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Seasonal and spatial dispersal patterns of select ambrosia beetles (Coleoptera: Curculionidae) from forest habitats into production nurseries

Christopher T. Werle^{1*}, Juang-Horng Chong², Blair J. Sampson¹, Michael E. Reding³, and John J. Adamczyk¹

Abstract

Exotic ambrosia beetles (Coleoptera: Curculionidae) are important pests of ornamental tree nurseries. Although these beetles reportedly disperse in early spring from peripheral forested areas into nurseries, few studies have determined how far they fly to infest new host trees, or whether a mass-trapping strategy can adequately protect a nursery crop. Field monitoring with ethanol baits in South Carolina (2011–2012), Mississippi (2013–2014), and Louisiana (2013–2014), USA, determined the timing of peak ambrosia beetle flights, dispersal distance, and optimal trap location. In addition to the well-documented spring flight peak, southeastern nursery managers may need to be aware of a second, late-summer flight. Captures from traps placed in a nursery at various distances (–25 to 200 m) from the forest–nursery interface showed a significant linear and quadratic trend in decreasing numbers of beetles captured with increasing distance from the forest in South Carolina, whereas significant linear, quadratic, and cubic trends were detected in Louisiana and Mississippi. Although captures at the nursery edge were lower than within the forest, traps placed at the nursery edge may still represent the optimal tool for both monitoring and mass-trapping programs because of easier access for personnel. Susceptible tree cultivars may gain added protection when placed deeper within nursery interiors and when baited traps line adjacent nursery edges.

Key Words: push-pull; volatile; IPM; population ecology; Xyleborina; trap

Resumen

Escarabajos ambrosia exóticos (Coleoptera: Curculionidae) son plagas importantes en viveros de árboles ornamentales. Aunque se indica que estos escarabajos se dispersan a principios de la primavera de la área periferia del bosque a los viveros, pocos estudios han determinado hasta dónde vuelan para infestar nuevos árboles hospederos, o si una estrategia masiva que atrapen los escarabajos pueda proteger adecuadamente las plantas del vivero. El monitoreo de campo con cebos de etanol en los estados de Carolina del Sur (2011–2012), Mississippi (2013–2014) y Louisiana (2013–2014) determinó el pico del tiempo de vuelo de los escarabajos ambrosia, la distancia de dispersión, y la ubicación óptima para las trampas. Además de tener el pico de vuelo de la primavera bien documentado, los gerentes de los viveros del sur-este deben de estar alertas de un segundo vuelo, a finales del verano. La captura de trampas colocadas en un vivero a diferentes distancias (–25 hasta 200 m) desde la interfaz del bosque-vivero mostró una tendencia lineal significativa y cuadrática en la disminución del número de escarabajos capturados al incrementar la distancia desde el bosque en Carolina del Sur, mientras se detectaron tendencias significativas lineales, cuadráticas y cúbicas en Louisiana y Mississippi. Aunque las capturas en el borde del vivero fueron menores que en el bosque, las trampas colocadas la periferia del vivero siempre pueden representar la herramienta óptima para los programas de monitoreo y de captura masiva debido a un acceso más fácil por partre del personal. Los cultivares de árboles susceptibles pueden obtener mayor protección cuando se colocan más profundo dentro del interior del vivero y cuando trampas cebadas se alinean a los bordes adyacentes del vivero.

Palabras Clave: empujar-halar; volátil; IPM; ecología de la población; Xyleborina; trampa

Exotic ambrosia beetles, particularly *Xylosandrus crassiusculus* (Motschulsky), *Xylosandrus germanus* (Blandford), *Xylosandrus compactus* (Eichhoff), and *Cnestus mutilatus* (Blandford) (Coleoptera: Curculionidae), have been important tree pests in the southeastern United States at nurseries and in landscapes for decades. These species have gained prominence in recent years due to their wide host range, frequency of attacks, and difficulty of control (Mizell et al. 1994; Oliver & Mannion 2001; Fulcher et al. 2012). Foundress beetles tunnel into trees and inoculate their brood gallery with a symbiotic fungus, which is then consumed by adults and larvae (Biedermann & Taborsky 2011). These

primary fungal symbionts, as well as secondary fungal pathogens, contribute to host plant mortality (Weber & McPherson 1984; Kuhnholz et al. 2001). Larval development of ambrosia beetles is completed within the gallery, and newly-eclosed, mated females disperse to new tree hosts (Weber & McPherson 1984). Although ambrosia beetles invading ornamental nurseries were presumed to originate from peripheral forested areas, few studies have fully investigated invasion source.

Standard management recommendations for ambrosia beetles include using ethanol lures to monitor adult flight in early spring, followed by applications of pyrethroid insecticides every 3 to 4 wk after

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the first beetle flights are detected (Hudson & Mizell 1999; Ranger et al. 2010, 2012; Reding et al. 2010, 2011). Prior studies describe an early spring population peak followed by a summer decline, and possibly a second, late summer peak for southern populations (Hudson & Mizell 1999; Oliver & Mannion 2001; Reding et al. 2010; Werle et al. 2012).

In natural environments, the directed flight of ambrosia beetles occurs within forests where wind speed is relatively low, particularly close to the ground where most beetle flight occurs (Browne 1961; Reding et al. 2011). However, within large open nurseries, where fewer windbreaks exist, higher wind speeds make directed flight significantly more difficult for small beetles (Pasek 1988). In a mark-recapture study, the striped ambrosia beetle, Trypodendron lineatum (Olivier) (Coleoptera: Curculionidae), which is a coniferous forest tree pest in the western United States, only exhibited non-directed flight for distances of 100 m or more, whereas recaptures at 500 m were primarily downwind of the release point (Salom & McLean 1989). Mean dispersal distances of marked lesser grain borers, Rhyzopertha dominica (F.) (Coleoptera: Bostrichidae), were significantly longer in wooded sites as compared with open sites (Mahroof et al. 2010). Similarly, T. lineatum was recaptured in significantly higher numbers from baited traps in forested as opposed to open settings, likely due to wind speeds roughly 4 times higher in the open settings (Salom & McLean 1991). Further knowledge of ambrosia beetle dispersal patterns may augment available cultural measures; for example, there may be a distance from the forest edge beyond which ambrosia beetles are unlikely to fly and attack trees. In large nurseries encompassing at least 50 hectares, we hypothesize that locating susceptible cultivars at the interior may provide added protection from ambrosia beetle attack.

Mass trapping is a technique that has been used successfully to suppress or even eradicate incipient populations of invasive insects at their advancing front (Brockerhoff et al. 2010). Even for established populations, mass trapping can offer cost-effective control when an attractant is perceived by a high proportion of the target insects and has a stronger pull than its ambient source (i.e., stressed trees), when traps collect insects throughout the dispersal period, and when traps, lures, and labor are cost effective (El-Sayed et al. 2006). Traps used in conventional ambrosia beetle monitoring programs meet all of these criteria; therefore, by capturing and killing a large proportion of dispersing females, mass trapping could be used as a population management tactic. In some cases, mass trapping can become a stand-alone control measure, but mass trapping also can be effective when combined with a delayed or reduced insecticide application (Huber et al. 1979). In a long-term study in commercial forests, mass trapping of several western ambrosia beetles (T. lineatum, Gnathotrichus sulcatus [LeConte], and Gnathotrichus retusus [LeConte]) yielded a benefit/cost estimate of five-to-one with associated savings of over US\$500,000 (Lindgren & Fraser 1994). Trap position may play an important role in trapping efficacy, because traps placed 15 to 25 m inside the forest captured significantly more ambrosia beetles than did traps placed at the forest margin (Lindgren et al. 1983).

Because ambrosia beetle population monitoring is important for properly-timed insecticide applications, for choosing the best location within a nursery for tree crops, and for the development of a push-pull management strategy, study objectives included: 1) determining the source and timing of ambrosia beetle flights; 2) estimating dispersal distances into ornamental nurseries; and 3) identifying the best location for trap placement based on capture rate and convenience.

Materials and Methods

EXPERIMENTAL LOCATIONS

Four commercial nurseries were used as research sites, including Tangipahoa Parish (30°47'30.39"N, 90°20'37.91"W), Louisiana (LA);

Stone County ($30^{\circ}47'59.92''N$, $89^{\circ}15'21.64''W$), Mississippi (MS); Georgetown County ($33^{\circ}14'40.78''N$, $79^{\circ}22'52.80''W$), South Carolina (SC); and Pickens County ($34^{\circ}45'50.34''N$, $82^{\circ}39'47.75''W$), SC. All nurseries were large (> 60 ha) open landscapes with diverse arrays of containerized crops and greenhouses (Tangipahoa Parish, Stone County, and Georgetown County sites) and field-grown ornamental trees (Pickens County site). The LS site was surrounded by a combination of managed pine and natural mixed hardwood stands on 3 sides, with a road and residential area on the 4th. The pine stand at the LA site was subjected to a prescribed burn during our study in Feb 2014. The MS site was bordered by managed pine forest on 2 sides, a barren sand/

gravel pit on the 3rd side, and a road with residential areas on the 4th. The pine stand at the MS site last received a prescribed burn in 2011. The 2 SC sites were surrounded by pine-hardwood mix on all 4 sides and had not been burned within 5 yr of the experiment.

TRAPPING METHOD

Baker traps were constructed using 2 recycled soda bottles attached with a Tornado Tube (Steve Spangler Science, Englewood, Colorado, USA) (Oliver et al. 2004; Ranger et al. 2010; Reding et al. 2011). The upper 2 L bottle had 3 rectangular openings (length 15 cm, width 6 cm) in the sides to allow beetle entry, whereas the lower 592 mL bottle was partially filled with propylene glycol to kill and preserve insects. Traps were baited with a slow-release (65 mg/d at 25 °C) ethanol lures (AgBio, Westminster, Colorado, USA) and suspended about 1 m above the ground with Japanese beetle trap stands (Tanglefoot, Grand Rapids, Michigan, USA) (LA and MS sites) or stands constructed of lumber and metal shelf support brackets (SC sites). The experimental design was randomized complete block. Treatments tested were traps placed at distances into the nursery from the edge of: -25, 25, 50, 100, and 200 m (LA and MS sites in 2013), or -13, 0, 13, 25, 50, and 100 m (SC sites in 2011 and 2012; LA and MS sites in 2014) (Fig. 1). Each treatment was a trap placed within its own row at a randomly assigned distance, with rows separated laterally from neighbors by 20 m (SC sites) or 25 m (LA and MS sites) to lessen the interference from adjacent treatments within the block. The number of blocks at each site was limited by nursery size and number of treatments tested. In 2013, each site held 5 blocks with 5 distance treatments in each for 25 traps in total, whereas in 2011, 2012, and 2014, there were 4 blocks with 6 treatments each for 24 traps in total. Research plots also were separated from the lateral and distal nursery edges by at least 200 m (LA and MS sites in 2013) or 100 m (SC sites in 2011 and 2012, LA and MS sites in 2014).

Traps were deployed in the spring with samples collected every 2 wk, and lures were replaced every 8 wk. Collections were made 1 Apr to 16 Dec 2011, 13 Jan to 28 Dec 2012, 22 Apr to 26 Aug 2013, and 21 Feb to 23 Oct 2014. The Scolytinae collected from individual traps were brought back to the laboratory for abundance and species determination using standard keys (Rabaglia et al. 2006).

STATISTICAL ANALYSES

Data from each collection year and site were analyzed separately because of variation in experimental design among the research sites and years. The effects of trap distance and collection time period were analyzed for the pooled numbers of *C. mutilatus, X. compactus, X. crassiusculus,* and *X. germanus* because these are the major pestiferous ambrosia beetle species in ornamental tree nurseries. Other ambrosia beetles captured were identified to species and counted but not used in the analyses. Mean captures of the 4 target species per trap per 2 wk sampling period were analyzed using repeated measures analysis of variance (ANOVA), with distance and collection time period



Fig. 1. Satellite image of the Mississippi research site (Google, Mountain View, California, USA) with an overlay showing a randomized complete block design of 5 blocks. Representing the 2013 test, each block shown here had a trap placed at –25, 25, 50, 100, and 200 m from the nursery–forest interface.

as factors (PROC MIXED, SAS Institute 2011). A first-order autoregressive covariance structure was included in the repeated measures statement. A trend analysis using polynomial contrasts was conducted to properly interpret significant distance effects. Because the distances were unequally spaced, a coefficient matrix for orthogonal contrasts was generated using PROC IML (SAS Institute 2011). The coefficient matrix was then used in contrast statements in PROC GLM to detect significant linear, quadratic, and cubic trends (SAS Institute 2011).

Results

Including all other non-target ambrosia beetle species, 2,345 and 1,961 specimens were collected from the Georgetown County (SC) and Pickens County (SC) sites, respectively, from 2011 to 2012, whereas 1,671 and 1,702 specimens were collected from the Tangipahoa Parish (LA) and Stone County (MS) sites, respectively, from 2013 to 2014. Ten, 11, 11, and 13 ambrosia beetle species were captured in ornamental tree nurseries located in Stone County, Tangipahoa Parish, Georgetown County, and Pickens County, respectively (Table 1). When pooled together, the 4 target species (*C. mutilatus, X. compactus, X. crassiusculus,* and *X. germanus*) composed 86.4% (Tangipahoa Parish, LA), 91.7% (Stone County, MS), 69.6% (Georgetown County, SC), and 63.7% (Pickens County, SC) of the total ambrosia beetles collected over 2 yr. *Xylosandrus crassiusculus* was consistently one of the most abundant species at all research sites. Similar to findings from other regional studies, *X. germanus* was not recovered from nurseries located in Stone County and Tangipahoa Parish, whereas *C. mutilatus* was not collected from the nursery located in Georgetown County, SC (Werle et al. 2012, 2014).

The numbers of ambrosia beetles captured biweekly were significantly different (P < 0.05) among distances from the nursery edges and sampling times at all nurseries and in all years (Table 2). The 2-way interactions between distances and sampling times also were significant for all nurseries and years (Table 2).

Ambrosia beetles of the 4 target species were active from Mar to Nov at all sampled nurseries (Figs. 2 and 3). Populations in LA and MS did not appear to begin flight activities earlier than the more northerly populations in SC. In the 1st years of this research in LA (2013), MS (2013), and SC (2011), the sampling efforts began too late to detect the initiation of spring flight. In the 2nd years, we detected the initiation of spring flight in late Feb (at LA and Georgetown County [SC] sites) to early Mar (at MS and Pickens County [SC] sites), which quickly developed into peaks in late Mar in SC (Fig. 2) and early Apr in LA and MS (Fig. 3). At nurseries in SC, the numbers of ambrosia beetles slowly declined with a 2nd peak in May–Jun (Fig. 2). Following a summer decline at nurseries in LA and MS, a 2nd surge in ambrosia beetle captures was detected beginning in late Jul 2013, and at the LA nursery in 2014 (Fig. 3), indicating the possible emergence of a 2nd generation.

Across sampling dates, trap distance from the nursery edge had a significant influence on the numbers of ambrosia beetles captured at all nurseries (Table 2). Trend analysis of the distance effect for ambrosia beetles showed significant linear and quadratic trends (P < 0.05) for nurseries located in SC (both years) and the nursery in MS (2014)

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 Table 1. Species composition of ambrosia beetles (Coleoptera: Curculionidae) captured in ethanol-baited Baker traps at ornamental tree nurseries in Louisiana (LA; 2013–2014), Mississippi (MS; 2013–2014), and South Carolina (SC; 2011–2012).

	% total specimens					
Species	Tangipahoa Parish, LA	Stone County, MS	Georgetown County, SC	Pickens County, SC		
Ambrosiodmus obliquus (LeConte)	_	_	0.3	0.1		
Ambrosiodmus rubricollis (Eichhoff)	0.3	0.2	0.6	0.3		
Ambrosiodmus tachygraphus (Zimmermann)	_	_	_	< 0.1		
Ambrosiophilus atratus (Eichhoff)	< 0.1	_	—	< 0.1		
Cnestus mutilatus (Blandford)	1.3	0.6	_	1.7		
Cyclorhipidion bodoanum (Reitter)	_	_	< 0.1	_		
Dryoxylon onoharaensis (Murayama)	0.5	0.2	0.9	0.8		
Euwallacea validus (Eichhoff)	0.6	0.5	_	_		
Xyleborinus octiesdentatus (Murayama)	_	0.2	—	_		
Xyleborinus saxesenii (Ratzeburg)	8.5	2.2	14.4	29.5		
Xyleborus affinis Eichhoff	1.6	3.0	0.6	0.5		
Xyleborus celsus Eichhoff	0.1	_	_	_		
Xyleborus ferrugineus (F.)	1.9	2.0	0.4	0.3		
Xyleborus pubescens Zimmermann	_	_	13.1	4.7		
Xylosandrus compactus (Eichhoff)	13.9	18.3	0.4	0.2		
Xylosandrus crassiusculus (Motschulsky)	71.2	72.8	69.1	58.5		
Xylosandrus germanus (Blandford)	_	_	< 0.1	3.3		

only) (Table 3). The numbers of beetles captured were greatest at -13 m inside the forest, decreasing sharply at 0 and 13 m into the nursery (Fig. 4). The numbers declined further but at a slower rate or remained similar from 25 to 100 m in SC (Fig. 4) or 13 to 100 m in MS (2014; Fig. 5). The distance effect showed significant linear, quadratic, and cubic trends for the numbers of ambrosia beetles captured at nurseries in LA (2013 and 2014) and MS (2013 only) (Table 3). Similar to nurseries in SC, the greatest numbers of ambrosia beetles were captured at -13 or -25 m inside the forest at the sites in LA and MS (Fig. 5). However, at these sites, the numbers captured from 0 to 200 m fluctuated, with the

numbers captured at greater distances occasionally higher than those at shorter distances (Fig. 5).

Discussion

Ambrosia beetle trap capture peaks at nurseries in the southeastern United States were recorded from Mar through Apr, and again in SC from May to Jun and in LA and MS from late Jul through Aug. The timing of the 2nd peak flight in SC agrees with the observations of a May–Jun

Table 2. Statistics of repeated measure ANOVA for effects of distance from nursery edge and collection time period on the numbers of *Cnestus mutilatus, Xylos*andrus compactus, X. crassiusculus, and X germanus captured per trap per 2 wk sampling period at ornamental tree nurseries in Louisiana (LA), Mississippi (MS), and South Carolina (SC).

	Georgetown County, SC (2011)			Georgetown County, SC (2012)			
Effect	df	F	<i>P</i> > <i>F</i>	df	F	<i>P</i> > <i>F</i>	
Distance	5, 18	15.91	< 0.0001	5, 18	9.46	0.0001	
Time	16, 288	11.22	< 0.0001	24, 432	11.42	< 0.0001	
Distance × time	80, 288	2.02	< 0.0001	120, 432	2.13	< 0.0001	
	Pickens County, SC (2011)			Pickens County, SC (2012)			
	df	F	P > F	df	F	P > F	
Distance	5, 18	27.27	< 0.0001	5, 18	31.18	< 0.0001	
Time	18, 324	14.06	< 0.0001	22, 396	18.54	< 0.0001	
Distance × time	90, 324	1.91	< 0.0001	110, 396	2.57	< 0.0001	
	Stone County, MS (2013)		Stone County, MS (2014)				
	df	F	P > F	df	F	<i>P</i> > <i>F</i>	
Distance	4, 20	14.43	< 0.0001	5, 18	4.23	0.0101	
Time	10, 200	2.84	0.0025	17, 306	8.02	< 0.0001	
Distance × time	40, 200	1.71	0.0093	85, 306	1.54	0.0043	
	Tangipahoa Parish, LA (2013)			Tangipahoa Parish, LA (2014)			
	df	F	P > F	df	F	P > F	
Distance	4, 20	5.75	0.0030	5, 18	10.57	< 0.0001	
Time	10, 200	3.64	0.0002	17, 306	5.48	< 0.0001	
Distance × time	40, 200	2.42	< 0.0001	85, 306	1.40	0.0214	

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Fig. 2. Mean captures of *Cnestus mutilatus, Xylosandrus compactus, X. crassiusculus,* and *X. germanus* in ethanol-baited Baker traps at 2 sites in South Carolina in 2011 and 2012.

Fig. 3. Mean captures of *Cnestus mutilatus, Xylosandrus compactus, X. crassiusculus,* and *X. germanus* in ethanol-baited Baker traps at 2 sites in Louisiana and Mississippi in 2013 and 2014.

Table 3. Results of trend analysis for effects of distance from nursery edge on the numbers of *Cnestus mutilatus, Xylosandrus compactus, X. crassiusculus,* and *X. germanus* captured at ornamental tree nurseries in Louisiana (LA), Mississippi (MS), and South Carolina (SC).

Contrast	Georgetown County, SC (2011)			Georgetown County, SC (2012)			
	df	F	<i>P</i> > <i>F</i>	df	F	P > F	
Linear	1	28.91	< 0.0001	1	16.21	< 0.0001	
Quadratic	1	6.71	0.0099	1	8.66	0.0034	
Cubic	1	0.00	0.9904	1	0.06	0.8076	
	Pickens County, SC (2011)			Pickens County, SC (2012)			
	df	F	<i>P</i> > <i>F</i>	df	F	P > F	
Linear	1	59.23	< 0.0001	1	43.03	< 0.0001	
Quadratic	1	26.79	< 0.0001	1	21.27	< 0.0001	
Cubic	1	2.47	0.1164	1	2.58	0.1088	
	Stone County, MS (2013)			Stone County, MS (2014)			
	df	F	<i>P</i> > <i>F</i>	df	F	P > F	
Linear	1	59.78	< 0.0001	1	20.08	< 0.0001	
Quadratic	1	26.55	< 0.0001	1	10.98	0.0010	
Cubic	1	12.18	0.0006	1	0.50	0.4793	
	Tangipahoa Parish, LA (2013)			Tangipahoa Parish, LA (2014)			
	df	F	<i>P</i> > <i>F</i>	df	F	P > F	
Linear	1	53.04	< 0.0001	1	9.44	0.0023	
Quadratic	1	65.70	< 0.0001	1	38.69	< 0.0001	
Cubic	1	17.35	< 0.0001	1	8.40	0.0040	



Fig. 4. Mean (± SE) captures of *Cnestus mutilatus, Xylosandrus compactus, X. cra`ssiusculus,* and *X. germanus* in ethanol-baited Baker traps deployed at various distances from the nursery–forest interface at 2 sites in South Carolina in 2011 and 2012.

emergence of *X. crassiusculus* and May–Jul emergence of *X. germanus* in middle Tennessee (Oliver & Mannion 2001). Our documentation of this 2nd peak in ambrosia beetle activity should help southern nursery managers to more accurately monitor populations and alter management strategies accordingly. It may be best for nursery managers to operate a trapping program throughout the spring and summer months as verification of peak flight activity, and potentially as a mass-trapping strategy. Tree crops exposed to the abiotic stress of late summer heat can experience a variety of symptoms including inhibition of growth, reduction in ion flux, and production of reactive oxygen species (Wahid et al. 2007), which may increase vulnerability to attack by a 2nd generation of dispersing females.

Each nursery site had a unique ambrosia beetle community (Table 1), likely influenced by the surrounding natural plant communities that serve as hosts. Plant communities are in turn shaped by soil and landscape features and by micro-climactic conditions (Ohmann & Spies 1998). Although study site differences were likely due in part to natural habitat variability, there also were different forest and nursery management practices at the sites. With no recent prescribed burns at the MS and SC sites, fire-sensitive species including cherry (*Prunus serotina* Ehrh.; Rosales: Rosaceae), sweetgum (*Liquidambar styraciflua* L.; Saxifragales: Altingiaceae), redbud (*Cercis canadensis* L.; Fabales: Fabaceae), and sweetbay magnolia (*Magnolia virginiana* L.; Magnoliales: Magnoliaceae), all known hosts of ambrosia beetles, were able to proliferate in adjacent forests (Mizell et al. 1994). However, at the LA site, a prescribed burn in Feb 2014 occurred before the start of our 2nd year of data collection. This prescribed burn destroyed much of the hardwood undergrowth at the LA site, and with it possibly many of the overwintering ambrosia beetles, contributing to a relatively low spring peak at this site (Fig. 4). Superficially, it may appear that properly timed prescribed fires, by lowering ambrosia beetle population size in surrounding forests, could reduce infestations within nurseries. However, due to greater tree stress, areas subjected to prescribed burns can experience an increase in populations of Xyleborina in subsequent years, and any nursery benefit gained from a fire-induced reduction in ambrosia beetle populations may be temporary (Sullivan et al. 2003; Campbell et al. 2008).

Nursery management practices also can be highly variable, contributing further to study site differences. In 2014, a large block of > 100 containerized redbud trees located between 13 and 50 m from the edge of the MS nursery was colonized by a pathogenic fungus (*Fusarium lateritium* Nees; Hypocreales: Nectriaceae), as well as a substantial ambrosia beetle population. After the trees were cut in Jun and brought back to the laboratory for examination, over 3.5 beetle galleries on average were observed per tree, and > 200 specimens of adult Xyleborina were collected. These trees contained a significant portion of the future reproductive capacity of the ambrosia beetles within that area, and when the trees were removed before a 2nd gen-



Fig. 5. Mean (± SE) captures of *Cnestus mutilatus, Xylosandrus compactus, X. crassiusculus,* and *X. germanus* in ethanol-baited Baker traps deployed at various distances from the nursery–forest interface at 2 sites in Louisiana and Mississippi in 2013 and 2014.

eration could emerge, trap capture data may have been impacted in terms of both trap distance and capture date variables (Figs. 2 and 4). Without the removal of these beetle-infested redbuds, it is possible we might have had experienced a more pronounced late summer peak at the MS site in 2014, as well as additional trap captures at or near the forest interface.

A linear and quadratic trend for trap captures could be observed with increasing distance from the nursery edge at nurseries in SC (2011 and 2012) and MS (2014) (Figs. 4 and 5). Although fewer beetles were captured by traps placed at the nursery edge (0 m) compared with traps within the forest (-13 and -25 m), edge placement was more convenient and easily accessible. When compared with all other traps within the nursery interior (13, 25, 50, 100, and 200 m), the traps at the nursery edge (0 m) did capture more beetles, supporting our hypothesis that the source of the ambrosia beetle population was within the peripheral forested areas as opposed to within the nursery. The effectiveness of the edge traps, combined with the benefit of avoiding daily operations within the nursery and the natural obstacles within the forest, would suggest that the optimal trap location would be at the nursery–forest interface.

The effects of weather patterns would certainly play a role in the beetles' detection of ethanol, as well as their ability to fly. A related curculionid species, *Trypodendron lineatum* (Olivier), was able to com-

plete upwind oriented flights to baited traps at distances of up to 25 m, but beyond this distance the flights were largely downwind and undirected (Salom & McLean 1989). Similarly, study results support that with increasing distance into the nursery interior, and away from ambrosia beetle source populations, susceptible nursery stock may be subjected to less beetle pressure. The effect of prevailing winds may play an important role, as beetles attracted to volatile emissions may not detect stressed trees that are placed downwind, or conversely may find upwind flight more strenuous (Salom & McLean 1989; Ranger et al. 2015).

The use of a perimeter trapping program may augment the protection offered to nursery trees located at a greater distance from the nursery edge. Significantly more *T. lineatum* were captured in traps placed 100 m from the forest edge when intermediate traps at 5 or 25 m were not present (Salom & McLean 1989). Therefore, a ring of baited traps at the forest–nursery interface may protect tree crops, as the availability of more proximal perimeter traps would likely intercept dispersing females from longer-distance flights into the nursery interior. Although traps located as close to the forest as 13 m had significantly lower beetle captures than traps at the edge or within the forest, vulnerable nursery stock may not gain adequate protection from placement at 13 m. At nurseries deploying perimeter traps, placing susceptible cultivars at least 50 m from the nursery edge could help Werle et al.: Dispersal patterns of ambrosia beetles

trees escape ambrosia beetle attacks, based on the low trap captures observed in this study at $^{\rm 3}$ 50 m.

Perimeter trapping can provide advance warning of ambrosia beetle activity and potentially divert large numbers of dispersing females from susceptible tree crops. When combined with cultural measures including maintaining tree vigor and locating vulnerable stock at nursery interiors, and a judicious spray program based on monitoring data from the traps, these cumulative efforts may lead to a highly effective, low-cost management program beneficial to nursery owners nationwide.

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