POPULATION ECOLOGY

Attraction of Ambrosia Beetles (Coleoptera: Scolytidae) to Different Tropical Pine Species in Brazil

C.A.H. FLECHTMANN,[1] A.L.T. OTTATI,[1] AND C. W. BERISFORD[2]

Environ. Entomol. 28(4): 649–658 (1999)

ABSTRACT Ambrosia beetles are the predominant Scolytidae in Brazil. Little is known about the attractiveness of exotic conifer tree volatiles to native scolytids. Objectives were to compare the attractiveness of logs with and without bark of *Pinus oocarpa* Schiede, *P. caribaea* variety *bahamensis* Barrett & Golfari, *P. car.* variety *caribaea* Barrett & Golfari and *P. car.* variety *hondurensis* Barrett & Golfari over time to native scolytids in different pine stands, to compare the relative attractiveness of logs relative to ethanol traps, to determine how long it takes for logs to become attractive to ambrosia beetles and when attraction peaks occur, and to determine if volatiles released by live standing trees would mask volatiles released by logs of the same species. In young stands, *Hypothenemus* was the predominant insect genus, whereas in older stands *Xyleborus* predominated. Debarked logs trapped more beetles than logs with bark. Pine log species attractiveness was not influenced by volatiles present in the stand. Beetles were divided into the following 3 groups, based on response to log volatiles and ethanol: (1) species attracted to ethanol and not responding to pine terpenes *Ambrosiodmus hagedorni* (Iglesia), *A. retusus* (Eichhoff), *X. spinulosus* Blandford, *Corthylus schaufussi* Schiede, *Cryptocarenus heveae* (Hagedorn), *H. obscurus* (F.), (2) species attracted to ethanol but responding to pine terpenes *Xyleborinus gracilis* (Eichhoff), *X. affinis* Eichhoff, *H. eruditus* Westwood, *Premnobius cavipennis* Eichhoff, and (3) species more attracted to pine terpenes and less responsive to ethanol, *A. obliquus* (Le Conte), *X. ferrugineus* F., *X. catulus* Blandford. *Pinus car.* variety *bahamensis* was the least attractive pine, *P. oocarpa* the most attractive. The attraction peak varied according to the season; logs were not attractive to beetles 10 wk after cutting.

KEY WORDS ambrosia beetles, primary attraction, tropical pines, attractiveness peak, pine terpenes versus ethanol response

MORE THAN 95% of the reforested area in Brazil consists of 2 genera of trees, *Pinus* and *Eucalyptus.* Tropical (*Pinus oocarpa* and *Pinus caribaea*) and subtropical pines, (*Pinus taeda* L.) comprise ≈35% of the total reforested area, whereas eucalypts represent ≈63% (ANFPC 1996). Although these forests occupy large areas, reforestation in Brazil is relatively new; establishment for most of these plantations began in the mid-1960s because of government tax incentives (Schönherr et al. 1974).

Records of pests in eucalypts are abundant and appeared early in the main establishment of these forests (Berti F. 1981, Iede 1985). This is because of the presence of many native plants of the same family (Myrtaceae), apparently making it easier for native insects to switch from their patchily distributed native hosts to the vast monocultures of potential new hosts. Pine plantations, however, remained surprisingly free of pests for many years, and to this date few insects have obtained the status of regular, economically important pests (Schönherr and Pedrosa-Macedo 1979, Flechtmann et al. 1995). This may occur because there are only 3 narrowly distributed, native conifers in Brazil (Marchiori 1996). None of these are in the genus *Pinus,* which leaves predominantly hardwood native insects to adapt to the exotic pines.

Beetles of the family Scolytidae are major insect pests in conifer forests throughout the world (Wood 1982). Bark beetles are the most predominant group in temperate forests, whereas xylomycetophagous ambrosia beetles are most abundant throughout the tropics (Schedl 1958; Beaver 1977, 1979).

In Brazil, surveys on scolytids in pine forests started in the early 1970s, and few species were recorded (Schönherr 1991). However, as the forests grew older and occupied larger areas, longer and more intensive surveys revealed a significant increase in the abundance and diversity of scolytid beetles (Schönherr 1991, Flechtmann et al. 1995). Those surveys found ambrosia beetles as the most important group of scolytids in pine forests in Brazil (Flechtmann et al. 1995).

Bark beetles in temperate climates cause millions of dollars of damage in outbreak years (Lie and Bakke 1981, Drooz 1985, Niemeyer 1985, Miller et al. 1987). However, in Neotropical regions, damage inflicted by the predominant ambrosia beetles is comparatively less severe and more difficult to quantify (Samaniego and Gara 1970). Occasionally ambrosia beetles attack live (mainly stressed) trees (Atkinson et al. 1988, Bea-

---

[1] Department of Biology–FEIS/UNESP, Av Brasil, 56, 15 385-000-Ilha Solteira-SP, Brazil.

[2] Department of Entomology, University of Georgia, 413 Biological Sciences Bldg., Athens, GA 30605-2655.

ver 1988), but they become pests by attacking felled trees. Ambrosia beetle infestations cause dark-stained pinholes, galleries, and blue-staining of lumber and veneer. The resulting loss of grade reduces the value of the lumber or it may be banned as an export (Gray and Borden 1985, McLean 1985, Orbay et al. 1994). Ambrosia beetles in the Neotropics are frequently characterized as a constant nuisance (Fisher et al. 1953), but in Peru these scolytids cause losses of 30–80% of lumber volume (Dourojeanni 1965). In certain temperate regions, such as British Columbia, ambrosia beetle damage can amount to millions of dollars per year by degradation of lumber (Lindgren and Fraser 1994).

In Brazil, records of ambrosia beetle damage in pines are becoming more common. So far, damage has been restricted to newly felled trees, stumps, and lumber banned from export (Flechtmann et al. 1995). Attacks on live pines have not been recorded.

Xylomycetophagous ambrosia beetles are polyphagous, with generally low host specificity (Beaver 1979). Little is known about the importance and relationship of tree host kairomones and ambrosia beetle host preference (Kelsey and Joseph 1997). Some ambrosia beetles respond to primary pine host attractants, using them as cues in host location (Bauer and Vité 1975, Hines and Heikkenen 1977, Fatzinger 1985). Ethanol is the best known primary attractant for ambrosia beetles (Samaniego and Gara 1970, Carpenter et al. 1988, Kelsey 1994a, Kelsey and Joseph 1997).

Ethanol can be produced in living plants (MacDonald and Kimmerer 1991, Kelsey 1994a), but it occurs in much greater quantities in felled trees (Moeck 1970, Carpenter et al. 1988, Lindelöw et al. 1992, Kelsey 1994a), as a result of continued anaerobic respiration in dying tissues. Ethanol alone attracts a wide variety of ambrosia beetles and acts as a synergist for host kairomones or pheromones for both ambrosia and bark beetles (Bauer and Vité 1975, Chénier and Philogène 1989, Schroeder and Lindelöw 1989, Byers 1995, Werner 1995). In Brazil, ethanol (used as baits in traps) is a good attractant for many Brazilian ambrosia beetles (Marques 1984, Carrano-Moreira 1985, Flechtmann et al. 1995). Although several Brazilian ambrosia beetles respond to ethanol-baited traps, very little is known about the relative attractiveness of host volatiles.

Secondary attraction occurs in many bark beetle species (see Borden 1982 for a review), but in scolytid ambrosia beetles, it is recognized in just a few Corthylini (*Gnathotrichus*) and Xyloterini (*Trypodendron*) (Byrne et al. 1974, Macconnell et al. 1977, Borden and McLean 1979). In Xyleborini, it appears that pheromone production is lacking (Beaver 1977, Klimetzek et al. 1986), although no specific experiments proving that are found in the literature.

The main objective of this study was to compare the attractiveness of logs with and without bark to native scolytids in pine stands in Brazil. Species of pines evaluated included *Pinus oocarpa* Schiede, *Pinus caribaea* Morelet variety *bahamensis* Barrett & Golfari, *Pinus caribaea* Morelet variety *caribaea* and *Pinus caribaea* Morelet variety *hondurensis* Barrett & Golfari. The attractiveness of logs was compared with ethanol used in a bait. The influence of volatiles emitted by the healthy standing trees present on the study sites on the attractiveness of logs also was investigated. Specific objectives were as follows: (1) to determine when logs become attractive to ambrosia beetles after felling, (2) when peak attraction occurs, and (3) how long the logs remain attractive to the beetles.

Materials and Methods

Sites and Deployment. Four tests were conducted in Agudos, São Paulo, Brazil, at the forest company Duraflora S.A. from December 1992 through September 1995. Agudos is located at 22° 22′ S and 48° W. The region is characterized by high summer temperatures and dry winters. The average temperature is 18.6°C in the winter and 23.3°C in the summer.

In experiment I, we tested the attractiveness of bark-on and debarked logs of *P. oocarpa*, *P. car.* variety *bahamensis*, *P. car.* variety *caribaea* and *P. car.* variety *hondurensis* to different Scolytidae species. Log ends were not sealed, and bark was removed by hand spudding in debarked logs. Two logs (≈20 cm diameter, 70 cm long) of each pine species were placed inside each tent trap (Flechtmann and Gaspareto 1997). Tent traps allow volatiles from logs to be released into the environment and trap attracted beetles before they can attack the billets, thus avoiding any possible chemical change in the log bait from insect attack and also the production of any possible secondary attractants (pheromones). The traps were deployed in lines (blocks) in each stand, 20 m apart within a line with 30 m between lines. Each line consisted of 4 log-baited and 1 control (unbaited) tent traps. The position of the different baits in the tent traps was randomly assigned. One ESALQ-84 trap (Berti F. and Flechtmann 1986) baited with 95% ethanol was deployed 200 m from the end of each line of tent traps so they did not to interfere with the attractiveness of the volatiles released by the logs. Ethanol release rate was ≈0.52 g/d at 21°C (determined gravimetrically).

To determine the influence of odors released by standing pines on the attractiveness of logs of the same pine species, traps were deployed in stands of the same pine species that were used as baits—*P. oocarpa*, *P. car.* variety *bahamensis*, *P. car.* variety *caribaea* and *P. car.* variety *hondurensis.* In each stand, 5 blocks were used, with each line of tent traps containing bark-on logs alternating with another containing debarked logs. Altogether, 100 tent traps and 20 ESALQ-84 traps were used.

In *P. oocarpa* and *P. car.* variety *caribaea* stands, 3 blocks of traps with bark-on logs and 2 blocks of debarked logs as baits were installed, whereas for *P. car.* variety *bahamensis* and *P. car.* variety *hondurensis* stands, there were 2 blocks with bark-on and 3 blocks with debarked logs, respectively. Stand characteristics were as follows: (1) *P. oocarpa* - 111.14 ha, planted in November 1967, diameter at breast height (dbh) of 36.34 cm and tree height of 27.51 m; (2) *P. car.* variety *bahamensis* - 65.41 ha, planted in February 1967, dbh of 32.17 cm and tree height of 27.03 m; (3) *P. car.* variety *caribaea* - 31.41 ha, planted in January 1969, dbh of 31.00 cm and tree height of 25.90 m; (4) *P. car.* variety *hondurensis* - 56.77 ha, planted in November 1968, dbh of 34.89 cm and tree height of 28.73 m. All 4 stands had a density of 200 trees per hectare.

The collection bottles on both trap types were filled with water plus a small amount of detergent. Traps were first baited on 22 December 1992, and collections were made every 7 d for a period of 10 wk (after which logs were not attractive). The liquid was replaced on each collection.

In experiments II-IV, logs of the same 4 pine species, with the same dimensions as described for experiment I, were used as baits. However, only bark-on logs were used, and all traps were placed in a single *P. car.* variety *hondurensis* stand. Log ends were not sealed.

The *P. car.* variety *hondurensis* stand in experiment II had an area of 16.34 ha; it was planted in January 1972 and had a dbh of 28.77 cm, tree height of 24.04 m, and tree density of 300 trees per hectare. In experiment III, the stand area was 17.35 ha, planted in April 1984, and had 2,000 trees per hectare. In experiment IV, the stand had 39.93 ha, was planted in April 1984, and also had 2,000 trees per hectare.

There were 5 blocks per stand, each block consisting of a line with 5 tent traps (4 baited + 1 unbaited) and 1 or 2 ESALQ-84 traps, with the same spacing as used in experiment I. In experiment II, only 1 ESALQ-84 trap (baited with 95% ethanol) per line was used. In experiments III and IV, 2 ESALQ-84 traps were used (1 at each end of the line); 1 trap was baited with 95% ethanol and the other was unbaited. In experiments II-IV, the insects were collected weekly for 10 wk. The first collections were made on 27 July 1993, 12 April 1994, and 4 July 1995 in experiments II, III, and IV, respectively.

In all experiments, trees selected to be cut were from stands other than where traps were deployed. All billets were kept in plastic bags (to avoid any insect attack) in the shade until placed in the tent traps (within 24 d of tree cutting). No stand had any thinning or logging within 12 mo after trap deployment.

Experiments I and III were initiated in the warm season (daily temperatures of 25.34 ± 0.24°C and 22.8 ± 0.23°C [mean ± SE] for the first 5 wk, respectively); experiments II and IV started in the cold season (daily temperatures of 17.80 ± 0.43°C and 18.91 ± 0.50°C for the first 5 wk, respectively).

Voucher specimens have been deposited at the Entomology Museum of the Faculdade de Engenharia de Ilha Solteira (FEIS/UNESP), Ilha Solteira, São Paulo state, Brazil.

Experimental Design and Data Analysis. The experiments were randomized complete block designs. Data were transformed into $\sqrt{(x + 1)}$ to correct for non-normality (Phillips 1990). Beetle catches were analyzed by PROC GLM with treatment means separated by the Tukey test (SAS Institute 1990) at the 5% level of significance.

Results

Experiment I. In total, 16,815 Scolytidae (23 species) were trapped. The tribe Bothrosternini was represented by *Cnesinus dryographus* Schedl and Corthylini by *Corthylus nudipennis* Schedl and *Corthylus schaufussi* Schedl; those species were trapped in very low numbers (<1% total abundance).

Eight species were trapped in the tribe Cryphalini, including *Cryptocarenus heveae* (Hagedorn), *Cryptocarenus diadematus* Eggers, *Cryptocarenus seriatus* Eggers, *Cryptocarenus* spp. (2 species), *Hypothenemus bolivianus* (Eggers), *Hypothenemus eruditus* Westwood and *Hypothenemus obscurus* (F.). Cryphalini represented ≈22% of the total number of scolytids trapped.

The greatest diversity and abundance were found in the Xyleborini (essentially xylomycetophagous ambrosia beetles), of which 12 species were trapped. Catches included *Ambrosiodmus hagedorni* (Iglesias), *Ambrosiodmus obliquus* (LeConte), *Premnobius cavipennis* Eichhoff, *Xyleborinus gracilis* (Eichhoff), *Xyleborus affinis* Eichhoff, *Xyleborus biconicus* Eggers, *Xyleborus ferrugineus* F., *Xyleborus catulus* Blandford, *Xyleborus linearicollis* Schedl, *Xyleborus spinulosus* Blandford, *Xylosandrus curtulus* (Eichhoff) and *Xylosandrus retusus* (Eichhoff), which altogether accounted for ≈78% of all scolytids captured.

Despite the fact that 23 species were trapped, only 12—*A. hagedorni, A. obliquus, A. retusus, P. cavipennis, X. gracilis, X. affinis, X. ferrugineus, X. catulus, X. spinulosus, C. heveae, H. eruditus*, and *H. obscurus*—were trapped in numbers sufficient to be analyzed statistically.

There was a statistically significant difference for the main factors of presence of bark, stand, bait, and week, and for the interactions bark*bait and bark*bait*stand ($P < 0.05$).

Overall, for the 12 above-mentioned species, catches were numerically higher on tent traps baited with debarked than with bark-on logs over the 10 wk and the 4 pine stands. Significantly more *X. ferrugineus* ($F = 25.33$; df = 1, 194; $P = 0.0001$), *X. catulus* ($F = 3.06$; df = 1, 194; $P = 0.0405$) and *H. eruditus* ($F = 5.25$; df = 1, 194; $P = 0.023$) were attracted to debarked *P. car.* variety *bahamensis* logs than on respective bark-on logs. Significantly more *X. ferrugineus* ($F = 11.32$; df = 1, 194; $P = 0.0009$) and *H. eruditus* ($F = 12.84$; df = 1, 19; $P = 0.0004$) were attracted to debarked *P. car.* variety *caribaea* logs than to corresponding bark-on logs. There were no significant differences between debarked and bark-on *P. car.* variety *hondurensis* logs and *P. oocarpa* logs for any beetle species. Mean comparisons of beetle catches on debarked and bark-on logs by each of the 10 wk also showed that scolytids were more attracted to debarked logs.

Among debarked logs, some scolytids showed a significant preference for logs of a particular species. *Hypothenemus eruditus* was more attracted to *P. car.* variety *bahamensis* than to any other pine logs; *X. ferrugineus* was equally attracted to *P. car.* variety *caribaea, P. car.* variety *hondurensis* and *P. car.* variety

Table 1. Mean ± SE of Scolytidae species attracted to traps baited with ethanol or logs of different species of tropical pines and placed in different tropical pine stands. Agudos, São Paulo State, Brazil, December 1992–March 1993 (experiment I)

Species	Etoh	Pcb	Pcc	Pch	Poo	Ctr
			Exp. I: debarked logs, attractant			
Xaff	1.86 ± 0.30a	0.36 ± 0.21b	0.20 ± 0.08b	0.14 ± 0.04b	0.42 ± 0.29b	0.02 ± 0.01b
Heru	14.60 ± 1.56a	1.35 ± 0.22b	0.96 ± 0.18bc	0.70 ± 0.16bc	0.51 ± 0.16bc	0.11 ± 0.04c
Xfer	1.00 ± 0.20c	13.62 ± 1.85a	19.94 ± 2.85a	14.82 ± 1.85a	5.80 ± 0.81b	1.82 ± 0.27c
Xgra	2.55 ± 0.71a	0.05 ± 0.03b	0.04 ± 0.02b	0.06 ± 0.03b	0.03 ± 0.02b	0.02 ± 0.02b
Ahag	0.54 ± 0.16a	0.09 ± 0.04b	0.03 ± 0.02b	0.03 ± 0.02b	0.08 ± 0.04b	0.02 ± 0.01b
Chev	1.09 ± 0.20a	0.01 ± 0.01b	0.02 ± 0.02b	0.00 ± 0.00b	0.00 ± 0.00b	0.00 ± 0.00b
Aobl	0.07 ± 0.04bc	0.19 ± 0.05abc	0.36 ± 0.10a	0.32 ± 0.08ab	0.39 ± 0.09a	0.06 ± 0.03c
Hobs	0.81 ± 0.13a	0.08 ± 0.04b	0.03 ± 0.02b	0.02 ± 0.01b	0.02 ± 0.01b	0.01 ± 0.01b
Xcat	0.01 ± 0.01b	0.51 ± 0.15a	0.55 ± 0.18a	0.24 ± 0.07ab	0.14 ± 0.06ab	0.01 ± 0.01b
Aret	5.18 ± 0.72a	0.00 ± 0.00b	0.00 ± 0.00b	0.00 ± 0.00b	0.00 ± 0.00b	0.00 ± 0.00b
Xspi	8.47 ± 1.50a	0.10 ± 0.10b	0.01 ± 0.01b	0.02 ± 0.01b	0.03 ± 002b	0.00 ± 0.00b
Pcav	0.20 ± 0.06a	0.00 ± 0.00b	0.00 ± 0.00b	0.01 ± 0.01b	0.02 ± 0.02b	0.00 ± 0.00b
			Exp. I: bark-on logs, attractant			
Xaff	1.09 ± 0.13a	0.08 ± 0.03b	0.06 ± 0.03b	0.11 ± 0.08b	0.45 ± 0.24b	0.07 ± 0.04b
Heru	10.74 ± 0.89a	0.27 ± 0.07b	0.13 ± 0.04b	0.24 ± 0.06b	0.13 ± 0.04b	0.13 ± 0.06b
Xfer	0.77 ± 0.12e	3.03 ± 0.37cd	4.76 ± 0.59bc	9.67 ± 1.68a	8.65 ± 1.17ab	1.81 ± 0.36de
Xgra	2.18 ± 0.41a	0.02 ± 0.01b	0.03 ± 0.02b	0.00 ± 0.00b	0.02 ± 0.01b	0.00 ± 0.00b
Ahag	0.85 ± 0.17a	0.01 ± 0.01b	0.03 ± 0.02b	0.03 ± 0.02b	0.02 ± 0.01b	0.02 ± 0.01b
Chev	1.24 ± 0.18a	0.00 ± 0.00b	0.00 ± 0.00b	0.00 ± 0.00b	0.00 ± 0.00b	0.00 ± 0.00b
Aobl	0.17 ± 0.05a	0.12 ± 0.04a	0.15 ± 0.05a	0.13 ± 0.04a	0.15 ± 0.05a	0.12 ± 0.04a
Hobs	1.44 ± 0.24a	0.03 ± 0.02b	0.01 ± 0.01b	0.02 ± 0.01b	0.01 ± 0.01b	0.00 ± 0.00b
Xcat	0.01 ± 0.01a	0.05 ± 0.02a	0.09 ± 0.03a	0.09 ± 0.05a	0.04 ± 0.02a	0.07 ± 0.07a
Aret	5.46 ± 0.99a	0.00 ± 0.00b	0.00 ± 0.00b	0.00 ± 0.00b	0.00 ± 0.00b	0.00 ± 0.00b
Xspi	9.69 ± 1.13a	0.00 ± 0.00b	0.00 ± 0.00b	0.00 ± 0.00b	0.02 ± 0.02b	0.01 ± 0.01b
Pcav	0.14 ± 0.04a	0.00 ± 0.00b	0.00 ± 0.00b	0.00 ± 0.00b	0.02 ± 0.01b	0.00 ± 0.00b

Means back-transformed from $\sqrt{(x + 0.5)}$; means followed by same letters are not significantly different within rows ($P > 0.05$; Tukey test). Etoh, ethanol-baited ESALQ-84 trap; Pcb, *P. car.* variety *bahamensis* log; Pcc, *P. car.* variety *caribaea* log; Pch, *P. car.* variety *hondurensis* log; Poo, *P. oocarpa* log; Ctr, unbaited tent trap. Xaff, *X. affinis;* Heru, *H. eruditus;* Xfer, *X. ferrugineus;* Xgra, *X. gracilis;* Ahag, *A. hagedorni;* Chev, *C. heveae;* Aobl, *A. obliquus;* Hobs, *H. obscurus;* Aret, *A. retusus;* Xspi, *X. spinulosus;* Pcav, *P. cavipennis;* Xcat, *Xyleborus catulus.*

bahamensis, A. obliquus to *P. oocarpa, P. car.* variety *caribaea* and *P. car.* variety *hondurensis* and *X. catulus* to *P. car.* variety *caribaea* and *P. car.* variety *bahamensis* (Table 1). Analyses for each week showed similar results.

The attractiveness of the different debarked logs was compared for each beetle and each stand. In the *P. car.* variety *bahamensis* stand, *X. ferrugineus* was significantly more trapped on *P. car.* variety *bahamensis* and *P. car.* variety *caribaea* logs ($F = 29.00$; df = 5, 172; $P = 0.0001$). In the *P. car.* variety *caribaea* stand, *X. ferrugineus* was more attracted to *P. car.* variety *caribaea* and *P. car.* variety *hondurensis* logs ($F = 12.44$; df = 5, 113; $P = 0.0001$), *A. obliquus* was more attracted to *P. car.* variety *caribaea* logs ($F = 4.57$; df = 5, 113; $P = 0.0008$), and *X. catulus* was more attracted to *P. car.* variety *caribaea* logs ($F = 2.85$; df = 5, 113; $P = 0.0185$). In the *P. car.* variety *hondurensis* stand, *X. ferrugineus* had a preference for *P. car.* variety *bahamensis, P. car.* variety *caribaea,* and *P. car.* variety *hondurensis* logs ($F = 31.54$; df = 5, 172; $P = 0.0001$). In the *P. oocarpa* stand, more *X. ferrugineus* were caught on *P. car.* variety *caribaea* and *P. car.* variety *bahamensis* logs ($F = 7.38$; df = 5, 113; $P = 0.0094$), and *A. obliquus* had a preference for *P. oocarpa* and *P. car.* variety *hondurensis* logs ($F = 4.65$; df = 5, 113; $P = 0.0007$). For all other scolytid species, there were no differences between treatments.

Only *X. ferrugineus* showed a preference for bark-on logs, being more attracted to *P. car.* variety *hondurensis* and *P. oocarpa* logs when grouping all stands and weeks (Table 1). A similar result was observed when breaking down the analysis by week.

The comparison of the attractiveness of different bark-on logs in each stand resulted in responses similar to those observed when all stands were grouped. *X. ferrugineus* was more attracted to *P. oocarpa* and *P. car.* variety *caribaea* in the *P. car.* variety *bahamensis* stand ($F = 9.90$; df = 5, 113; $P = 0.0001$), to *P. car.* variety *hondurensis* and *P. oocarpa* in the *P. car.* variety *caribaea* stand ($F = 18.59$; df = 5, 172; $P = 0.0001$), and to *P. oocarpa* in the *P. oocarpa* stand ($F = 4.92$; df = 5, 172; $P = 0.0003$). There were no significant differences among log baits in the *P. car.* variety *hondurensis* stand.

Periods of peak attractiveness to scolytids were calculated taking into consideration the catches observed on control and ethanol-baited traps, to ensure that greater numbers were not a function of greater seasonal abundances. For debarked logs, significantly more *H. eruditus* were trapped on weeks 4 and 5 ($F = 16.56$; df = 9, 388; $P = 0.0001$); *X. ferrugineus* on weeks 4, 5, and 7 ($F = 6.77$; df = 9, 388; $P = 0.0001$); *A. hagedorni* ($F = 2.81$; df = 9, 388; $P = 0.0033$), *A. obliquus* ($F = 5.10$; df = 9, 388; $P = 0.0001$), and *H. obscurus* ($F = 2.50$; df = 9, 388; $P = 0.0086$) on week 5; *X. catulus* ($F = 18.75$; df = 9, 388; $P = 0.0001$) on week 6; and *X. gracilis* ($F = 3.41$; df = 9, 388; $P = 0.0005$) on week 1. For the remainder of the species, there were no statistically significant differences among weeks.

For bark-on logs, the results were similar for 2 species; more *X. ferrugineus* were trapped on weeks 4, 7,

Table 2. Mean ± SE number of Scolytidae species attracted to traps baited with ethanol or logs of different species of tropical pines within *P. caribaea* variety *hondurensis* stand. Agudos, São Paulo State, Brazil, July–October 1993 (experiment II)

Species	Exp. II - attractant					
	Etoh	Pcb	Pcc	Pch	Poo	Ctr
Xaff	1.62 ± 0.37a	1.44 ± 0.33a	2.22 ± 0.36a	2.16 ± 0.38a	1.42 ± 0.27a	1.12 ± 0.28a
Heru	3.00 ± 0.40a	1.52 ± 0.23ab	2.08 ± 0.41ab	1.56 ± 0.28b	1.44 ± 0.28b	2.14 ± 0.42ab
Xfer	1.30 ± 0.46a	1.86 ± 0.58a	2.92 ± 0.78a	3.28 ± 0.89a	1.66 ± 0.34a	1.46 ± 0.38a
Xgra	2.08 ± 0.49a	0.72 ± 0.17b	0.66 ± 0.17b	1.48 ± 0.47ab	0.46 ± 0.16b	0.88 ± 0.22ab
Chev	0.68 ± 0.16a	0.12 ± 0.05b	0.14 ± 0.07b	0.08 ± 0.04b	0.04 ± 0.03b	0.26 ± 0.09b
Aobl	0.04 ± 0.03b	0.36 ± 0.11ab	0.30 ± 0.10ab	0.64 ± 0.15a	0.80 ± 0.21a	0.06 ± 0.04b
Pcav	0.18 ± 0.07a	0.14 ± 0.06a	0.12 ± 0.05a	0.20 ± 0.07a	0.12 ± 0.05a	0.06 ± 0.03a

See footnote in Table 1.

and 8 ($F = 4.29$; df = 9, 388; $P = 0.0001$), whereas more *X. catulus* were trapped on weeks 6 and 8 ($F = 5.24$; df = 9, 388; $P = 0.0001$). However, *H. eruditus* ($F = 3.72$; df = 9, 388; $P = 0.0002$), *A. hagedorni* ($F = 2.41$; df = 9, 388; $P = 0.0113$), and *A. obliquus* ($F = 3.62$; df = 9, 388; $P = 0.0002$) exhibited a somewhat different pattern; *H. eruditus* and *A. obliquus* were more attracted to pine logs on weeks 1 and 5, whereas *A. hagedorni* was more common on week 8.

A comparison of attractiveness of bark-on and debarked logs over time also was performed for each stand, and the results were generally the same.

Overall, *X. affinis, H. eruditus, X. gracilis, A. hagedorni, C. heveae, H. obscurus, A. retusus, X. spinulosus,* and *P. cavipennis* responded significantly more to ethanol than to any log baits, regardless of presence or absence of bark, with all weeks and stands combined (Table 1). *X. ferrugineus, A. obliquus,* and *X. catulus* were more attracted to pine log volatiles, and ethanol-baited trap catches were significantly lower than the control traps, suggesting ethanol alone may be repellent. Also, only on debarked logs, catches of *A. obliquus* and *X. catulus* were significantly higher on log-baited than on ethanol-baited traps (Table 1). The above-mentioned results were not influenced by analyses done by each week and also by each stand. It is notable that *C. heveae, H. obscurus, A. retusus, X. spinulosus,* and *P. cavipennis* showed lower responses to pine logs than to the unbaited control traps (Table 1).

Experiment II. Scolytids collected throughout the 10 wk of trapping included 1,680 specimens among 3 tribes and 20 species. Corthylini (1 species) accounted for <1%, whereas Cryphalini (8 species) represented ≈26% of the total. Xyleborini (11 species) accounted for 73% of all scolytids. Only *X. affinis, H. eruditus, X. ferrugineus, X. gracilis, C. heveae, A. obliquus,* and *P. cavipennis* were trapped in numbers sufficient for statistical analyses.

Xyleborus affinis ($F = 18.07$; df = 9, 186; $P = 0.0001$), *H. eruditus* ($F = 20.53$; df = 9, 186; $P = 0.0001$), *X. ferrugineus* ($F = 43.24$; df = 9, 186; $P = 0.0001$), *C. heveae* ($F = 3.22$; df = 9, 186; $P = 0.0012$), *A. obliquus* ($F = 8.09$; df = 9, 186; $P = 0.0001$), and *P. cavipennis* ($F = 5.84$; df = 9, 186; $P = 0.0001$) catches were significantly higher on log-baited traps in week 9, whereas more *X. gracilis* were caught on week 6 ($F = 4.53$; df = 9, 186; $P = 0.0005$). Analyses for each log species showed similar results.

Over the 10-wk period, *H. eruditus, X. gracilis,* and *C. heveae* catches were significantly higher in traps baited with ethanol. *A. obliquus* was the only species more attracted to log-baited treatments, with higher catches observed on traps baited with *P. car.* variety *hondurensis* and *P. oocarpa* logs. For this species, catches in ethanol-baited traps were similar to unbaited traps and were significantly lower than in any of the log-baited traps. Conversely, for *C. heveae,* the log-baited catches were similar to the unbaited control traps (Table 2). Similar results were observed when analyses were done by week, except for *X. ferrugineus,* which was significantly more attracted to *P. car.* variety *hondurensis, P. car.* variety *caribaea,* and *P. oocarpa* baits over the other log treatment ($F = 2.88$; df = 5, 20; $P = 0.0406$).

Experiment III. Sixteen scolytid species were trapped (3 tribes), totaling 3,585 specimens. Although Corthylini (2 species) represented <1% and Xyleborini (7 species) ≈27% of the total abundance, Cryphalini (7 species) accounted for ≈73% of the scolytids captured. *Hypothenemus eruditus* alone in the Cryphalini accounted for 67% of the total. *X. affinis, H. eruditus, X. ferrugineus, A. hagedorni, C. heveae, H. obscurus, P. cavipennis,* and *C. schaufussi* were included in the statistical analyses.

Only Xyleborini species exhibited a preference among the species of pine logs. *X. affinis* was more attracted to all log species over remaining treatments, but *X. ferrugineus* had higher catches on traps baited with *P. car.* variety *caribaea, P. car.* variety *bahamensis,* and *P. oocarpa* logs. For these 2 species, catches on ethanol-baited traps were equivalent to the unbaited control traps. The least preferred log species (trapping equal or lower than unbaited traps) for *X. ferrugineus* was *P. car.* variety *hondurensis* and for *P. cavipennis* it was *P. oocarpa* (Table 3).

Hypothenemus eruditus, A. hagedorni, C. heveae, C. schaufussi, and *X. spinulosus* were clearly more attracted to ethanol. *P. cavipennis* showed a mixed response, where catches were highest on *P. car.* variety *caribaea, P. car.* variety *hondurensis* and also ethanol-baited traps (Table 3). Results were similar when they were analyzed by week.

The attractiveness of the pine logs varied over time. For *X. affinis,* the highest catches were observed on week 3 ($F = 17.45$; df = 9, 186; $P = 0.0001$), *X. ferrugineus* ($F = 5.78$; df = 9, 186; $P = 0.0001$) on weeks

Table 3. Mean ± SE numbers of Scolytidae species attracted to traps baited with ethanol or logs of different species of tropical pines within *P. caribaea* v. *hondurensis* stand. Agudos, São Paulo State, Brazil, April–June 1994 (experiment III); June–September 1995 (experiment IV)

Species	Etoh	Pcb	Pcc	Pch	Poo	nEtoh	Ctr
				Exp. III: attractant			
Xaff	0.40 ± 0.09c	1.20 ± 0.22ab	1.56 ± 0.24a	0.96 ± 0.19abc	1.08 ± 0.22abc	0.34 ± 0.09c	0.66 ± 0.17bc
Csch	0.54 ± 0.11a	0.10 ± 0.04b	0.04 ± 0.03b	0.04 ± 0.03b	0.02 ± 0.02b	0.16 ± 0.07b	0.00 ± 0.00b
Heru	27.24 ± 2.93a	15.88 ± 2.88b	15.20 ± 3.31b	7.50 ± 1.53b	9.38 ± 2.55b	17.00 ± 3.45b	14.90 ± 3.08b
Xfer	0.26 ± 0.07cd	1.12 ± 0.18ab	1.44 ± 0.22a	0.64 ± 0.13bc	0.90 ± 0.16ab	0.08 ± 0.04d	0.64 ± 0.16bcd
Ahag	1.68 ± 0.27a	0.48 ± 0.13b	0.38 ± 0.11b	0.72 ± 0.14b	0.28 ± 0.09b	0.68 ± 0.137b	0.22 ± 0.07b
Chev	1.48 ± 0.23a	0.60 ± 0.16b	0.44 ± 0.15b	0.38 ± 0.13b	0.72 ± 0.21b	1.04 ± 0.18ab	1.02 ± 0.20ab
Aobl	0.20 ± 0.07a	0.12 ± 0.05a	0.10 ± 0.04a	0.18 ± 0.06a	0.10 ± 0.05a	0.06 ± 0.03a	0.06 ± 0.03a
Xspi	2.36 ± 0.52a	0.12 ± 0.05b	0.16 ± 0.06b	0.08 ± 0.05b	0.02 ± 0.02b	0.56 ± 0.20b	0.14 ± 0.06b
Pcav	2.08 ± 0.41ab	1.74 ± 0.36abc	2.46 ± 0.48a	2.38 ± 0.51ab	0.56 ± 0.14c	0.58 ± 0.14c	0.90 ± 0.18bc
				Exp. IV: attractant			
Xaff	6.54 ± 0.86a	3.47 ± 0.53ab	4.21 ± 0.93ab	3.68 ± 0.70b	5.54 ± 1.35ab	1.86 ± 0.35b	1.86 ± 0.45b
Heru	13.89 ± 1.61a	6.79 ± 1.22b	8.78 ± 1.51b	6.07 ± 1.25b	5.57 ± 0.90b	7.82 ± 2.01b	3.58 ± 0.67b
Xfer	0.06 ± 0.03ab	0.21 ± 0.07ab	0.12 ± 0.06ab	0.18 ± 0.06ab	0.30 ± 0.09a	0.12 ± 0.07ab	0.03 ± 0.02b
Xgra	2.10 ± 0.26a	0.52 ± 0.10b	0.68 ± 0.19b	0.68 ± 0.14b	0.41 ± 0.10b	0.77 ± 0.20b	1.18 ± 0.31b
Chev	1.73 ± 0.24a	0.12 ± 0.05c	0.40 ± 0.14bc	0.22 ± 0.08bc	0.27 ± 0.08bc	0.36 ± 0.11bc	0.84 ± 0.25b
Hobs	0.33 ± 0.08a	0.12 ± 0.05ab	0.22 ± 0.08ab	0.02 ± 0.02b	0.09 ± 0.04b	0.12 ± 0.06ab	0.13 ± 0.05ab
Aret	0.83 ± 0.29a	0.00 ± 0.00b	0.02 ± 0.02b	0.00 ± 0.00b	0.00 ± 0.00b	0.00 ± 0.00b	0.28 ± 0.12b
Pcav	0.46 ± 0.12a	0.13 ± 0.05ab	0.18 ± 0.06ab	0.12 ± 0.05b	0.13 ± 0.06ab	0.16 ± 0.05ab	0.31 ± 0.11ab

Means back-transformed from $\sqrt{(x + 0.5)}$; means followed by same letters are not significantly different within rows ($P > 0.05$; Tukey test). Etoh, ethanol-baited ESALQ-84 trap; Pcb, *P. car.* variety *bahamensis* log; Pcc, *P. car.* variety *caribaea* log; Pch, *P. car.* variety *hondurensis* log; Poo, *P. oocarpa* log; Ctr, unbaited tent trap, *C. schaufussi*; nEtOh, unbaited ESALQ-84 trap. Xaff, *X. affinis;* Heru, *H. eruditus;* Xfer, *X. ferrugineus;* Xgra, *X. gracilis;* Ahag, *A. hagedorni;* Chev, *C. heveae;* Aobl, *A. obliquus;* Hobs, *H. obscurus;* Aret, *A. retusus;* Xspi, *X. spinulosus;* Pcav, *P. cavipennis;* Xcat, *Xyleborus catulus*.

3 and 5, *X. spinulosus* ($F = 3.07$; df = 9, 186; $P = 0.0019$) on week 5, *P. cavipennis* ($F = 13.97$; df = 9, 186; $P = 0.0001$) on weeks 3 and 4, and *A. hagedorni* on week 9 ($F = 9.35$; df = 9, 186; $P = 0.0001$). Similar results were found when data were analyzed separately for each of the 4 pine species used as baits.

Experiment IV. In total, 16 species distributed among 2 tribes and representing 5,220 individuals were trapped. Beetles of the tribe Xyleborini (9 species) comprised 38%, and Cryphalini (7 species) constituted 62% of the total, most of which (56%) were *H. eruditus.* Statistical analyses were limited to *X. affinis, H. eruditus, X. ferrugineus, X. gracilis, C. heveae, H. obscurus, A. retusus,* and *P. cavipennis.*

No beetle species demonstrated a preference for any pine species during the entire trapping period or in any week. However, there was a variation in the attractiveness of these logs over time. *X. affinis* ($F = 21.45$; df = 8, 167; $P = 0.0001$) and *X. ferrugineus* ($F = 3.17$; df = 8, 167; $P = 0.0023$) were trapped in significantly greater numbers on week 3, *H. eruditus* ($F = 56.34$; df = 8, 167; $P = 0.0001$) and *C. heveae* ($F = 6.32$; df = 8, 167; $P = 0.0001$) on week 8, and *X. gracilis* ($F = 16.70$; df = 8, 167; $P = 0.0001$) on week 9. Those trends were not influenced by the species of logs.

Xylebous affinis, H. eruditus, X. gracilis, C. heveae, H. obscurus, A. retusus, and *P. cavipennis* were significantly more attracted to ethanol-baited traps than to log-baited traps; of those, catches of *H. eruditus, X. gracilis, C. hevea,* and *A. retusus* were not different from unbaited controls (Table 3). However, more *X. ferrugineus* were trapped in *P. oocarpa*-baited traps, whereas ethanol trap catches were similar to unbaited traps (Table 3).

Discussion

The *P. car.* variety *hondurensis* stands used in experiments I and II were mature (>21 yr old) and nearing harvest, whereas in experiments III and IV they were relatively young (10 yr old). Marques (1989) reported high catches of *H. eruditus* and low catches of *Xyleborus* in ethanol-baited traps placed in young *Pinus taeda* and *Pinus elliottii* stands, but the opposite occurred in more mature stands. We observed similar results for *P. car.* variety *hondurensis* sites. The abundance of *Xyleborus* and *H. eruditus* in the younger stands averaged 23 and 62%, respectively; for the older stands it was ≈68 and 19%, respectively.

Xylomycetophagous beetles are considered to be the principal scolytid group in the Neotropics (Chandra 1981, Atkinson and Equihua-Martinez 1986). The predominance of *H. eruditus* (a non-xylomycetophagous beetle) in younger stands may be caused by more intense management practices. Repeated thinnings in young stands produce abundant breeding material (in the form of slash) for this myelophagous species. In older stands with less frequent thinnings, the scolytid population shifts to more aggressive xyleborine beetles.

Debarked logs trapped more scolytids than bark-on logs. The higher attractiveness of debarked logs to ambrosia beetles generally results in a higher initial infestation of debarked logs (Browne 1935, Fisher et al. 1953). Debarking exposes all the sapwood, generating a much greater surface area from which host volatiles can be released, as opposed to logs with bark, where only the cut ends allow rapid semiochemical release. Thus, the attractiveness of debarked logs may be attributed to the release of greater amounts of volatiles.

The humidity of a log is extremely important for host colonization (Beaver 1977); usually logs are not colonized by ambrosia beetles if the water content drops below 40–50% (Saunders et al. 1967, Samaniego and Gara 1970). Debarked logs dry out more rapidly (Beaver 1977), and it is expected that bark-on logs would ultimately show a higher infestation and more degradation than debarked logs (Fisher et al. 1953, Roonwal 1958). However, in our experiment debarked logs were more attractive than bark-on logs throughout the entire 10-wk period. Under natural conditions, debarked logs could still release attractive volatiles weeks after bark removal, but upon landing, and after probing the potential breeding material (at this time with unsuitable humidity levels), beetles might reject it and search for another host. In this experiment, beetles did not have access to the logs, which makes it difficult to assess if this attractiveness to potentially drier logs would indeed result in an initial attack and establishment. However, for a few xylomycetophagous scolytids, the presence of bark appears to be essential for them to initiate an attack (Browne 1961).

It appears that the higher attractiveness of a particular pine log species was not influenced by the volatiles predominant in the environment (stand) where the log was placed. Accordingly, a higher or lower attractiveness of one pine species over the others did not change over time.

Ethanol is a common compound produced in fallen trees (Moeck 1970; Kelsey 1994a, b), and it is very likely that it also was produced in our log baits at some point after they were cut. Based on the response of the selected scolytids to pine log volatiles and ethanol, they could be divided into 3 main groups (Tables 1–3) as follows: (group I) species that were attracted to ethanol but not to pine terpenes: *A. hagedorni*, *A. retusus*, and *X. spinulosus* in the Xyleborini, and *C. schaufussi*, *C. heveae*, and *H. obscurus* in the Cryphalini; (group II) species more attracted to ethanol but still responding to pine terpenes: *X. gracilis*, *X. affinis*, and perhaps *P. cavipennis* (C.A.H.F., unpublished data) in the Xyleborini, and *H. eruditus* in the Cryphalini; (group III) species more attracted to pine terpenes and less responsive to ethanol: *A. obliquus*, *X. ferrugineus*, and *X. catulus*, all in the Xyleborini.

Following similar classifications by Klimetzek et al. (1986) and Gil et al. (1985), the more polyphagous species are found in group I, where ethanol is the main semiochemical cue to host location. None of these species attacks pines in Brazil. Ethanol apparently synergizes host odors for group II species. Group III species, which tend to be the most aggressive scolytids (Klimetzek et al. 1986), appear to congregate mainly in response to host odors, and ethanol seems to be less important in host location. Species in the groups II and III have been reported to breed in pines. The *Xyleborus* species classified as group III typically attack hardwoods (Wood 1982). It appears that this is the first report in the literature showing that these 3 xyleborine beetles have a stronger response to pine volatiles than to ethanol alone. Of the 3 species, *X. ferrugineus* is by far the most ubiquitous in pine forests in Brazil, and it is frequently observed attacking fallen trees in Agudos. This species, along with *X. affinis*, are considered to be the most important economically in the country (Pedrosa-Macedo 1988).

The existence of xylomycetophagous ambrosia beetles that prefer pine volatiles over ethanol alone is another indication that native scolytid species are adapting to the exotic pine species. There are reports of ambrosia beetle attacks on pine stumps but no documented attacks on live, standing trees. It is hard to predict with certainty if and when these beetles will evolve to the next logical step (i.e., attacks on live, stressed trees) as they already do with hardwoods.

Over the 4 experiments involving logs with bark, *X. affinis*, *X. catulus*, *P. cavipennis*, and *A. hagedorni* exhibited a preference for ≥1 pine species in a single test, mainly for *P. car.* variety *caribaea* for the first 3 species, and for *P. car.* variety *hondurensis* for the last. Only *X. ferrugineus* and *A. obliquus* exhibited a differential attractiveness among the pine species in >1 occasion. For *X. ferrugineus*, there were small variations among the experiments. Combining all results, it appears that *P. car.* variety *caribaea* and *P. oocarpa* were the most attractive species, whereas *P. car.* variety *bahamensis* was the least attractive. As for *A. obliquus*, overall *P. car.* variety *hondurensis* and *P. oocarpa* were the most preferred pines, and *P. car.* variety *bahamensis* was again the least preferred.

Species in the genus *Xyleborus* can reproduce parthenogenetically (Beaver 1977, Norris 1979) because endosymbiotic microorganisms activate haploid embryonic development in virgin females (Peleg and Norris 1972). These females produce only males, which then mate with their maternal parents; the resulting isolated genome may lead to a new clone or even a new species (Norris 1992). Thus, *Xyleborus* species, breeding in logs in Brazil, could develop a clone specialized for pines. Normally there is no specialization by ambrosia beetles, but cases of unnatural specialization are known, such as for *Xyleborus fornicatus* Eichhoff in plantations of tea, *Thea sinensis* L., in Sri Lanka (Browne 1958).

Once a tree is felled, the basic composition of semiochemicals present in the boles changes through time. Usually hydrocarbon monoterpenes decrease (Byers et al. 1989) and oxygenated monoterpenes and ethanol increase (Leufvén and Birgersson 1987, Kelsey 1994b). Changes in volatiles released by the logs affect the arrival sequence of scolytids. More aggressive species usually appear first and secondary scolytids tend to come later (Dixon and Payne 1979).

We observed 2 general periods of peak attractiveness of the logs. In experiments I and III, the peak was near the intermediate weeks (weeks 4–7 in experiment I and weeks 3–5 in experiment III), but for experiments II and IV, the peak occurred in the later weeks (8 and 9). Those trends were followed closely by *H. eruditus* (Fig. 1).

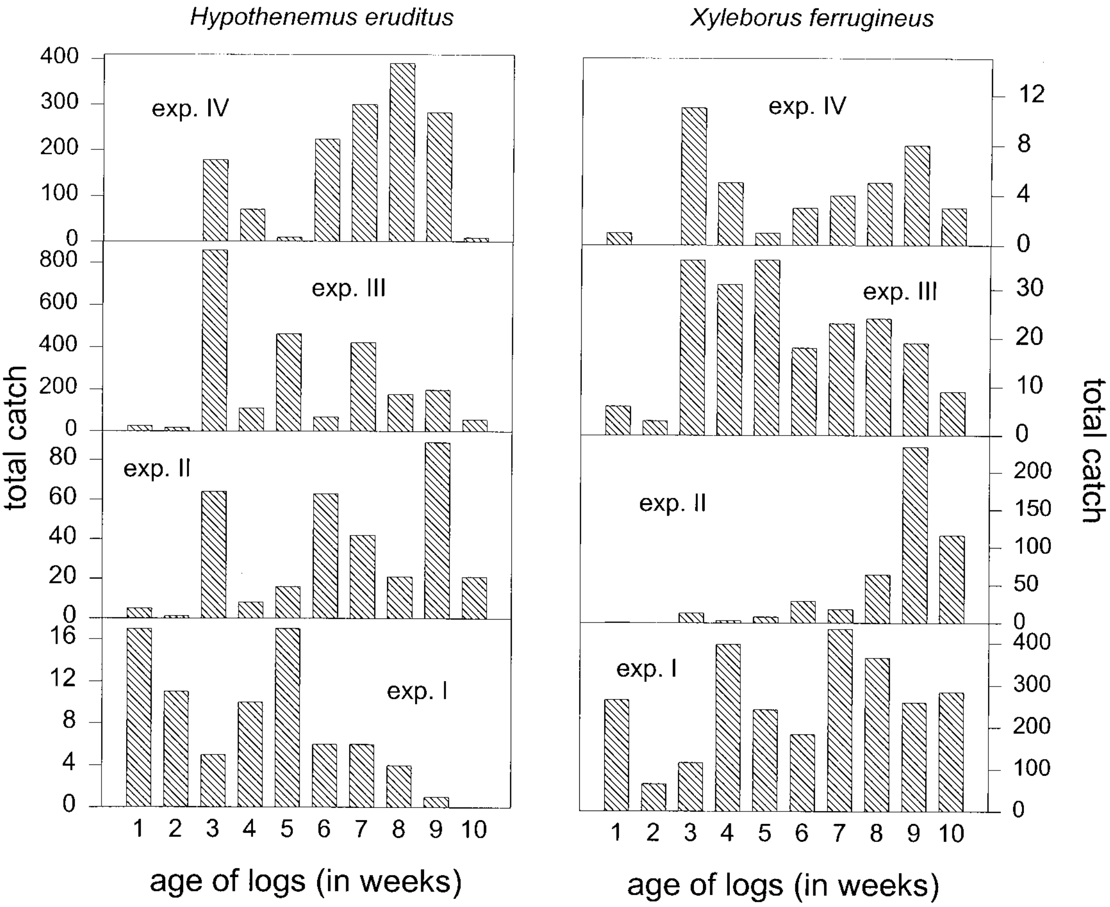

Fig. 1. Abundance of *H. eruditus* and *X. ferrugineus* trapped in tropical bark-on pine log-baited traps over time in 4 different tropical pine stands. Agudos, São Paulo State, Brazil, from December 1992 to September 1995.

Scolytid flights are more abundant in October through March, but they are still present in significant numbers in the other months (Flechtmann et al. 1995). It appears that the lower temperatures prevalent in experiments II and IV caused a reduction in the rate of change of the volatile composition of the pine logs (Kelsey 1994b).

If results based on logs inside traps accurately represent attacks on natural logs, they might indicate that logs could be stored in the forest during winter months for a longer time than during summer months if absolutely necessary (although not recommended) before ambrosia beetle attacks occur. However, *X. ferrugineus*, a species that responds more to pine logs than to ethanol alone, consistently arrived within the first 3 wk (Fig. 1). This early arrival suggests that this species may be one of the most aggressive among the scolytids present in the study sites.

Acknowledgments

We thank Mark Dalusky (Department of Entomology, University of Georgia), Gary DeBarr and Jim Hanula (Forestry Science Laboratory, U.S. Forest Service, Athens, GA), and Robert Rabagglia (Forest Pest Management, Maryland Department of Agriculture, Annapolis) for critical review of the manuscript; and J. Kelley (UCNS, University of Georgia) for assistance in SAS code writing. We also thank J.L.S. Maia and Duraflora S.A. for technical and financial support of the experiments.

References Cited

ANFPC. 1996. Relatório estatístico florestal. ANFPC, São Paulo, Brazil.

Atkinson, T. H., and A. Equihua-Martinez. 1986. Biology of bark and ambrosia beetles (Coleoptera: Scolytidae and Platypodidae) of a tropical rain forest in southeastern Mexico with an annotated checklist of species. Ann. Entomol. Soc. Am. 79: 414–423.

Atkinson, T. H., J. L. Foltz, and R. C. Wilkinson. 1988. *Xylosandrus crassiusculus* (Motschulksky), an Asian ambrosia beetle recently introduced into Florida (Coleoptera: Scolytidae). Fla. Dep. Agric. Cons. Serv. Entomol. Circ. 310.

Bauer, J., and J. P. Vité. 1975. Host selection by *Trypodendron lineatum.* Naturwissenschaften 62: 539.

Beaver, R. A. 1977. Bark and ambrosia beetles in tropical forests, pp. 133–149. *In* BIOTROP Special Publication 2: Bogor.

Beaver, R. A. 1979. Host specificity of temperate and tropical animals. Nature (Lond.) 281: 139–141.

Beaver, R. A. 1988. Biological studies on ambrosia beetles of the Seychelles (Col., Scolytidae and Platypodidae). Z. Angew. Entomol. 105: 62–73.

Berti F., E. 1981. Insetos associados a plantações de espécies do gênero *Eucalyptus* nos estados da Bahia, Espírito Santo, Mato Grosso do Sul, Minas Gerais e São Paulo. Full-Prof. thesis, Universidade de São Paulo, Piracicaba.

Berti F., E., and C.A.H. Flechtmann. 1986. A model of ethanol trap to collect Scolytidae and Platypodidae (Insecta, Coleoptera). IPEF (34): 53–56.

Borden, J. H. 1982. Aggregation pheromones, pp. 74–139. *In* J. B. Mitton and K. B. Sturgeon [eds.], Bark beetles in North American conifers. University of Texas Press, Austin.

Borden, J. H., and J. A. McLean. 1979. Secondary attraction in *Gnathotrichus retusus* and cross-attraction of *G. sulcatus* (Coleoptera: Scolytidae). J. Chem. Ecol. 5: 79–88.

Browne, F. G. 1935. Borer attack on logs of meranti tembaga. Malay. For. 4: 182–186.

Browne, F. G. 1958. Some aspects of host selection among ambrosia beetles in the humid tropics of South-East Asia. Malay. For. 21: 164–182.

Browne, F. G. 1961. The biology of Malayan Scolytidae and Platypodidae. Malay. For. Rec. 22: 1–255.

Byers, J. A. 1995. Host-tree chemistry affecting colonization in bark beetles, pp. 154–213. *In* R. T. Cardé and W. J. Bell [eds.], Chemical ecology of insects 2. Chapman & Hall, New York.

Byers, J. A., B. S. Lanne, and J. Löfqvist. 1989. Host tree unsuitability recognized by pine shoot beetles in flight. Experientia 45: 489–492.

Byrne, K. J., A. A. Swigar, R. M. Silverstein, J. H. Borden, and E. Stokkink. 1974. Sulcatol: population aggregation pheromone in the scolytd beetle, *Gnathotrichus sulcatus.* J. Insect Physiol. 20: 1895–1900.

Carpenter, S. E, M. E. Harmon, E. R. Ingham, R. G. Kelsey, J. D. Lattin, and T. D. Schowalter. 1988. Early patterns of heterotroph activity in conifer logs. Proc. R. Soc. Edinb. Sect. B (Biol. Sci.) 94: 33–43.

Carrano-Moreira, A. F. 1985. Análise faunística de Scolytidae em comunidades florestais no estado do Paraná. M.S. thesis, Universidade Federal do Paraná, Curitiba.

Chandra, A. 1981. Bioecology of wood destroying *Xyleborus* and their control (Insecta: Scolytidae). Indian J. For. 4: 286–289.

Chénier, J.V.R., and B.J.R. Philogéne. 1989. Field responses of certain forest Coleoptera to conifer monoterpenes and ethanol. J. Chem. Ecol. 15: 1729–1745.

Dixon, W. N., and T. L. Payne. 1979. Sequence of arrival and spatial distribution of entomophagous and associate insects on southern pine beetle-infested trees. Tex. Agric. Exp. Stn. Bull. MP-1432.

Dourojeanni, M. J. 1965. Los gorgojos de ambrosia de las familias Scolytidae y Platypodidae (Coleoptera) en el Peru. An. Cient. 3: 9–32.

Drooz, A. T. 1985. Insects of eastern forests. U.S. Dep. Agric. Misc. Publ. 1426.

Fatzinger, C. W. 1985. Attraction of the black turpentine beetle (Coleoptera: Scolytidae) and other forest Coleoptera to turpentine-baited traps. Environ. Entomol. 14: 768–775.

Fisher, R. C., G. H. Thompson, and W. E. Webb. 1953. Ambrosia beetles in forest and sawmill: their biology, economic importance and control. For. Abstr. 15: 3–15.

Flechtmann, C.A.H., and C. L. Gaspareto. 1997. A new trap for capturing Scolytidae (Coleoptera), based on primary attraction. Z. Angew. Entomol. 121: 357–359.

Flechtmann, C.A.H., H.T.Z. Couto, C. L. Gaspareto, and E. Berti F. 1995. Scolytidae em Reflorestamento com Pinheiros Tropicais. IPEF, Piracicaba.

Gil, J., J. Pajares, and M. G. Viedma. 1985. Estudios acerca de la atracción primaria en Scolytidae (Coleoptera) parasitos de coniferas. Bol. Estac. Cent. Ecol. 14: 107–125.

Gray, D. R., and J. H. Borden. 1985. Ambrosia beetle attack on logs before and after processing through a dryland sorting area. For. Chron. 61: 299–302.

Hines, J. W., and H. J. Heikkenen. 1977. Beetles attracted to severed Virginia pine (*Pinus virginiana* Mill.). Environ. Entomol. 6: 123–127.

Iede, E. T. 1985. Perspectivas da pesquisa na área de entomologia para controle de pragas florestais no sul do Brasil, pp. 129–134. *In* Proceedings, IUFRO Workshop on Protection of Forests in the Tropics, 24–30 November 1985. Universidade Federal Paraná, Curitiba.

Kelsey, R. G. 1994a. Ethanol and ambrosia beetles in Douglas fir logs with and without branches. J. Chem. Ecol. 20: 3307–3319.

Kelsey, R. G. 1994b. Ethanol synthesis in Douglas-fir logs felled in November, January, and March and its relationship to ambrosia beetle attack. Can. J. For. Res. 24: 2096–2104.

Kelsey, R. G., and G. Joseph. 1997. Ambrosia beetle host selection among logs of Douglas fir, Western hemlock, and. Western red cedar with different ethanol and α-pinene concentrations. J. Chem. Ecol. 23: 1035–1051.

Klimetzek, D., J. Köhler, J. P. Vité, and U. Kohnle. 1986. Dosage response to ethanol mediates host selection by "secondary" bark beetles. Naturwissenschaften 73: 270–272.

Leufvén, A., and G. Birgersson. 1987. Quantitative variation of different monoterpenes around galleries of *Ips typographus* (Coleoptera: Scolytidae) attacking Norway spruce. Can. J. Bot. 65: 1038–1044.

Lie, R., and A. Bakke. 1981. Practical result from the mass trapping of *Ips typographus* in Scandinavia, pp. 175–181. *In* Proceedings, Management of Insect Pests with Semiochemicals: Concepts and Practice, 23–28 March 1980. Plenum, New York.

Lindelöw, Å., B. Risberg, and K. Sjödin. 1992. Attraction during flight of scolytids and other bark- and wood-dwelling beetles to volatiles from fresh and stored spruce wood. Can. J. For. Res. 22: 224–228.

Lindgren, B. S., and R. G. Fraser. 1994. Control of ambrosia beetle damage by mass trapping at a dryland log sorting area in British Columbia. For. Chron. 70: 159–163.

Macconnell, J. G., J. H. Borden, R. M. Silverstein, and E. Stokkink. 1977. Isolation and tentative identification of lineatin, a pheromone from the frass of *Trypodendron lineatum* (Coleoptera: Scolytidae). J. Chem. Ecol. 3: 549–561.

MacDonald, R. C., and T. W. Kimmerer. 1991. Ethanol in the stems of trees. Physiol. Plant. 82: 582–588.

Marchiori, J.N.C. 1996. Dendrologia das Gimnospermas. Editora da Universidade Federal de Santa Maria, Santa Maria, Ser. Livros Didáticos.

Marques, E. N. 1984. Scolytidae e Platypodidae em *Pinus taeda.* M.S. thesis, Universidade Federal do Paraná, Curitiba.

Marques, E. N. 1989. Índices faunísticos e grau de infestação por Scolytidae em madeira de *Pinus* spp. Ph.D. thesis, Universidade Federal do Paraná, Curitiba.

McLean, J. A. 1985. Ambrosia beetles: a multimillion dollar degrade problem of sawlogs in Coastal British Columbia. For. Chron. 61: 295–298.

Miller, M. C., J. C. Moser, M. D. McGregor, J. C. Gregoire, M. Baisier, D. L. Dahlsten, and R. A. Werner. 1987. Potential for biological control of native North American *Dendroctonus* beetles (Coleoptera: Scolytidae). Ann. Entomol. Soc. Am. 80: 417–428.

Moeck, H. A. 1970. Ethanol as the primary attractant for the ambrosia beetle *Trypodendron lineatum* (Coleoptera: Scolytidae). Can. Entomol. 102: 985–995.

Niemeyer, H. 1985. Field response of *Ips typographus* L. (Col., Scolytidae) to different trap structures and white versus black flight barriers. Z. Angew. Entomol. 99: 44–51.

Norris, D. M. 1979. The mutualistic fungi of Xyleborini beetles, pp. 53–63. *In* Proceedings, Insect-Fungus Symbiosis, 27 August–3 September 1977. University of Florida, Tampa.

Norris, D. M. 1992. Xyleborus ambrosia beetles: a symbiotic ideal extreme biofacies with evolved polyphagous privileges at monophagous prices. Symbiosis 14: 229–236.

Orbay, L., J. A. McLean, B. J. Sauder, and P. L. Cottell. 1994. Economic losses resulting from ambrosia beetle infestation of sawlogs in coastal British Columbia, Canada. Can. J. For. Res. 24: 1266–1276.

Pedrosa-Macedo, J. H. 1988. Atividades de pesquisas em entomologia florestal na UFPR, pp. 1–6. *In* Encontro Sobre Pragas Florestais, 7–8 December 1988. Instituto de Pesquisas e Estudos Florestais, São Paulo.

Peleg, B., and D. M. Norris. 1972. Bacterial symbiote activation of insect parthenogenetic reproduction. Nature New Biol. 236: 111–112.

Phillips, T. W. 1990. Responses of *Hylastes salebrosus* to turpentine, ethanol, and pheromones of *Dendroctonus.* Fla. Entomol. 73: 286–292.

Roonwal, M. L. 1958. Forest entomology in India (1947–1955), pp. 317–322. *In* Proceedings, 10th International Congress of Entomology, vol. 1, 17–25 August 1956, Montreal.

Samaniego, A., and R. I. Gara. 1970. Estudios sobre la actividad de vuelo y selección de huéspedes por *Xyleborus* spp. y *Platypus* spp. (Coleoptera: Scolytidae y Platypodidae). Turrialba 2: 471–477.

SAS Institute. 1990. SAS/STAT user's guide, vol. 2. SAS Institute, Cary, NC.

Saunders, J. L., D. M. Norris, and J. K. Knoke. 1967. Insect–host tissue interrelations between *Xyleborus ferrugineus* (Coleoptera: Scolytidae) and *Theobroma cacao* in Costa Rica. Ann. Entomol. Soc. Am. 60: 419–423.

Schedl, K. 1958. Breeding habits of arboricole insects in central Africa, pp. 183–197. *In* Proceedings, 10th International Congress of Entomology, vol. 1, 17–25 August 1956, Montreal.

Schönherr, J. 1991. Proteção florestal: duas décadas de pesquisa em Curitiba, pp. 188–203. *In* Simpósio, O Desafio das Florestas Neotropicais, 7–12 April 1991, Univiversidade Federal, Paraná, Curitiba.

Schönherr, J., and J. H. Pedrosa-Macedo. 1979. Tierische Schädlinge in forstlichen Monokulturen im Süden Brasiliens. Allg. Fosts Z. (29): 788–790.

Schönherr, J., J. H. Pedrosa-Macedo, and D. Hoffmann. 1974. Pragas animais nos reflorestamentos da região sul do Brasil, pp. 161–162. *In* Anais, II Congresso Florestal Brasileiro, 17–21 September 1973. Federação das Indústrias do Estado do Paraná, Curitiba.

Schroeder, L. M., and A. Lindelöw. 1989. Attraction of scolytids and associated beetles by different absolute amounts and proportions of α-pinene and ethanol. J. Chem. Ecol. 15: 807–817.

Werner, R. A. 1995. Toxicity and repellency of 4-allylanisole and monoterpenes from white spruce and tamarack to the spruce beetle and eastern larch beetle (Coleoptera: Scolytidae). Environ. Entomol. 24: 372–379.

Wood, S. L. 1982. The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae): a taxonomic monograph. Great Basin Nat. Mem. 6: 1–1361.

Received for publication 14 July 1998; accepted 16 December 1998.