursery Station included *Carphoborus tentativus bifurcus* Eichhoff, *Hylastes salebrosus* Eichhoff, *Ips grandicollis* Eichhoff, *Pityogenes hopkinsi* Swaine, *Pityogenes meridianus* Blackman, *Pityophthorus liquidambar* Blackman, and *Xyleborus sayi* Hopkins. In the former list, *P. liquidambar* and *X. sayi* also occurred at the Tarlton site (Table 1). *Hylastes salebrosus* and *P. meridianus* are new state records for Tennessee. With the exception of *Hylocurus rudis* (LeConte), no new beetle species were collected from Davidson and Franklin Counties. *Hylocurus rudis* is a new state record for Tennessee.

Trap collections of the primary tree-attacking ambrosia beetle species (*X. crassiusculus*, *X. germanus*, and *X. saxeseni*) peaked from early April to June at the Nursery Station (Fig. 1). A second peak in *X. crassiusculus* and *X. saxeseni* collections began around early August and extended into November. Seasonal patterns in trap collections were similar in 1998 and 1999 at the Nursery Station. At the Tarlton and Dibrell sites, trap collections of the three primary species were similar to the Nursery Station site, with the exception of *X. germanus* at the Dibrell site, which was not collected in 1998 and only collected twice in 1999 (30 April and 30 July). Among the three sites, the earliest and latest yearly collections of *X. saxeseni*, *X. crassiusculus*, and *X. germanus* were 3 January and 9 December, 8 February and 17 December, and 9 March and 3 September, respectively. *Xyleborinus saxeseni* was collected during every month of the year, and *X. crassiusculus* was collected during every month except January. With the exception of August, *X. germanus* was collected during every month between March and September.

In general, trap collections of other ambrosia beetles had similar spring peaks, a decline during summer

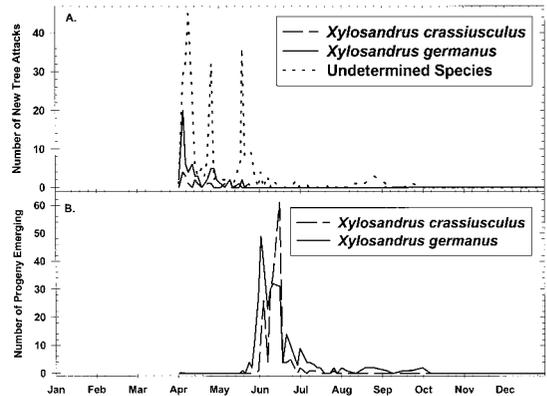


Fig. 2. Seasonal timing and total number of A) tree attacks by *Xylosandrus crassiusculus*, *Xylosandrus germanus*, and undetermined ambrosia beetles, and B) progeny of *X. crassiusculus* and *X. germanus* emerging from chestnut (*Castanea mollissima*) at the Nursery Crop Research Station, McMinnville, TN, during 1999.

months, and then an increase (for some species) in fall trap captures. *Monarthrum fasciatum* had trap collections that began in late January and extended to early December, with peaks in early April and mid-September, whereas *M. mali* had collections from late January to mid-October, with peaks in late March to early April. *Ambrosiodmus rubricollis* Eichhoff had trap collections that began in early May and extended to early July, with peak captures occurring mid- to late-May. *Ambrosiodmus tachygraphus* Zimmermann had trap collections that began in late January and extended to mid-June, with peak capture in early April. *Xyleborus atratus* had trap collections that began in late March and extended to early July, with peak captures in early April and mid-May. *Xyleborus pelliculosus* had trap collections that began in early February and extended to early May, with peak collections in early February and early March. Peak collections of *X. pelliculosus* and *A. rubricollis* were the latest and earliest among ambrosia beetle species, respectively.

Timing of Tree Attack. Tree attacks began on 2 April at a time when trees were exhibiting signs of dormancy break (i.e., swelling and green color change in buds) (Fig. 2A). New tree attacks by *X. crassiusculus* and *X. germanus* first occurred on 2 and 5 April, respectively, based on the species of progeny that subsequently emerged from the galleries (Fig. 2A). Among the 20 study trees, five were not attacked, ambrosia beetles apparently killed three trees, and the remaining trees were damaged. A total of 387 separate attacks occurred among 15 trees from 2 April to 23 September. Because only 195 galleries were caged and progeny did not emerge in all cages ($n = 96$), the species responsible for the majority of tree attacks were undetermined (Fig. 2A). Based on galleries from which progeny emerged, tree attacks by *X. crassiusculus* ($n = 16$) had an 85.0 and 15.0% occurrence in April and May, respectively, and tree attacks by *X. germanus* ($n = 64$) had a 91.0, 5.0, and 1.0% occurrence

Table 2. Total and percent emergence of different species of ambrosia beetle from chestnut at the Nursery Crop Research Station, McMinnville, TN, in 1999

Species	No. Cages	No. emerging		
		Males	Females	Total
No Emergence	96	—	—	—
Solitary				
<i>Hypothenemus</i> sp. 2	2	0	4	4
<i>Hypothenemus</i> sp. 3	2	0	2	2
<i>Hypothenemus</i> sp. 4	1	0	1	1
<i>Xyleborinus saxeseni</i>	1	0	3	3
<i>Xylosandrus crassiusculus</i>	15	10	148	158
<i>Xylosandrus germanus</i>	61	16	257	273
Mixed				
<i>Xylosandrus crassiusculus</i>	4	1	28	29
<i>Xylosandrus germanus</i>		4	12	16
<i>Hypothenemus</i> sp. 2	1	0	1	1
<i>Hypothenemus</i> sp. 4		0	2	2
<i>Xyleborinus saxeseni</i>	1	0	1	1
<i>Xylosandrus germanus</i>		1	3	4
Total	184	32	462	494

203 galleries were not caged.

in April, May, and June, respectively. Total tree attack occurrence (both determined and undetermined species) was 68.9, 24.7, 3.3, 0.5, 2.1, and 0.5% during the months of April, May, June, July, August, and September, respectively (Fig. 2A). Timing of tree attacks by *X. crassiusculus* and *X. germanus* closely coincided with spring trap collections at the Nursery Station (Figs. 1 and 2). An increase in fall trap collections of *X. crassiusculus* and *X. saxeseni* at the Nursery Station also coincided with renewed tree attacks in the fall. *Xylosandrus germanus* was the dominant species attacking chestnut, but it was poorly represented in Lindgren trap collections ($\leq 1.7\%$ of total collections). New tree attacks continued after May (Fig. 2A), but *X. crassiusculus* and *X. germanus* did not emerge from any galleries formed after May. Based on progeny emergence from galleries, the only tree attacks that could be attributed to *X. saxeseni* ($n = 2$) occurred on 16 April, and attacks attributed to *Hypothenemus* spp. occurred from 17 May to 3 June ($n = 10$) and the 18–25 of August ($n = 2$).

Progeny Species Composition, Date of Emergence, and Related Data. At least four species of ambrosia beetle attacked chestnut based on progeny emergence from galleries (Table 2). A total of 184 galleries were caged for progeny collection. Ambrosia beetle species did not emerge from 52.2% of the caged galleries, and *X. germanus*, *X. crassiusculus*, *Hypothenemus* spp., and *X. saxeseni* emerged from 35.9, 10.3, 3.3, and 1.1% of the remaining galleries, respectively. Mixed species of ambrosia beetle were found in 3.3% of collection cages, including *X. crassiusculus* with *X. germanus*, two species of *Hypothenemus*, and *X. germanus* with *X. saxeseni*. The largest number of beetles collected from a single gallery was 59 *X. crassiusculus*. Emerging *X. crassiusculus* and *X. germanus* progeny were female biased at 94.1 and 92.8%, respectively (Table 2). *Xylosandrus crassiusculus* and *X. germanus* produced significantly more progeny than *Hypothenemus* spp. (Table 3).

Table 3. Average height, stem caliper, compass direction, and number of progeny emerging for the primary species of ambrosia beetles collected from chestnut at the Nursery Crop Research Station, McMinnville, TN, in 1999

Species	Gallery site measurements (mean \pm SE)			
	Height, cm	Stem caliper, cm	Compass direction, °	Progeny per gallery (mean \pm SE)
<i>Xylosandrus germanus</i>	24.3 \pm 4.1a	11.5 \pm 0.5a	195.2 \pm 13.1a	4.4 \pm 0.5a
<i>Xylosandrus crassiusculus</i>	28.7 \pm 4.1a	10.2 \pm 0.7a	238.6 \pm 22.0a	9.9 \pm 4.0a
<i>Hypothenemus</i> sp.	60.4 \pm 6.9b	5.5 \pm 0.4b	185.4 \pm 33.4a	1.2 \pm 0.2b
Statistics	Height	Stem	Compass	Progeny
MSE	0.18	0.18	1.53	0.16
MST	1.44	1.44	0.69	0.59
df _{MST, MSE}	2, 70	2, 70	2, 70	2, 70
F	8.01	8.01	0.45	3.59
P	0.0007	0.0007	0.6407	0.0328

Means within a column followed by a different letter were significantly different ($P < 0.05$; LSD test). Analysis of variance statistics at the bottom of the table are for the species main treatment effect. Location and the interaction of species with location were not significantly different ($P > 0.05$).

The primary emergence period of *X. crassiusculus* and *X. germanus* was similar, with the exception that emergence of *X. germanus* extended over a longer period of time (Fig. 2B). Emergence of *X. crassiusculus* began on 19 of May and was 95% completed by 21 of June. Emergence of *X. germanus* began on 24 of May and was 95% completed by 14 of July. The average period from first attack to progeny emergence was 55.2 and 54.3 d for *X. crassiusculus* and *X. germanus*, respectively. Trap collections of *X. crassiusculus* and *X. germanus* did not increase during the periods of peak progeny emergence from galleries (Figs. 1 and 2B). Tree attacks also did not increase during June through July periods of progeny emergence (Fig. 2). Progeny of both species did not exit from individual galleries at the same time, but were collected in cages across multiple dates (Table 4). The collection of progeny on different sample dates was defined as "emergence events." Progeny of *X. crassiusculus* and *X. germanus* had a maximum of four and seven separate emergence events from individual galleries, which ranged from 0.2 to 14.3 d and 7.7–19.8 d apart, respectively. *Xylosandrus crassiusculus* progeny initially exited galleries in greater number (i.e., 93.2% on first two events) than *X. germanus* progeny (i.e., 68.4% on first two events). Emergence of *X. germanus* progeny ranged from one to two beetles during each emergence event, while emergence of *X. crassiusculus* progeny ranged from six to seven beetles on the first two events to one to two on subsequent events. However, the total number of days from first to last emergence was similar for both *Xylosandrus* species. In general, *X. crassiusculus* males tended to emerge on the first emergence event (six out of nine galleries), while male *X. germanus* tended to emerge on the second or third emergence event (nine out of 14 galleries). Both *X. crassiusculus* and *X. germanus* males occasionally had more than one

Table 4. Emergence timing and number of progeny produced at each emergence interval for the primary species of ambrosia beetle attacking chestnut at the Nursery Crop Research Station, McMinnville, TN, in 1999

Variable measured	Emergence event	Species	
		<i>Xylosandrus crassiusculus</i>	<i>Xylosandrus germanus</i>
No. of days from first attack (mean \pm SE)	1st	55.2 \pm 3.6	54.3 \pm 1.9
	2nd	66.5 \pm 2.9	64.8 \pm 3.2
	3rd	74.2 \pm 3.2	68.6 \pm 4.7
	4th	94.0 \pm 7.4	74.5 \pm 8.0
	5th	—	74.7 \pm 9.1
	6th	—	74.5 \pm 7.9
	7th	—	89.0 \pm 5.1
No. progeny per gallery (mean \pm SE)	1st	6.8 \pm 3.1	1.9 \pm 0.2
	2nd	6.0 \pm 2.9	2.1 \pm 0.2
	3rd	1.5 \pm 0.3	1.8 \pm 0.3
	4th	1.0 \pm 0.0	2.1 \pm 0.4
	5th	0	1.0 \pm 0.0
	6th	0	1.0 \pm 0.0
	7th	0	1.0 \pm 0.0
No. of galleries with emergence ^a	1st	19	66
	2nd	8	45
	3rd	6	27
	4th	4	16
	5th	0	9
	6th	0	6
	7th	0	4
Percent of total emerging ^b	1st	67.9	39.6
	2nd	25.3	28.8
	3rd	4.7	15.2
	4th	2.1	10.5
	5th	0	2.8
	6th	0	1.9
	7th	0	1.2

^a This is the sample size for means calculated under number of days from first attack and number of progeny per gallery.

^b Total refers to the sum of all beetle progeny collected for each species during the study (i.e., 187 and 293 *X. crassiusculus* and *X. germanus*, respectively).

emergence event from the same gallery. A total of seven *X. germanus* females emerged from five galleries the following spring. Spring 2000 emergence ranged from 283 to 368 d after initial 1999 gallery formation. One gallery with *X. germanus* emergence during 2000 previously had 59 *X. crassiusculus* emerging in 1999.

Table 5. Gallery location or other characteristics associated with different species of ambrosia beetle attacking chestnut at the Nursery Crop Research Station, McMinnville, TN, in 1999

Species emerging	Nothing recorded ^a	No. galleries observed			
		Bud	Terminal bud	Leaf scar	Toothpick strands
<i>Hypothenemus</i> spp.	6	5	1	0	0
<i>Xyleborinus saxeseni</i> Ratzeburg	0	0	0	0	1
<i>Xylosandrus crassiusculus</i> (Motschulsky)	8	0	0	0	8
<i>Xylosandrus germanus</i> Blandford	29	2	0	1	32
<i>X. crassiusculus</i> \cup <i>X. germanus</i>	0	0	0	0	4
<i>X. saxeseni</i> \cup <i>X. germanus</i>	1	0	0	0	0
Undetermined species ^b	198	64	2	4	21
Total	242	71	3	5	66

Bud = galleries that occurred in the lateral stem buds; terminal bud = galleries that occurred in the terminal stem bud; leaf scar = galleries that occurred in leaf scars; toothpick strands = galleries that had excavated sawdust or frass extending from the entrance in a cylindrical, toothpick-like manner.

^a These galleries either had no unique feature or nothing was recorded for the gallery.

^b Undetermined because gallery not caged.

Gallery location, as well as characteristics of the gallery entrance, was indicative of some species of ambrosia beetle (Tables 3 and 5). *Hypothenemus* spp. preferentially attacked terminal and lateral buds of chestnut. In addition, stems attacked by *Hypothenemus* usually were dead at the time of attack. The genus *Hypothenemus* is in the tribe Cryphalini, and therefore is not considered a true ambrosia beetle. *Xylosandrus germanus* was the only species that bored into leaf scars. Toothpick-like strands were extended from galleries that had *X. saxeseni*, *X. crassiusculus*, or *X. germanus* emergence. *Xylosandrus crassiusculus* and *X. germanus* preferred to attack lower on the tree than *Hypothenemus* spp. (Table 3). As a result, the stem size at the location of *X. crassiusculus* and *X. germanus* galleries was significantly greater than stem size associated with *Hypothenemus* spp. galleries (Table 3). Although average height of *X. crassiusculus* and *X. germanus* galleries did not differ ($P > 0.05$), the height of *X. crassiusculus* attacks were distributed normally about the mean, while the height of *X. germanus* attacks linearly decreased with increasing height. Average gallery direction of *X. crassiusculus*, *X. germanus*, and *Hypothenemus* spp. ranged from near south (i.e., 195°) to near southwest (i.e., 239°), but was not different among the three species (Table 3). At the termination of the study, live trees had an average height of 98.0 cm and caliper of 1.3 cm (at a height of 15.2 cm).

Discussion

Ambrosia Beetle Trapping. A diverse number of scolytid species were captured at each survey site in this study. Among the species collected, 11 are new state records (Wood and Bright 1992; USDA Cooperative Agricultural Pest Survey Database). *Xylosandrus crassiusculus*, *X. saxeseni*, and *M. fasciatum* were the most common species trapped in this study. Because *X. crassiusculus* has a broad host range and frequently kills the host tree, it is a serious nursery pest. *Xyleborinus saxeseni* was the most abundant scolytid year

round in this and other southeastern studies (Roling and Kearby 1975; Turnbow and Franklin 1980; Kovach 1986; Atkinson et al. 1988a). In this study, some species had minimal trap collections (e.g., *C. columbianus*, *Gnathotrichus materiarius* Fitch, *H. salebrosus*, *Hypotheremus* spp., *X. affinis*), but were common in other states (Roling and Kearby 1975; Turnbow and Franklin 1980; Atkinson et al. 1988a). *Ips grandicollis*, *Pityophthorus* spp., and *X. ferrugineus* had low trap densities in this study and in Florida, but were abundant on sticky traps (Atkinson et al. 1988a).

Scolytid collection in traps likely is affected by variation in regional scolytid faunas, the method of trapping used, and the environment. The presence of attractive host material in the vicinity of traps modified the response of *M. fasciatum*, *M. mali*, and *X. saxeseni* to ethanol-baited traps (Roling and Kearby 1975). Wood boring beetles likely colonize trees when conditions are optimal for the development of their progeny. A tree condition that is optimal for infestation may be signaled by changes in olfactory (Dunn and Potter 1991) or visual cues. Trap features like height, location, shape, color, design type, bait location, volume of ethanol released, and population of beetles in the vicinity all affect trapping rates (Roling and Kearby 1975; Turnbow and Franklin 1980; Lindgren 1983; Atkinson et al. 1988a). At the Nursery Station, *X. germanus* was poorly represented in trap collections (particularly in 1999), but was the most common species attacking chestnut. *Xylosandrus germanus* was commonly trapped in another Tennessee study (Weber and McPherson 1983). Other factors like the presence of attractive host material in the vicinity may have affected the response of *X. germanus* to traps in this study. Other studies cited in the previous section all used traps made from clear Plexiglas in a vane or single-sheet configuration (Roling and Kearby 1975; Wilkening et al. 1981; Kovach 1986). Traps with clear Plexiglas windows would be more likely to attract scolytids by olfactory signals than visual cues. In contrast, Lindgren traps used in this study would have provided both an olfactory stimulus from ethanol baits, as well as a visual stimulus from the multiple black funnels.

Trap collections of both *Xylosandrus* species began in early April in this study. *Xylosandrus crassiusculus* appeared to have two distinct trap periods (April to June and August to October), which may indicate two generations per year. In Florida, trap collections of *X. crassiusculus* ranged from early February to early March (<http://www.ifas.ufl.edu/1005a.htm>), whereas in Texas, collections fluctuated from mid-February to late April depending on survey year (<http://aggie-horticulture.tamu.edu/county/smith/industry/aab.html>). *Xylosandrus crassiusculus* was reported to have one generation per year in South Carolina, and up to four generations per year in Taiwan (Wu et al. 1978; Kovach 1986). Low *X. germanus* collections among Tennessee sites prevent conclusions about the number of probable generations per year. Under favorable conditions in New Jersey, *X. germanus* had two to three generations per year (Hoffman 1941). In Illinois,

NC, Ohio, and another Tennessee study, *X. germanus* was reported to have only two generations per year, and were in flight from late March to September depending on the state (Schneider and Farrier 1969; Weber 1982; Weber and McPherson 1983).

Species only collected during the spring in middle Tennessee included *A. rubricollis*, *A. tachygraphus*, *X. atratus*, and *X. pelliculosus*. Both *Ambrosiodmus* species had unimodal collection patterns. In South Carolina, *A. tachygraphus* also had a unimodal spring peak, but *A. rubricollis* had a spring and fall peak, with some specimens captured all summer (Kovach 1986). *Monarthrum fasciatum* and *M. mali* collected in the spring and fall in middle Tennessee, had similar patterns in Georgia, FL, Missouri, and South Carolina (Roling and Kearby 1975; Turnbow and Franklin 1980; Kovach 1986; Atkinson et al. 1988a). In all studies, fall trap collections of *M. fasciatum* and *M. mali* were always lower. Multiple peaks in trap capture of *X. saxeseni* were observed in Tennessee, which would be consistent with a multivoltine biology. *Xyleborinus saxeseni* can have four to five generations per year in South Carolina (Kovach 1986). Ambrosia beetle trap collections generally were lowest during summer months.

Timing of Tree Attack. In this study, attacks on chestnut by ambrosia beetles occurred primarily from early April to early June and again in September and October. Although *X. crassiusculus* and *X. germanus* may have continued attacking chestnuts during the summer and fall, in terms of progeny emergence, no tree attacks could be attributed to these species after early June. In Florida, trees were attacked immediately after *X. crassiusculus* began emerging in February (Mizell et al. 1998). Attacks by *X. crassiusculus* in Alabama were reported as early spring (Davis and Dute 1995), and in Virginia, *X. crassiusculus* emergence occurred at the same time as the first flush of new growth (Baker 1999). In Illinois, walnut was attacked by *X. germanus* in late April and attacks continued until late June (Weber and McPherson 1983). The heaviest attacks by *X. germanus* in Illinois, NC, and another Tennessee study occurred during April (Weber 1982; Weber and McPherson 1983). *Xylosandrus germanus* attacks on elm roots in New Jersey were observed ≈ 1 mo later than this study (i.e., 10 May) (Hoffman 1941). *Xyleborinus saxeseni* had a peak emergence from late April to early May in Germany (Fischer 1954) and during March in South Carolina (Kovach 1986). Peak trap collection of *X. saxeseni* in this study was in April, and the only tree attacks that could be attributed to this species occurred in April.

In 1999, both *X. crassiusculus* and *X. germanus* began attacking chestnuts before dormancy was broken on 2 April. However, some trees had begun to exhibit signs of leafing by 1 April, as indicated by swelling and color change of buds. Two trees that had small visible leaves by 7 April were not attacked during the study. Other trees began to break dormancy near the base of the tree, but were heavily attacked and eventually killed. All chestnuts that were not killed had broken dormancy by the end of April. During 1999, $\approx 70\%$ of the yearly tree attacks occurred in April with $\approx 74\%$ of

those tree attacks occurring before the 15 April, the period when most chestnuts were attempting to break dormancy. In Florida and Georgia, attacks on certain plants ceased after leafing was complete (Hudson and Mizell 1999). The phenological state of tree growth apparently is an important determinant of tree susceptibility to ambrosia beetles.

The primary periods of attack in middle Tennessee coincided with peak trap collections of *X. crassiusculus*, *X. germanus* and *X. saxeseni*. Consequently, trap collections of *Xylosandrus* and *Xyleborinus* species may indicate the timing of tree attacks and when protective measures should be applied to trees. *Xylosandrus germanus* was not captured in traps after June at the Nursery Station, but did have May, July, and September collections at the Tarlton site. Traps proved valuable for timing chemical applications against *X. crassiusculus* in Florida and Georgia, because initiation of beetle flights varied between years (Hudson and Mizell 1999). Mizell et al. (1998) observed a close relationship between *X. crassiusculus* trap capture and tree attacks. Although traps can indicate when ambrosia beetles are active, a direct relationship between trap capture and tree attack does not always occur. *Xylosandrus crassiusculus* and *X. germanus* progeny were actively emerging from late May to July at the Nursery Station, but trap collections and tree attacks did not increase at this time.

Progeny Species Composition, Date of Emergence, and Related Data. Although *X. saxeseni* was the most common species in middle Tennessee trap collections, progeny of *X. germanus* and *X. crassiusculus* were the majority of species emerging from chestnut. *Hypothenemus* spp. progeny only emerged in the late spring from galleries in or directly below buds occurring on dead stems. Consequently, it is doubtful that *Hypothenemus* spp. had a significant impact on chestnut growth or survival. Progeny of *X. crassiusculus* and *X. germanus* apparently did not continue attacking chestnut upon emergence in this study, because tree attacks or trap capture did not increase during periods of peak emergence. In other studies, the first generation of *X. germanus* was more damaging than the second generation (Heidenreich 1960; Mizell et al. 1998). Differences in the phenological state of dormant versus actively growing-trees, might explain the absence of attacks by second-generation beetles. Progeny also may disperse soon after emergence. The apparent lack of beetle response to ethanol-baited traps also may relate to differences in beetle behavior during emergence periods.

The development periods of *X. crassiusculus* and *X. germanus* may be similar, because both species required ≈ 55 d from initial gallery formation until first emergence in this study. *Xylosandrus germanus* brood emerged from tree sections after ≈ 60 d in the laboratory (Buchanan 1941), while brood reared on artificial diet at 24.0°C required about 25 d to develop from egg to adult (Kaneko 1965; Weber and McPherson 1983). Mass collections of *X. germanus* progeny from recently attacked elm roots occurred ≈ 28 –35 d later in early- to mid-July and then again in early- to mid-

August (Hoffman 1941). If *X. germanus* had a similar 4–5 wk developmental period in this study, then adult progeny remained in the maternal brood chamber for another 4 wk. Development time of *Xylosandrus crassiusculus* varied from ≈ 30 –40 d in Florida to 20–120 d in South Carolina (Mizell et al. 1998), which is consistent with this study. The extended progeny emergence in this study for both *X. crassiusculus* and *X. germanus* may be explained by continuous maternal oviposition. All life stages of *X. germanus* are commonly found together from June to September, because the female oviposits over a 3-wk period (Hoffman 1941). On diet, *X. germanus* oviposited for ≈ 26 d (Weber and McPherson 1983). *Xylosandrus crassiusculus* had about three times more progeny emerging than *X. germanus* during the first two emergence events, suggesting egg lay by *X. crassiusculus* occurred over a shorter period.

The maximum progeny number from a single gallery in chestnut was 59 *X. crassiusculus* (mean = 9.9) and 18 *X. germanus* (mean = 4.4) beetles, which may be considered low relative to other tree species (Hoffman 1941; Weber 1982; Weber and McPherson 1983; Mizell et al. 1994). *Xylosandrus crassiusculus*, *X. germanus*, and *X. saxeseni* each have a primary species of ambrosia fungus, which includes *Ambrosiella* spp. (close to *A. xylebori*), *Ambrosiella hartigii* Batra, and *Ambrosiella sulphurea* Batra, respectively (Batra 1967; Weber 1978; Roeper 1996). In addition, *Xylosandrus crassiusculus* and *X. germanus* commonly are associated with *Fusarium* fungi (Kessler 1974; Weber 1978; Weber and McPherson 1984; Kovach 1986; Davis and Dute 1995). The growth requirements for these different species of fungi might vary with moisture and substrate quality of different tree species. A low progeny average for *X. crassiusculus* and *X. germanus* on chestnut may indicate this host is less suitable than other reported hosts.

Some characteristics of gallery entrances were associated with certain species of ambrosia beetle. *Xylosandrus crassiusculus* and *X. germanus* mainly attacked chestnut near the base of the main trunk (0–29 cm), while *Hypothenemus* spp. emerged from galleries on apical branches. Toothpick-like strands of sawdust and beetle excrement emanating from galleries have been associated with *X. crassiusculus* in numerous studies (Atkinson et al. 1988b; Mizell et al. 1994, 1998; Davis and Dute 1995; Baker 1999; Hudson and Mizell 1999; Schultz and Whitaker 1999). In this study, these strands also were associated with galleries that produced *X. crassiusculus*, *X. germanus*, and *X. saxeseni* progeny. *Xylosandrus germanus* has been reported to produce the toothpick-like strands in other studies (Hoffman 1941; Weber and McPherson 1983). *Xyleborinus saxeseni* may not have produced the strands because it also emerged from galleries producing *X. germanus*.

Three unusual observations were made during this study. First, mixed-species were observed emerging from single galleries, which has not been previously reported. Some scolytid species are reported to share galleries with members of their own species, to evict

other scolytids from their galleries (e.g., *Sampsonius* spp.), to have galleries that cross in the tree, or to construct galleries from the entrance/exit holes of other species (Wood 1982, Macias-Samano and Borden 2000). Four of the five galleries with mixed species emergence occurred on the same tree and were all within a height of 2.6–10 cm from the ground. The proximity of these four galleries could indicate that some galleries connected within the tree.

Secondly, male *X. crassiusculus* and *X. germanus* occasionally exited galleries in this study (6.5% of total collections). In contrast, most reports indicate male Xyleborini never (or rarely) leave the maternal brood chamber (Hoffman 1941; Bright 1968, 1976; Schneider and Farrier 1969; Weber 1982; Wood 1982; Atkinson et al. 1988b; Davis and Dute 1995; Baker 1999). Dead male *X. saxeseni* frequently were ejected from galleries by emerging female brood (Kovach 1986). In this study, most *X. crassiusculus* and *X. germanus* males were found live in the cages, but emerging females may have forcibly ejected live males.

Finally, emergence of ambrosia beetles continued into the following spring with progeny collected from five galleries during February, March, April, and May of 2000. It is not known whether beetles emerging in 2000 were F₁ progeny that overwintered in the gallery or were from an F₂ generation produced in the original maternal gallery. Female progeny of *X. germanus* sometimes overwinter in older galleries (Hoffman 1941). Xyleborini (i.e., *Xyleborus* and *Xylosandrus*) ambrosia beetles can produce successive generations in the same host if moisture is adequate for fungal growth (Bright 1968; 1976). No *X. crassiusculus* were collected in 2000 from galleries made during 1999. However, one of the galleries with a *X. germanus* female emerging during the spring of 2000, had only *X. crassiusculus* emergence in 1999. *Xylosandrus crassiusculus* progeny may not overwinter in the same maternal brood chamber, or it was not detected in this study.

In conclusion, *X. crassiusculus* and *X. germanus* were the major species attacking chestnut in middle Tennessee. However, *X. crassiusculus* and *X. saxeseni* were the most common species collected in traps, while *X. germanus* was poorly represented. Timing of peak trap captures in the spring and fall coincided with attacks on chestnut, but not during early summer. Therefore, it is concluded that initial spring collections of ambrosia beetles are probably the most critical indicator for risk of tree damage to chestnut. In the case of *X. germanus*, presence of this species in a trap, and not its overall abundance, may be a more important determinant of potential tree attack. Study trees were not equally attacked. This phenomenon of sporadic attacks within individual nurseries has been reported elsewhere (Kessler 1974; Hall et al. 1982; Mizell et al. 1998). A large number of factors affect tree susceptibility, including tree vigor, tree age and size, presence of disease, genetics of seed stock, timing of bud break, unfavorable weather (e.g., late frost, drought), previous insect attack, shipment of trees to new regions, breeding habitat that favors large beetle populations (e.g., fallen branches), type of dominant vegetation in

the area, and site conditions (e.g., shading, soil fertility, and humidity) (Hall et al. 1982; Weber 1978; 1982; Kovach 1986; Mizell et al. 1998; Baker 1999). Regarding the previous list, an important future step in ambrosia beetle management will be to develop a clear understanding of how these factors affect tree susceptibility, interrelate, and can be modified to reduce tree susceptibility.

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