Ambrosia Beetle (Coleoptera: Scolytidae) Species, Flight, and Attack on Living Eastern Cottonwood Trees

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ABSTRACT In spring 2002, ambrosia beetles (Coleoptera: Scolytidae) infested an intensively managed 22-ha tree plantation on the upper coastal plain of South Carolina. Nearly 3,500 scolytids representing 28 species were captured in ethanol-baited traps from 18 June 2002 to 18 April 2004. More than 88% of total captures were exotic species. Five species [*Dryoxylon onoharaensum* (Murayama), *Euwallacea validus* (Eichhoff), *Pseudopityophthorus minutissimus* (Zimmermann), *Xyleborus atratus* Eichhoff, and *Xyleborus impressus* Eichhoff]) were collected in South Carolina for the first time. Of four tree species in the plantation, eastern cottonwood, *Populus deltoides* Bartram, was the only one attacked, with nearly 40% of the trees sustaining ambrosia beetle damage. Clone ST66 sustained more damage than clone S7C15. ST66 trees receiving fertilization were attacked more frequently than trees receiving irrigation, irrigation + fertilization, or controls, although the number of S7C15 trees attacked did not differ among treatments. The study location is near major shipping ports; our results demonstrate the necessity for intensive monitoring programs to determine the arrival, spread, ecology, and impact of exotic scolytids.

KEY WORDS ethanol, fertilization, invasive species, *Populus deltoides*, Xyleborini

NEARLY 50% OF EXTINCT or imperiled species in the United States were caused, in part, by invasive species (Wilcove et al. 1998). Pimentel et al. (2000) suggest that invasive species cost the U.S. economy $138 billion annually. There are >400 invasive insect species in U.S. forests, encompassing a wide range of feeding guilds (Mattson et al. 1994). Bark and ambrosia beetles (Coleoptera: Scolytidae) can be particularly hard to detect because of their cryptic lifestyle and the difficulty in effectively monitoring their populations in remote areas. Several invasive scolytids are of concern because of their unknown damage potential (Atkinson et al. 1988b, Mizell et al. 1994, Bright and Rabaglia 1999, Vandenberg et al. 2000, Haack 2001, Schiefer and Bright 2004). In the absence of effective monitoring, exotic species may persist undetected for many years before discovery (Liebhold et al. 1995, Humble 2003).

Ambrosia beetles, with the exception of a short flight period, spend their entire life within a woody stem (Rudinsky 1962). Native ambrosia beetles generally attack weakened or stressed trees; however, healthy trees are frequently attacked by exotic species (Rudinsky 1962, Wood 1982b, Kühnholz et al. 2001). Damage to sawn lumber can be particularly severe near logging operations, where felled logs serve as an attractant to ambrosia beetles (McLean 1985). Ambrosia beetle infestation of conifer pulp logs resulted in losses of >$77/m^3 of log and reduced value on high-grade logs by 57% (Orbay et al. 1994). In the southeastern United States, healthy peach trees as well as nursery trees and shrubs are at risk to boring and fungal inoculation, particularly by the exotic ambrosia beetle *Xylosandrus crassiusculus* (Motschulsky) (Kovach and Gorsuch 1985, 1988; Mizell et al. 1994).

Intensively managed forest plantations (Stanturf et al. 2001) may have production rates high enough to potentially offset the global increase in demand for wood and wood products (Fenning and Gershenzon 2002, Stanton et al. 2002). *Populus* species and hybrids are especially suited to intensive management because of their rapid growth, ease of propagation, and desirable wood qualities (Dickmann and Stuart 1983). Unfortunately, plantation monocultures make them prone to a suite of pests and diseases (Coyle et al. 2005).

In spring 2002, an ambrosia beetle infestation occurred on apparently healthy eastern cottonwood, *Populus deltoides* Bartram, in an intensively managed plantation in South Carolina. This infestation provided

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Table 1.   Average monthly weather from 18 June 2002 to 18 April 2004 at the Savannah River Site, Aiken, SC

Mo	Temp (°C)	Relative humidity (%)	Wind speed (km h^{-1})	Rainfall (cm)
Jan.	5.4	72.2	2.4	8.8
Feb.	7.4	79.0	3.4	20.6
Mar.	13.9	76.4	3.8	23.5
April	15.5	75.6	3.2	38.1
May	20.9	85.3	2.9	15.2
June	23.5	84.7	2.7	13.2
July	25.7	83.2	2.3	25.9
Aug.	25.1	84.4	2.3	4.6
Sept.	22.5	84.9	2.6	5.8
Oct.	17.6	88.2	1.9	7.7
Nov.	12.2	84.1	2.4	3.3
Dec.	5.9	79.2	2.5	13.6

an opportunity to document the composition and seasonal flight patterns of the local scolytid fauna, critical information for the detection and management of exotic species (Simberloff et al. 2005). We hypothesized that the majority of captured beetles would be exotic species (Kovach and Gorsuch 1985) because ports in South Carolina provide opportunities for exotic scolytids to establish after being imported in ballast or other wood products (Haack 2001).

We also hypothesized ambrosia beetle flight patterns would peak in spring and late summer, as documented previously (Roling and Kearby 1975, Turnbow and Franklin 1980, Atkinson et al. 1988a, Weber and McPherson 1991). Finally, because the incidence and severity of pest damage can differ among *P. deltoides* clones and resource amendment treatments (Coyle 2002, Herms 2002, Huberty and Denno 2004, Coyle et al. 2005), we hypothesized that the incidence of ambrosia beetle attack would differ between two *P. deltoides* clones and would be highest in trees receiving irrigation and fertilization amendments.

Materials and Methods

Experimental Setting. The study took place at the U.S. Department of Energy Savannah River Site, a National Environmental Research Park, near Aiken, SC (33° 23′ N, 81° 40′ W). A detailed description of the plant material, silvicultural treatments, and experimental design can be found in Coleman et al. (2004) and Coyle and Coleman (2005). Before logging in 1999, vegetation included 14-yr-old pulp quality loblolly pine, *Pinus taeda* L., and 38-yr-old pole timber quality longleaf pine, *Pinus palustris* Miller, with an oak, *Quercus* spp., understory; this flora surrounded the site on three sides, with a small town to the north. After logging in 1999, all soil and debris were homogenized to a depth of 30 cm. Temperature, relative humidity, wind speed, and rainfall data (Table 1) were recorded continuously during the study period by a weather station (Campbell Scientific, Inc., Logan UT) installed in a cleared area 50 m west of the site.

In spring 2000, eastern cottonwood; American sycamore, *Platanus occidentalis* L.; sweetgum, *Liquidambar styraciflua* L.; and loblolly pine were planted. Two eastern cottonwood clones (ST66 of Issaquena County, Mississippi, and S7C15 of Brazos County, Texas) were planted as unrooted hardwood cuttings stored at 3°C and soaked in water for 48 h before planting.

Tree genotypes were arranged in a randomized complete block. Each 0.22-ha plot contained 14 rows of 21 trees (total of 294 trees), planted at 2.5 by 3-m spacing. Each of three blocks contained one plot per treatment for each genotype, grouped together to minimize within-site variation. Treatments consisted of control (C), irrigation (I), fertilization (F), and irrigation + fertilization (IF). We applied irrigation treatments (0.5 mm d^{-1}) via an automated system to both I and IF treatments. Liquid fertilizer was applied through the automated system to F and IF treatments at 40, 80, and 120 kg N ha^{-1} yr^{-1} in 2000, 2001, and 2002 (and thereafter), respectively, to correspond with the increasing demand of growing trees.

Weed control treatments included an oxyflourfen (Goal 2XL, Rohm and Haas Co., Philadelphia, PA) application before budbreak, and glyphosate (Roundup Pro, Monsanto Corp., St. Louis, MO) applications as needed throughout the growing season. Dicofol (Kelthane, Rohm and Haas Co.) was applied to control the mite *Tetra lobulifera* Kiefer (Coyle 2002). All pesticides were applied as needed according to label directions.

Beetle Trapping and Identification. Four 12-unit Lindgren multiple funnel traps (Lindgren 1983) were installed in June 2002 on the plantation perimeter with the bottom of the traps 1 m above ground. Traps were baited with ethanol released at 275 mg d^{-1} (L2–2041/500 UHR ethanol lure; Phero Tech, Inc., Delta, British Columbia, Canada) and checked at 7–14-d sampling periods from 18 June 2002 to 18 April 2004. To kill and preserve captured insects, sample cups were filled with a 50:50 mixture of water and propylene glycol. Weeds around the traps were controlled mechanically and were not allowed to obscure the trap. With the exception of two genera, all Scolytidae were identified to species (Wood 1982a, Wood and Bright 1992, Bright and Skidmore 1997). Voucher specimens were deposited in the Clemson University Entomology Museum and the personal collections of R. J. Rabaglia (Maryland Department of Agriculture) and D.R.C.

Beetle Attack. Two *P. deltoides* trees (clone S7C15) were destructively sampled in May 2002. Both had black discoloration on the lower bole, an indication of beetle attack; sap exuded from beetle entrance holes was the primary cause of discoloration. Trees were sampled from border rows in the F and IF treatments. All beetles within the basal 1 m of stem were excised and identified to species.

From 18 to 21 June 2002, we recorded the incidence (presence, 1; absence, 0) of beetle attack on 360 trees in each *P. deltoides* clone. For each *P. deltoides* clone, three rows of 10 trees, bordered by at least two rows of buffer trees, were monitored in each plot (n = 90 trees treatment^{-1}) by using bole discoloration as a presence or absence indicator. Any tree having bole

Table 2. Total number of Scolytidae captured using ethanol-baited lures from 18 June 2002 to 18 April 2004 at the Savannah River Site, Aiken, SC

Exotic	Tribe	Species	2002	2003	2004	Total	% of total
Yes	Xyleborini	*Ambrosiodmus rubricollis* (Eichhoff)	23	33	1	57	1.63
No	Xyleborini	*Ambrosiodmus tachygraphus* (Zimmermann)	0	5	3	8	0.23
No	Bothrosternini	*Cnesinus strigicollis* LeConte	0	0	1	1	0.03
Yes	Dryocoetini	*Dryoxylon onoharaensum* (Murayama)	42	145	7	194	5.55
Yes	Xyleborini	*Euwallacea validus* (Eichhoff)	0	1	0	1	0.03
No	Corthylini	*Gnathotrichus materiarius* (Fitch)	0	1	0	1	0.03
No	Hylesinini	*Hylastes tenuis* Eichhoff	1	2	1	4	0.11
No	Cryphalini	*Hypothenemus* spp.	72	146	34	252	7.21
No	Ipini	*Ips avulsus* (Eichhoff)	3	2	0	5	0.14
No	Ipini	*Ips calligraphus* (Germar)	0	1	0	1	0.03
No	Micracini	*Micracisella nanula* (LeConte)	0	2	0	2	0.06
No	Corthylini	*Monarthrum fasciatum* (Say)	0	10	2	12	0.34
No	Corthylini	*Monarthrum mali* (Fitch)	0	5	6	11	0.31
Yes	Ipini	*Orthotomicus caelatus* (Eichhoff)	1	0	3	4	0.11
No	Ipini	*Pityogenes hopkinsi* Swaine	0	1	0	1	0.03
No	Corthylini	*Pityophthorus* spp.	4	9	0	13	0.37
No	Corthylini	*Pseudopityophthorus minutissimus* (Zimmermann)	2	0	0	2	0.06
No	Corthylini	*Pseudopityophthorus pruinosus* Eichhoff	0	3	0	3	0.09
Yes	Xyleborini	*Xyleborinus saxeseni* (Ratzburg)	674	1,426	150	2,250	64.38
No	Xyleborini	*Xyleborus affinis* Eichhoff	1	6	0	7	0.20
Yes	Xyleborini	*Xyleborus atratus* Eichhoff	0	21	33	54	1.55
Yes	Xyleborini	*Xyleborus californicus* Wood	0	51	11	62	1.77
No	Xyleborini	*Xyleborus ferrugineus* (F.)	7	10	0	17	0.49
No	Xyleborini	*Xyleborus impressus* Eichhoff	18	36	0	54	1.55
No	Xyleborini	*Xyleborus pubescens* Zimmermann	1	9	1	11	0.31
Yes	Xyleborini	*Xylosandrus compactus* (Eichhoff)	0	2	0	2	0.06
Yes	Xyleborini	*Xylosandrus crassiusculus* (Motschulsky)	35	348	82	465	13.30
No	Xyloterini	*Xyloterinus politus* (Say)	0	0	1	1	0.03
		Total	884	2275	336	3,495	

discoloration was considered attacked. Attacks were not found on sycamore, sweetgum, or loblolly pine.

Statistical Analyses. Scolytidae biodiversity, H, was calculated using the Shannon–Weiner diversity index (Shannon 1948, Zar 1999)

$$H = [n \log n - \sum_{i=1}^{k}(f_i \log f_i)]/n,$$

where n is total number of beetles captured, k is total number of species (richness), and f is number of beetles in species i.

Evenness, J, was calculated as the ratio of H to H_{max} (H_{max} being the theoretical maximum possible diversity for a set of data with k categories; Pielou 1966, Zar 1999), where $H_{max} = \log k$.

H and J were calculated for beetles captured in this study and other southeastern United States studies (Turnbow and Franklin 1980, Atkinson et al. 1988a, Weber and McPherson 1991, Oliver and Mannion 2001, Grant et al. 2003) with which we compared our data.

To account for slight variations in our sampling periods and the occasional loss of a funnel trap because of wind, trap captures were standardized as number of beetles trap^{-1} d^{-1} over each sampling period. Attack incidence (the proportion of trees attacked) between *P. deltoides* clones was analyzed using Fisher's exact test for dichotomous data (Simple Interactive Statistical Analysis Software, Hilversum, The Netherlands). Mean separations among attack incidence in the four silvicultural treatments within clones were performed using the Tukey-type multiple comparison test among proportions (Zar 1999). In all cases, $\alpha = 0.05$.

Results

Species Composition. We captured 3,495 scolytids, mostly tribe Xyleborini, over 94 wk (Table 2). Seven of the 28 species were captured every year. Nine exotic species made up >88% of the total specimens collected. *Xyleborinus saxeseni* (Ratzburg) accounted for >64% of total trap captures alone (Table 2). *X. saxeseni*, *X. crassiusculus*, and *Hypothenemus* spp. accounted for nearly 85% of all specimens collected. Twenty species were represented by <20 individuals (Table 2). Diversity was calculated as 0.59, and evenness was 0.41 (Table 3). *Dryoxylon onoharaensum* (Murayama), *Euwallacea validus* (Eichhoff), *Pseudopityophthorus minutissimus* (Zimmermann), *Xyleborus atratus* Eichhoff, and *Xyleborus impressus* Eichhoff represented new records for South Carolina.

Flight Patterns. Beetle flight was fairly constant from late June through November 2002 (Fig. 1A). Noticeable decreases in flight occurred when temperatures or humidity were unusually high. The decreases in flight activity in mid-August and mid-September 2003 corresponded to mean temperatures >28°C and relative humidity >94%, respectively. Activity ceased from late November 2002 until the end of January 2003, when beetles occurred in very small numbers (<0.04 beetles trap^{-1} d^{-1}). Beginning in late February 2003, flight activity began to increase steadily (Fig.

Table 3. Number of Scolytidae captured and diversity indices compared with other published studies in the southeastern United States

Species	SC[a]	FL[b]	GA[c]	NC[d]	TN[e]	TN[f]
Ambrosiodmus devexulus (Wood)		16				
Ambrosiodmus lecontii Hopkins		37				
Ambrosiodmus obliquus (LeConte)						1
Ambrosiodmus rubricollis (Eichhoff)	57				82	1
Ambrosiodmus tachygraphus (Zimmermann)	8	1	83	16	110	13
Carphoborus bifurcus (Eichhoff)		3		1		
Chramesus hicoriae LeConte			1	1		
Cnesinus strigicollis LeConte	1	3	17			
Conophthorus resinosae Hopkins				68		
Corthylus columbianus Hopkins			26		11	
Corthylus punctatissimus (Zimmermann)		3				
Corthylus spinifer Schwartz		26				
Cryptocarenus seriatus Eggers		31				
Crypturgus alutaceus Schwartz		14	170			
Dendroctonus frontalis Zimmermann			136			
Dendroctonus terebrans (Oliver)		3	3			
Dryocoetes autographus (Ratzburg)			5			
Dryocoetes granicollis (LeConte)						2
Dryoxylon onoharaensum (Murayama)	194				16	
Euwallacea validus (Eichhoff)	1					
Gnathotrichus materiarius (Fitch)	1	4	53	1	1	
Hylastes porculus Erichson			106	1		
Hylastes salebrosus (Eichhoff)		2	38	1		
Hylastes tenuis Eichhoff	4	520	121	10		
Hylesinus aculeatus Say			4	5		
Hylocurus torosus Wood			1	1		
Hylurgopinus rufipes (Eichhoff)			2			
Hypothenemus californicus Hopkins				4		
Hypothenemus crudiae (Panzer)				8		
Hypothenemus dissimilis (Zimmermann)			109	7		4
Hypothenemus eruditus (Westwood)			4	3		
Hypothenemus interstitialis (Hopkins)			6	3		
Hypothenemus obscurus (Fabricius)				35		
Hypothenemus sp. 1					10	
Hypothenemus sp. 2					5	
Hypothenemus sp. 3					2	
Hypothenemus spp.	252	312				
Ips avulsus (Eichhoff)	5	227	20	13		4
Ips calligraphus (Germar)	1	91				
Ips grandicollis (Eichhoff)		366	46	16		6
Ips pini (Say)				20		
Lymantor decipiens (LeConte)				1		
Micracis swainei Blackman				1		
Micracisella nanula (LeConte)	2	7				
Micracisella opacicollis LeConte			68			
Monarthrum fasciatum (Say)	12	1	669	31	600	6
Monarthrum mali (Fitch)	11	25	280	104	278	3
Orthotomicus caelatus (Eichhoff)	4	4	9	16		9
Phloeosinus dentatus (Say)			3			
Phloeotribus frontalis (Oliver)			6	14		
Phloeotribus liminaris (Harris)			7	1		
Pityoborus comatus (Zimmermann)		12	1			
Pityogenes hopkinsi Swaine	1			69		
Pityogenes meridianus Blackman			1			
Pityogenes plagiatus (LeConte)				26		
Pityophthorus annectans LeConte			8			
Pityophthorus cariniceps LeConte				6		
Pityophthorus confusus bellus Blackman			9			
Pityophthorus consimilis LeConte				34		
Pityophthorus crinalis (Blackman)			16	7		
Pityophthorus liquidambarus Blackman					3	
Pityophthorus puberulus (LeConte)				3		
Pityophthorus pulchellus Eichhoff				2		
Pityophthorus pullus (Zimmermann)				4		
Pityophthorus sp. 1					1	
Pityophthorus sp. 2					1	
Pityophthorus spp.	13	538		1		
Pseudopityophthorus asperulus (LeConte)		3		1		
Pseudopityophthorus minutissimus (Zimmermann)	2		2	10		
Pseudopityophthorus pruinosus Eichhoff	3		2	8		1
Pseudopityophthorus pubescens Blackman			2	3		
Pseudothysanoes lecontei Blackman				7		

Table 3.   Continued

Species	SC[a]	FL[b]	GA[c]	NC[d]	TN[e]	TN[f]
Scolytus multistriatus Marsh.			14			
Scolytus quadrispinosus Say						3
Scolytus rugulosus (Muller)				2		
Thysanoes fimbricornis LeConte			1	3		
Thysanoes pallens Wood				1		
Trypodendron scabricollis (LeConte)			1			
Xyleborinus gracilis (Eichhoff)				2		
Xyleborinus saxeseni (Ratzburg)	2,250	10,929	2,143	3,507	2,390	5
Xyleborus affinis Eichhoff	7	786	15	11	2	15
Xyleborus atratus Eichhoff	54				136	8
Xyleborus californicus Wood	62				9	
Xyleborus celsus Eichhoff			1	1		
Xyleborus ferrugineus (Fabricius)	17	192	8	93	8	22
Xyleborus impressus Eichhoff	54					
Xyleborus intrusus Blandford				1		
Xyleborus obliquus (LeConte)				2		
Xyleborus pelliculosus Eichhoff					197	2
Xyleborus planicollis Zimmermann				5		
Xyleborus pubescens (Zimmermann)	11	143	61	6		20
Xyleborus sayi (Hopkins)			221	1	14	
Xyleborus viduus Eichhoff				1		
Xyleborus xylographus (Say)				126		
Xylosandrus compactus (Eichhoff)	2	13				
Xylosandrus crassiusculus (Motschulsky)	465				848	1
Xylosandrus germanus Blandford				76	83	
Xyloterinus politus (Say)	1			3	3	1
H	0.59	0.47	0.91	1.49	0.72	1.11
H_{max}	1.45	1.46	1.64	1.76	1.36	1.28
J	0.41	0.32	0.55	0.85	0.53	0.87

[a] Data from this study; conducted using Lindgren funnel traps with ethanol lures.

[b] Data from Atkinson et al. (1988a); conducted using both sticky and window traps with felled slash pine, *Pinus elliottii* Engelmann.

[c] Data from Turnbow and Franklin (1980); conducted using window traps with no lure.

[d] Data from Weber and McPherson (1991); conducted using window traps with no lure.

[e] Data from Oliver and Mannion (2001); conducted using Lindgren funnel traps with ethanol lures.

[f] Data from Grant et al. (2003); conducted using direct collections, sweep netting, beat-sheeting, deadwood dissection, light trapping, canopy fogging, malaise trapping, and pitfall trapping with no additional lures.

1A). A substantial rain (6.9 cm) on 20 March 2003 likely reduced trap catches just before their greatest levels (13 beetles $trap^{-1} d^{-1}$) on 1 April 2003. Heavy rain fell during the first 2 wk of April 2003 (14.6 cm), and again on 25 April 2003 (40.9 cm), decreasing trap captures a final time (Fig. 1A) before their natural decline. Flight activity remained consistent throughout the remainder of summer and fall, until ceasing completely in the beginning of December 2003 (Fig. 1A). Beetles first occurred in mid-March 2004, much later than in 2003, and exhibited consistent flight activity until we stopped trapping in April 2004.

Flight patterns of *X. saxeseni* (Fig. 1B) and *Hypothenemus* spp. (Fig. 1D) indicated that these species were present at all times except during the winter. *X. crassiusculus* activity peaked once in spring 2003, and the species was present only in low numbers the rest of the study duration (Fig. 1C). *D. onoharaensum* experienced a major flight peak in spring and several minor peaks in summer 2003 (Fig. 1E). *Xyleborus californicus* Wood (Fig. 1F) and *X. atratus* (Fig. 1I) showed two distinct peaks in activity in the spring of each year. *Ambrosiodmus rubricollis* (Eichhoff) (Fig. 1G) activity peaked in early May 2003, and it was inconsistently captured during the summer. *X. impressus* (Fig. 1H) had the most irregular flight patterns.

Attack Incidence. Initial destructive sampling revealed 10 *X. saxeseni*, four *X. affinis*, two *X. crassius-*

culus, and two *D. onoharaensum* colonizing live *P. deltoides* stems. Significantly more clone ST66 trees suffered beetle attacks than did S7C15 trees (42.5 versus 32.8% respectively; *P* = 0.0014; Fisher's exact test). The incidence of attack differed significantly among clone ST66 treatments only, with fertilized trees attacked at the highest rates compared with the other treatments (Fig. 2). No study trees were killed as a result of beetle attacks; however, mortality induced by beetle damage occurred in three trees outside of the study area.

Discussion

Species Composition. The majority of exotic specimens collected upheld our first hypothesis. The low diversity (*H*) and evenness (*J*), second lowest of six studies in this region (Table 3), were because of large captures of *X. saxeseni* and very low captures of several other species.

The predominance of *X. saxeseni* is in agreement with other southeastern U.S. studies (Roling and Kearby 1975, Flechtmann et al. 1999, Hanula et al. 2002; Table 3), including a survey 20 yr earlier in South Carolina peach orchards (Kovach and Gorsuch 1985). *X. saxeseni* attacks numerous species of dead or dying hardwoods and conifers, and is common across the southeastern United States (Drooz 1985). Its ambrosia
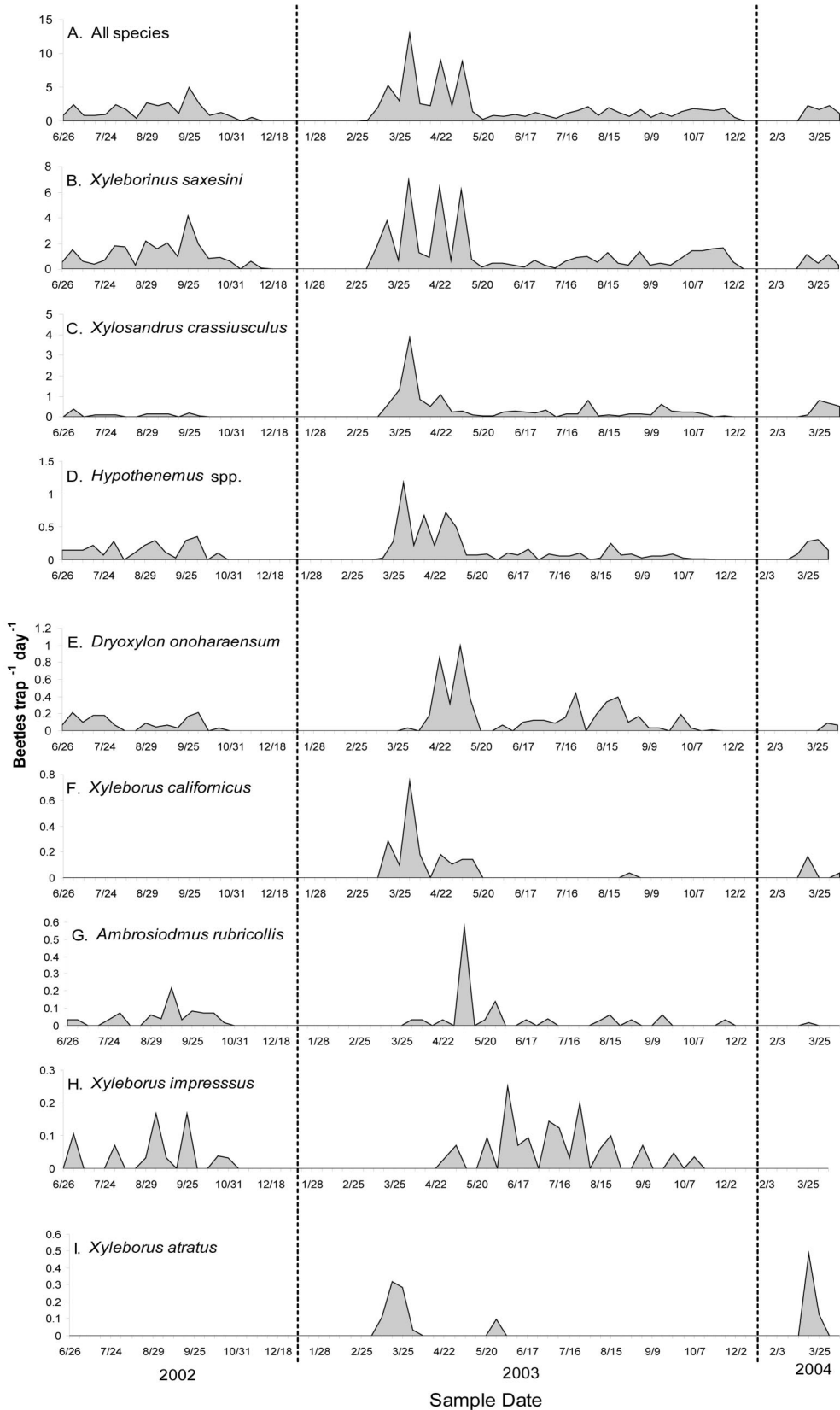
Fig. 1 Seasonal flight patterns of the total (A) and eight most common ambrosia beetles (B–I) captured at the Savannah River site near Aiken, SC, from June 2002 through April 2004.
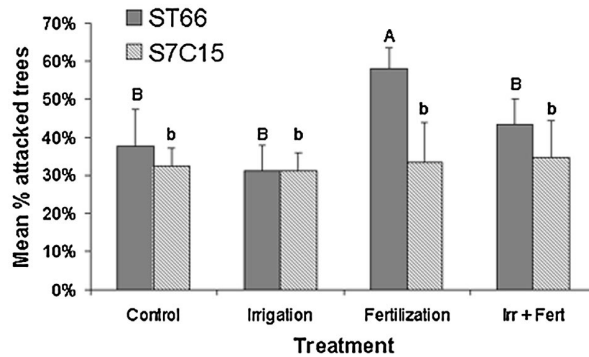
Fig. 2. Ambrosia beetle attack incidence in June 2002 on *P. deltoides* trees receiving various resource amendment treatments. Treatments within a clone sharing a letter are not significantly different ($\alpha = 0.05$; Tukey test).

fungus, *Ambrosiella sulfurea* Batra, is associated with (but has not been shown to cause) the decline of peach trees (Kovach and Gorsuch 1988). We observed fungal staining in destructively harvested trees, but the fungus was neither quantified nor identified.

X. crassiusculus was trapped in large numbers by using ethanol-baited traps in this and two other studies (Kovach and Gorsuch 1985, Oliver and Mannion 2001; Table 3) in addition to our study, possibly because these studies also used ethanol lures. Because of its propensity to attack and kill living trees (Atkinson et al. 1988b), which may at times emit ethanol (Kimmerer and Kozlowski 1982) and the apparent expansion of its range to the Pacific Northwest (ODA 1999), *X. crassiusculus* is a potentially serious pest of nursery stock, fruit orchards, and ornamental trees throughout North America (Kovach and Gorsuch 1985, Atkinson et al. 1988b, Mizell et al. 1994, Oliver and Mannion 2001). Up to 59 progeny have been shown to emerge from a single gallery (Oliver and Mannion 2001), demonstrating its capacity for population growth.

We captured *D. onoharaensum* (=*Xyleborus onoharaensis*) (Bright and Rabaglia 1999) in relatively large numbers compared with other studies in the southeastern United States (Table 3). Little is known regarding this species' biology, but it has now been captured in several southeastern states (Bright and Rabaglia 1999).

X. californicus was first reported in South Carolina in the early 1990s (Vandenberg et al. 2000), and it was caught in 2003 and 2004 (Table 2). We caught *X. californicus* and *A. rubricollis* in relatively large numbers considering reports of its capture are few (Kovach 1986, Oliver and Mannion 2001, Grant et al. 2003; Table 3). Other species, including *Micracisella nanula* (LeConte), *Pityogenes hopkinsi* Swaine, and *X. californicus* were only captured in one other southeastern U.S. study, and *E. validus* and *X. impressus* (recognized as a synonym of *X. ferrugineus* since 1960; Rabaglia 2005) were not reported elsewhere (Table 3).

Flight Patterns. Flight patterns, particularly for *X. saxeseni*, observed in our study (a large peak in early spring, and a smaller peak in autumn) agreed relatively well with other reports from the southeastern United States (Roling and Kearby 1975, Turnbow and

Franklin 1980, Kovach 1986, Atkinson et al. 1988a, Weber and McPherson 1991, Oliver and Mannion 2001). We observed a slightly earlier *X. crassiusculus* flight peak than in Tennessee (Oliver and Mannion 2001), possibly because of weather. The major activity peak in April and May for *Hypothenemus* spp. flight mirrored that reported by Atkinson et al. (1988a).

Attack Incidence. There is a wide range of susceptibility to pests as well as pest host preference among *P. deltoides* clones (Coyle et al. 2005). For example, clones in this plantation differed in their susceptibility to *T. lobulifera* (Coyle 2002). However, no studies have compared ambrosia beetle attack incidence on *Populus* clones, because attacks on healthy hosts are a relatively new phenomenon (Kühnholz et al. 2001). Clone ST66 was attacked more than clone S7C15 (Fig. 2), even though diameter between clones and among treatments was nearly identical (Coyle and Coleman 2005). However, we cannot determine whether this was because of host susceptibility or beetle preference.

The effect of resource amendments such as irrigation and fertilization on tree susceptibility to pests is under debate (Herms and Mattson 1992, Koricheva et al. 1998, Herms 2002, Huberty and Denno 2004). The growth-differentiation balance hypothesis (GDBH) for a resource-based balance between plant growth and defense (Herms and Mattson 1992) best explains the interaction between resource availability and host susceptibility. If resource availability limits growth, increases in resource availability will stimulate plant growth at the expense of defense. Our data suggest that the GDBH may differ among genotypes, because beetle attack incidence did not differ among resource amendment treatments in clone S7C15, yet ST66 trees receiving fertilization were attacked the most. The synthesis of Lorio (1986) of the ecology of the southern pine beetle, *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae), provides a compelling argument in support of the GDBH for southern pines. Attacks by Scolytidae are greatest in the spring when trees are allocating most of their resources to new growth and not defense. However, bark and ambrosia beetle attack rates dwindle throughout the summer as tree growth levels off and resources are converted into

defensive compounds (except for an occasional peak in late summer or fall, generally corresponding to a drought period and subsequent tree stress).

White pine weevil, *Pissodes strobi* (Peck), attack rates on spruce, *Picea glauca* (Moench) Voss × *P. engelmannii* Parry ex. Engelmann, also increased as fertilization rates increased (vanAkker et al. 2004). Fertilization increased plant material available for weevil feeding, but it did not affect induced resistance capabilities. With only two irrigation and fertilization treatments, this study was not designed to test the GDBH (Wilkens 1997, Stamp 2004), nor was that its original purpose (Coleman et al. 2004). Although growth losses to weevils were less than gains from fertilization, additional pest management tactics may be required if fertilization is used as a silvicultural treatment.

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