The Biology of the Black Twig Borer, *Xylosandrus compactus* (Eichhoff), in Hawaii[1 2]

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The black twig borer, *Xylosandrus compactus* (Eichhoff), belongs to the family Scolytidae and tribe Xyleborini. All species of Xyleborini are ambrosia beetles with the ambrosia fungus serving as the primary food for their development. *X. compactus* also occurs in southern Japan, Indonesia, Vietnam, Malaya, Sri Lanka, south India, Madagascar, Mauritius, Seychelles, across tropical Africa, Fiji and in the United States in Florida, Georgia, Alabama and Louisiana (LePelley 1968; Ngoan et al. 1976; USDA, APHIS 1976).

X. compactus is a serious pest of shrubs and trees. It attacks the live twigs and branches, especially if the host has suffered some setback such as transplanting or drought. Most other species of the tribe Xyleborini attack only unhealthy or newly felled trees. The black twig borer causes extensive economic damage to coffee and cacao throughout tropical Africa, Indonesia and southern India. Seedlings and twigs are readily killed after a single gallery formation by an adult female (LePelley 1968). In Japan, it is a major pest of tea causing extensive dieback (Kaneko et al. 1965).

The black twig borer was first reported in Hawaii by C.J. Davis in November 1961 at Kailua, Oahu, where it was found attacking pink tecoma, *Tabebuia pentaphylla* (L.) Hemsl. (Beardsley 1964). The black twig borer has spread to all major islands of the State (Hawaii Dept. of Agric. 1975). The list of hosts attacked in Hawaii has increased to 108 species of shrubs and trees in 44 families (Table 1). When the present study was begun little was known about the biology of *X. compactus* in Hawaii. Since its introduction, life history studies had not been conducted and the species of ambrosia fungus associated with it had not been confirmed. Four parasites of *X. compactus* introduced into Hawaii since 1961 apparently have failed to become established.

MATERIALS AND METHODS

Life history studies

Active brood galleries of *X. compactus* were field collected from various hosts for establishing laboratory cultures. They were collected on Oahu from Waiahole Valley on Koster's curse, *Clidemia hirta* (L.) D. Don, and from Manoa at the Lyon Arboretum on juniper berry, *Citharexylum caudatum* L.; bullocks-heart, *Annona reticulata* L.; and on Indonesian ginger, *Tapeinochilos ananassae* K. Schum. Infested stems were placed in humidity jars, of the type described by Napompeth (1969), for collection of newly emerged adult females. Infested stems were also placed in petri dishes containing two moist filter papers, and beetles were allowed to emerge. Observations were made on the time of emergence.

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For life history studies, three newly emerged female adults were introduced into each of several petri dishes containing three *Coffea arabica* L. stems, cut into 7.0 cm lengths with ends covered with parafilm, and laid on moist filter papers. All laboratory cultures of *X. compactus* were held at room temperature, which ranged from 23.3 to 27.2°C. Relative humidity ranged from 50 to 60%.

The duration of each of the immature stadia of *X. compactus* was determined by daily observations of stems containing colonies of known age. Beginning two days after initial boring by adult females, five infested coffee stems were opened each day and the contained immature stages counted. The duration of the egg and pupal stages were also determined by sealing the opened galleries with parafilm. Thereafter, the galleries were opened daily and observed.

Determination of the number of larval instars was made by measuring head capsule widths of 590 preserved larvae, using an eyepiece micrometer. These larvae were field collected from *C. hirta* in various stages of development, fixed in KAAD mixture (kerosene, acetic acid, alcohol, and dioxanne) and preserved in 70% alcohol.

The sex ratio was established based on beetles from field infested *C. hirta* and from laboratory rearings on coffee stems. Counts were made using galleries with teneral adults. Longevity studies were conducted on beetles reared on coffee stems in petri dishes. The mother beetles, which remained in the entry tunnels of their brood galleries throughout the period of development, were marked on the exposed portion of the elytra with Testors® enamel paint. Daily observations were made on 95 females which were marked on the 20th day after initiating brood galleries.

Associated ambrosia fungus

The fungus was isolated from three sources: (1) fungus lining the active gallery, (2) newly emerged females, (3) discolored vascular tissues near the site of infestation. The method of isolation from the first source involved aseptically transferring pieces of the ambrosia fungus lining active galleries directly into petri dishes containing Difco potato dextrose agar (PDA). The method of Baker and Norris (1968) for the isolation from female adults was followed. Isolations from discolored vascular tissues of the host plant were made by surface sterilizing infested twigs with 1% $HgCl_2$ for 1 to 5 minutes. After sterilization, each stem was washed, a small piece sliced off from each end so that residual sterilant was not carried over, and the center piece placed on PDA medium. All isolates were incubated in the dark at 28°C for 7 days.

Infestation in host plants

Various host plants infested with *X. compactus* were collected in the field and observed for symptoms of infestation.

Results and Discussion

Life history studies

Egg: The egg of *X. compactus* is oval, white, with a smooth surface. Measurements of 15 fresh eggs ranged from 0.53 × 0.26 mm to 0.59 × 0.30 mm with an average of 0.55 × 0.28 mm. Daily examination of galleries showed that the incubation period varied from 3 to 5 days with 81.1% hatching after 4 days. Only 4.7% failed to hatch (Table 2).

TABLE 1. *Host plants of* Xylosandrus compactus *(Eichhoff) in Hawaii*

Family	Scientific Name	Common Name	Reference
Amaranthaceae	*Charpentiera* sp.	papala	Smith (pers. comm.)
Annonaceae	*Annona cherimola* Mill.	cherimoya	HCEIR (Jan. 67)
	Annona glabra L.	pond apple	Hawaii Dept. of Agric. (1967)
	Annona montana Macf.	mountain soursop	HCEIR (Jan. 67)
	Annona muricata L.	soursop	HCEIR (Jan. 67)
	Annona reticulata L.	bullocks heart	HCEIR (Jan. 67)
	Annona squamosa L.	sugar-apple	HCEIR (Jan. 67)
	Rollinia emarginata Schlecht		Hawaii Dept. of Agric. (1967)
Araceae	*Anthurium andraeanum* Lind.	anthurium	Nakahara (1977)
Araucariaceae	*Araucaria heterophylla* (Salisb.) Franco	Norfolk Island Pine	HCEIR (Jan. 67)
Acanthaceae	*Graptophyllum pictum* (L.) Nees ex Griff.	caricature plant	Davis (1963)
Anacardiaceae	*Anacardium occidentale* L.	cashew nuts	HCEIR (May 73)
	Schinus terebinthifolius Raddi	Christmas berry	Davis (1968)
	Spondias purpurea L.	purple or red mombin	Hawaii Dept. of Agric. (1967)
Apocynaceae	*Vinca* spp.	periwinkle	Davis (1963)
Aquifoliaceae	*Ilex anomala* H.&A.	kawau	Gagne (1972)
Bignoniaceae	*Tabebuia pentaphylla* (L.) Hemsl.	pink tecoma	Davis (1963)
Boraginaceae	*Cordia alliadora* Cham.	laurel	HCEIR (Jan. 67)
Casuarinaceae	*Casuarina equisetifolia* Stickm.	common ironwood, she oak, beefwood	present study
Celastraceae	*Perrottetia sandwicensis* Gray	olomea	Davis (1969b)
Ebenaceae	*Diospyros* sp.	lama	HCEIR (May 73)
Euphorbiaceae	*Acalypha wilkesiana* Muell.-Arg.	painted copper leaf, jacob's coat	Hawaii Dept. of Agric. (1967)
	Aleurites moluccana (L.) Willd.	kukui	HCEIR (Dec. 68)
	Antidesma pulvinatum Hbd.	mehame	Davis (1969b)
	Claoxylon sandwicense Muell.-Arg.	po'ola	Yoshioka (pers. comm.)
Euphorbiaceae	*Croton reflexifolius* HBK.	colpalchi	HCEIR (Jan. 67)
	Drypetes phyllanthoides (Rock) Sherff	mehamehame	Gagne (1971)
Flacourtiaceae	*Flacourtia indica* (Burm.f.) Merr.	governors plum	Hawaii Dept. of Agric. (1967)
Hamameliadaceae	*Liquidambar formosana* Hance		Fujii (1977c)

TABLE 1 (Continued). *Host plants of* Xylosandrus compactus *(Eichhoff) in Hawaii*

Family	Scientific Name	Common Name	Reference
Lauraceae	*Persea americana* Mill.	avocado	Kajiwara (1964)
	Cryptocarya oahuensis (Deg.) Fosb.	holio	Gagne (1976)
Leguminosae			
Mimosoideae	*Acacia farnesiana* (L.) Willd.	klu	Hawaii Dept. of Agric. (1967)
	Acacia koa Gray	koa	HCEIR (Aug. 71)
	Acacia melanoxylon R.Br.	Australian blackwood	HCEIR (Jan. 67)
	Albizzia lebbeck (L.) Benth.	siris tree	HCEIR (Mar. 69)
	Inga paterno Harms		Hawaii Dept. of Agric. (1967)
	Leucaena leucocephala (Lam.) de Wit	koa-haole	Hawaii Dept. of Agric. (1967)
	Pithecellobium dulce (Roxb.) Benth.	opiuma	HCEIR (Dec. 68)
	Prosopis pallida (Humb. & Bonpl. ex Willd.) HBK.	kiawe	Davis (1966)
	Samanea saman (Jacq.) Merr.	monkeypod	HCEIR (Dec. 68)
Caesalpinioidea	*Cassia glauca* Lam.	kolomona	Davis (1969c)
	Cassia spp.	shower tree	Hawaii Dept. of Agric. (1967)
Papilionatae	*Andira inermis* (Wright) HBK.	angelin, patridge-wood	Hawaii Dept. of Agric. (1967)
	Crotalaria sp.		HCEIR (Dec. 68)
	Inocarpus fagifer (Parkins. ex Z) Fosb.	Tahitian chestnut	HCEIR (Jan. 67)
	Indigofera suffruticosa Mill.	indigo	Davis (1969c)
Liliaceae	*Asparagus myriocladus* Hort.	ornamental asparagus	Krauss (1965b)
Loganiaceae	*Buddleja asiatica* Lour.	huelo-'ilio, dogtail	Davis (1969b)
Malpighiaceae	*Byrsonima crassifolia* (L.) HBK	nance	HCEIR (Jan. 67)
Malvaceae	*Abutilon grandifolium* (Willd.) Sweet	hairy abutilon	HCEIR (Dec. 68)
	Hibiscus elatus Sw.	Cuba bast	Hawaii Dept. of Agric. (1967)
Malvaceae	*Hibiscus rosa-sinensis* L.	hibiscus	HCEIR (Jan. 67)
	Hibiscus tiliaceus L.	hau	Davis (1968)
	Malvastrum coromandelianum (L.)	Garcke false mallow	Davis (1969c)
Melastomataceae	*Clidemia hirta* (L.) D.Don	Koster's curse	Davis (1969a)
	Melastoma malabathricum L.	melastoma, Indian rhododendrom	Hawaii Dept. of Agric. (1967)
Meliaceae	*Melia azedarach* L.	pride of India	HCEIR (Dec. 68)
	Swietenia mahogoni (L.) Jacq.	West Indian mahogany	Hawaii Dept. of Agric. (1967)
	Toona ciliata var. *australis* (F. Muell.) C.DC.	Australian red cedar	Hawaii Dept. of Agric. (1967)

TABLE 1 (Continued). *Host plants of* Xylosandrus compactus *(Eichhoff) in Hawaii*

Family	Scientific Name	Common Name	Reference
Moraceae	*Pseudomorus sandwicensis* Deg.	Hawaiian false mulberry, a'ia'i	Yoshioka (Pers. Comm.)
Myrsinaceae	*Myrsine lessertiana* A.DC.	kolea	Yoshioka (Pers. Comm.)
Myrtaceae	*Eucalyptus pilularis* Sm.	blackbutt eucalyptus	HCEIR (Feb. 72)
	Eucalyptus robusta Sm.	Swamp mahogany	HCEIR (May 73)
	Eucalyptus sideroxylon A.Cunn. ex Benth.	red ironbark eucalyptus	HCEIR (Feb. 72)
	Eugenia cuminii (L.) Druce	Java plum	HCEIR (Dec. 68)
	Eugenia malaccensis L.	ohia ai, mountain apple	Davis (1968)
	Eugenia uniflora L.	Surinam cherry, pitanga	Davis (1963)
	Melaleuca leucadendra (Stickm.) L.	paper bark	Nelson & Davis (1972)
	Syncarpia glomulifera (Sm.) Niedz.	turpentine tree	Nelson & Davis (1972)
	Tristania conferta R.Br.	brushbox	Nelson & Davis (1972)
Oleaceae	*Fraxinus uhdei* (Wenzig) Lingelsh.	tropical ash	HCEIR (Jan. 67)
	Jasminum multiflorum (Burm.f.) Andr.	star jasmine	Davis (1963)
	Jasminum sambac (L.) Ait.	pikake	Davis (1963)
Orchidaceae	*Cattleya* spp.	cattleya orchids	Kim (1965)
	Dendrobium spp.	dendrobium orchids	Krauss (1965b)
	Epidendrum spp.	epidendrum orchids	Krauss (1965b) Yoshioka (1968)
Passifloraceae	*Passiflora edulis* Sims.	liliko'i, purple granadilla	HCEIR (Dec. 68)
Pittosporaceae	*Pittosporum tobira* (Thumb.) Ait.	pittosporum	Davis (1963)
Protaceae	*Macadamia ternifolia* var. *integrifolia*	macadamia (Maiden & Betche) Maid.& Bet.	Hawaii Dept. of Agric. (1967)
Rosaceae	*Rubus rosaefolius Sm.*	thimbleberry, 'akala	Davis (1969b)
Rubiaceae	*Coffea arabica* L.	Arabian Coffee	Davis (1968) Yoshioka (1968)
	Coprosma sp.	pilo	Davis (1969b)
	Gouldia sp.	manono	Davis (1969b)
Rutaceae	*Casimiroa edulis* LaLlave & Lex.	white sapote	Hawaii Dept. of Agric. (1967)
	Citrus reticulata Blanco	mandarin orange	Hawaii Dept. of Agric. (1967)
	Murraya paniculata (L.) Jack	mock orange	Hawaii Dept. of Agric. (1967)
	Pelea sp.	'alani	Davis (1969)
	Flindersia brayleyana F. Muell.	silkwood	Hodges & Stein (1977)
Santalaceae	*Santalum freycinetianum* Gaud.	Freycinet sandalwood	Fujii (1977) (pers. comm.)

TABLE 1 (Continued). *Host plants of* Xylosandrus compactus *(Eichhoff) in Hawaii*

Family	Scientific Name	Common Name	Reference
Sapindaceae	*Alectryon* sp.	mahoe	Yoshioka (pers. comm.)
	Euphoria longana Lam.	longan, dragons eye	HCEIR (May 73)
	Litchi chinensis Sonn.	litchi	Hawaii Dept. of Agric. (1967)
	Melicoccus bijugatus Jacq.	Spanish lime	Hawaii Dept. of Agric. (1967)
	Sapindus oahuensis Hbd.	lonomea	Yoshioka (Pers. Comm.)
Solanaceae	*Solanum sodomeum* L.	apple of Sodom	HCEIR (Dec. 68)
Sterculiaceae	*Melochia umbellata* (Houtt.) Stapf.	melochia	HCEIR (Jan. 67)
	Theobroma cacao L.	cocoa tree	HCEIR (Jan. 67)
Thymeliaceae	*Wikstroemia* sp.	'akia, false ohelo	Fujii (1977a)
Urticaceae	*Olmediella betschleriana* Loesen.	manzanote	HCEIR (Jan. 67)
	Pipturus albidus (H.&A.) Gray	mamaki	HCEIR (Jan. 67)
Verbenaceae	*Callicarpa pendunculata* R.Br.	beauty berry	HCEIR (Jan. 67)
	Citharexylum caudatum L.	juniper berry	present study
	Lantana camara L.	lantana	Davis (1969b)
	Stachytarpheta australis Mold.	Cayenne vervain	HCEIR (Dec. 68)
	Vitex trifolia L.	vitex	Davis (1963)
Vitaceae	*Vitis labruscana* Bailey	Isabella grape	Krauss (1965a)
Zingerberaceae	*Alpinia purpurata* (Vieill.) K. Schum.	red ginger	present study
	Tapeinochilos ananassae K. Schum	Indonesian ginger	present study

TABLE 2. *Incubation period of* X. compactus *eggs (n=106)*

Gallery No.	Number of eggs/gallery	Days after deposit 2	3	4	5	Nonviable eggs
		Numbers hatching				
1	6	0	0	4	2	0
2	5	0	2	2	0	1
3	7	0	0	3	4	0
4	12	0	3	5	2	2
5	11	0	3	6	2	0
6	16	0	5	9	0	2
7	8	0	2	6	0	0
8	14	0	4	9	1	0
9	8	0	1	5	2	0
10	9	0	0	9	0	0
11	10	0	4	4	2	0
TOTAL	106	0	24	62	15	5
% hatched & non-viable		0	22.6	58.5	14.1	4.7

Larva (Fig. 1): Two larval instars were indicated by the frequency distribution of head capsule widths of field collected larvae (Fig. 2). The first instar had an average width of 0.212 ± .025 mm and the second instar an average of 0.347 ± .021 mm.

There are two male as well as two female instars, but it is believed that because of the relatively small size of the males, head capsule widths of both male instars fell within the first peak of the graph, and were not distinguished by this method. Ngoan et al. (1976) suggested that this uncertainty could be resolved by measuring the all male progeny of the unmated females. However, all male progeny rarely occurred in the field, and a very low percentage of unmated females produced a brood in the laboratory.

The number of days after the female bored into the twig, at which the various instars were found was as follows: first, 7 to 20 days; second 10 to 21 days; and prepupae, 14 to 24 days (Table 3). The first pupa was dissected out of the twig 15 days after the female entered the twig. The minimum number of days for each stadium was: first, 3; second, 4; and prepupa, 1; for a total minimum duration (first instar to pupa) of 8 days at 25 ± 3°C.

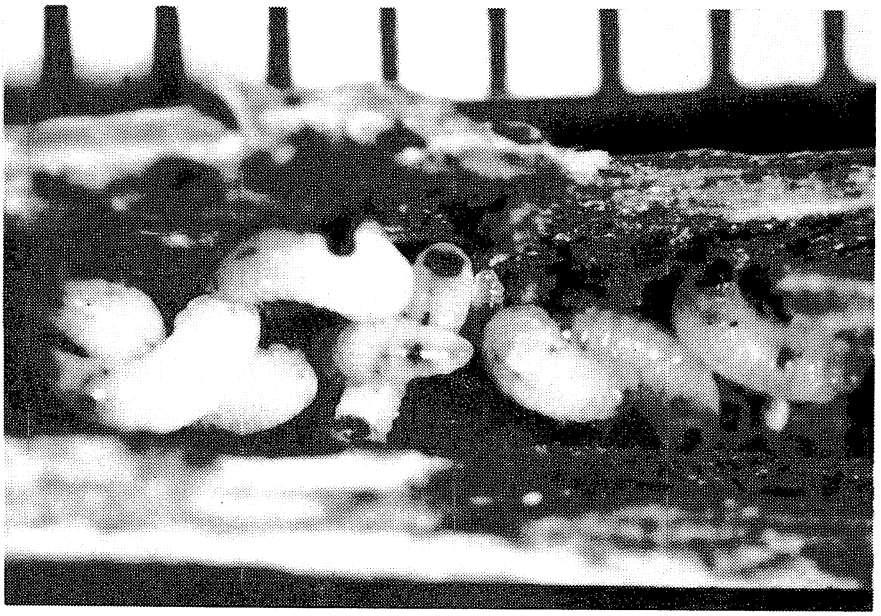

Fig. 1. Larvae of *X. compactus* in the leaf petiole of *Anthurium andraeanum* Lind. (1 division = 1 mm; Mag. 15X).

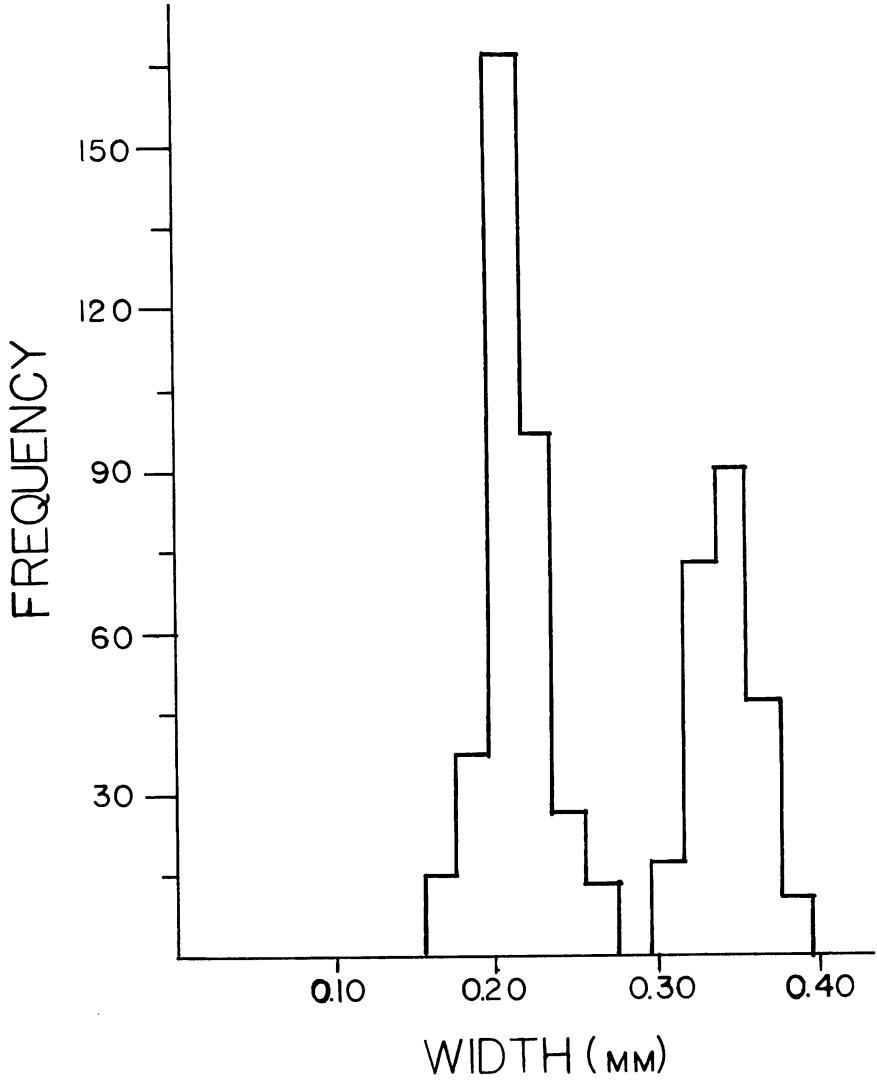

Fig. 2. Distribution of field-collected larval head capsule widths of *X. compactus* (n=590).

TABLE 3. *Numbers observed in laboratory galleries of* X. compactus *immatures* (n=1198, 5 twigs/day for 25 days)

Days after initial boring	Numbers Observed eggs	Larval Instars 1st	2nd	Prepupae	Pupae
2	-				
3	-				
4	5				
5	23				
6	38				
7	58	4			
8	41	11			
9	51	25			
10	42	29	7		
11	32	35	18		
12	21	28	22		
13	15	29	42		
14	6	23	25	11	
15		14	28	10	9
16		16	24	14	16
17		10	18	16	39
18		9	12	28	25
19		6	11	19	46
20		3	14	20	33
21			7	17	35
22				7	24
23				5	12
24				3	4
25					3

Pupa (Fig. 3): The pupal duration ranged from 6 to 7 days with an average of 6.6 days. There were distinct color changes in the body of the pupa with age. The development occurred as follows: First and second day, the entire body is white; third day, the eyes are tanned; fourth day, the mandibles are tanned; and fifth day, the tips of the metathoracic wings are black in females with the body light brown.
Adult (Fig. 4): After pupal ecdysis, the teneral female adult is light brown and turns shiny black in 3 to 4 days. The adult female has a body length of 1.6 to 1.8 mm and width of 0.72 to 0.74 mm (n=20). The male adult is light brown after pupal ecdysis and in 3 to 4 days turns reddish brown. It is smaller than the female, 0.90 to 1.3 mm in length and 0.42 to 0.46 mm in width (n=20). The male possesses degenerate metathoracic wings and is incapable of flying.

Preliminary observations revealed emergence taking place almost entirely between noon and 5:00 P.M. Data on beetle emergence between noon and 5:00 P.M. are presented in Table 4. Maximum emergence occurred between 3:00 and 4:00 P.M.

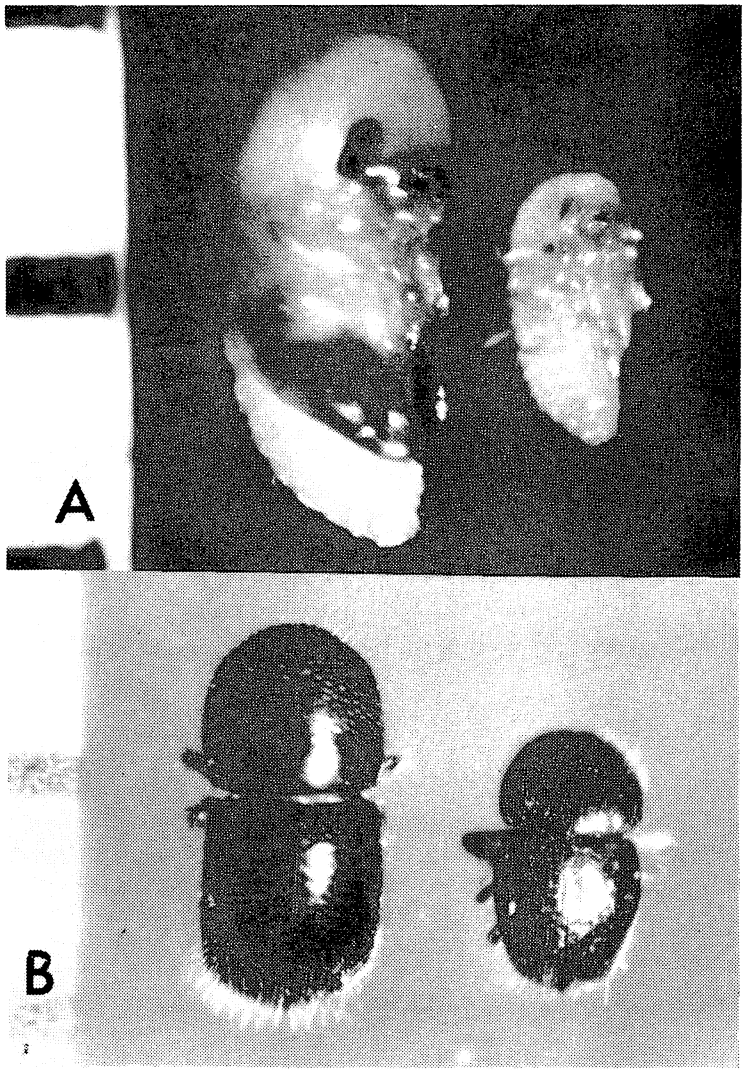

Fig. 3A. Female (left) and male (right) pupae, 5 days after formation (1 division = 1 mm; Mag. 40X). 3B. Female (left) and male (right) adult, 4 days after pupal ecdysis (1 division = 1 mm; Mag. 33X).

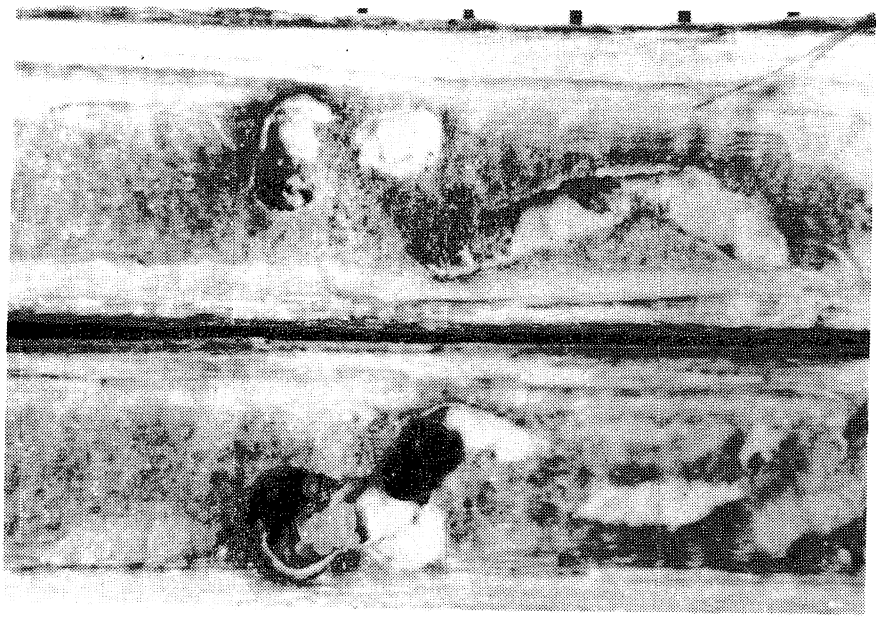

Fig. 4. Gallery in coffee stem split open 5 days after initial boring by the adult female. Ambrosia fungus and eggs are present (1 division = 1 mm; Mag. 14X).

TABLE 4. *Emergence of adult female* X compactus *from galleries*[a]

Time Observed	Number emerged
12:00 M	6
1:00 P.M.	36
2:00 P.M.	60
3:00 P.M.	123
4:00 P.M.	219
5:00 P.M.	8

[a] Observations made on field collected and laboratory reared beetles (n=452).

Female beetles emerging from field collected stems, were immediately transferred to fresh coffee stems in petri dishes. Beetles began boring into stems 30 minutes to 12 hours after release, and bored a distance equal to the length of their body in 2 to 3 hours. Females continued to bore, cutting through the vascular tissues, until they reached the pith, they bored out along the pith on either side of the entry tunnel. The length of time over which boring occurred was proportional to the number of eggs laid.

Observations made on 50 female beetles showed a preoviposition period (after pupal ecdysis to the deposit of the first egg) of 12 to 14 days. During the first 7 to 9 days after pupal ecdysis, the females remained within the parental gallery. Apparently, mating occurred during this time. Thereafter, the females emerged from the gallery and bored into a new host twig. Over a period of 5 to 7 days: (1) a gallery was constructed, (2) ambrosia fungus was introduced and cultivated by the female, (3) eggs were laid in clusters on the ambrosia fungus (Fig. 5). Eggs were found in galleries from the 4th to the 14th day after initial boring, for an oviposition period of approximately 7 to 9 days. Total egg production per female ranged from 2 to 16 eggs. The maximum number of eggs was found 7 to 9 days after initial boring. The mean number of eggs per gallery present at that time was 8.4 ± 3.5.

Fig. 5. Typical symptom of twig dieback of juniper berry, *Citharexylum caudatum* L. caused by *X. compactus*.

Field populations had male to female sex ratio of 1:9.0 ± 2.1 determined from a sample of 50 galleries, each with 13.6 ± 5.4 offspring. The laboratory population had a sex ratio of 1:6.1 ± 1.9 determined from 50 galleries, each with 8.7 ± 2.4 offspring. The t-test showed a highly significant difference, at the .01 probability level, between sex ratios of field and laboratory populations. In contrast to the normal average sex ratio, occasional galleries with all male progeny were also observed. Five out of 260 galleries sampled in the field and 2 out of 156 galleries in the laboratory were found to have all male progeny. No differences in size or structure were observed between males obtained from mated parents, and those from all male galleries.

Since unmated females of *X. compactus* produced only male progeny, Entwistle (1964) believed that the type of parthenogenesis involved was haploid arrhenotoky. Takenouchi and Takagi (1967) concluded that, in species with haploid males, the sex ratio fluctuated rather widely from strain to strain within species. Sex ratios could also be influenced to some extent, within the same species or strain, by various environmental factors, and often showed no tendency to conform to any fixed percentage of males. Thus, various sex ratios observed by different researchers (Lavabre 1958; Brader 1962; Entwistle 1964; Gregory 1954; Speyer 1923; Kaneko 1965; Kaneko *et. al.* 1965; Kalshoven 1958), and differences between field and laboratory population sex ratios obtained in this study, were probably due to different environments and/or different strains of *X. compactus*.

The mother beetles, which remained in the entry tunnels of their brood galleries throughout the period of brood development, emerged from entry tunnels after an average of 26.5 ± 1.3 days following initial boring. Their female progeny left the galleries after an average of 29.1 ± 1.1 days following initial boring. Longevity studies showed that after emergence, 83.3% of the mother beetles crawled on twigs and the filter paper, but did not initiate new galleries. These beetles had a total longevity of 38.6 to 41.6 days. The remaining 16.7% of the mother beetles, bored into twigs for a distance equal to the length of their body, but did not form galleries. These had a total longevity of 42 to 58 days. Observations on the male progeny of the marked mother beetles (1 to 2 males per brood gallery), showed that 83.9% of the males remained in the galleries, with a life span of approximately 4 to 6 days. The other 16.1% emerged 27 to 29 days after initial boring by the mother. These lived 7 to 10 days.

Associated ambrosia fungus

The three sources of the fungus produced mycelium and micro and macroconidia on the PDA medium. Identification was made by Dr. E. Trujillo of the Plant Pathology Department, University of Hawaii, who stated the fungus to be *Fusarium solani* (Mart.) Snyd. & Hans. This corresponded with the identification of Ngoan et al. (1976), who isolated *F. solani* from discolored xylem chips of the host plants, the ambrosia fungus lining the brood gallery, and from matured females. Contrary to the findings of these workers, Brader (1964) in the Ivory Coast considered the ambrosia fungus of *X. compactus* to be a new species and named it *Ambrosiella xylebori*. Batra (1967) did a taxonomic revision of the ambrosia fungi, considering the genus *Ambrosiella* to be the true ambrosia fungi with moniliod chains of cells.

The relationship between *F. solani* and *A. xylebori* is unclear. However, Trujillo (pers. comm.) suggested that the latter may be a synonym of *F. solani*. The sprout

cells of the ambrosial phase, which bear their conidia in chains, are usually confined to the active galleries and fungal repositories, the mycangia. This growth form is not found in *F. solani* in culture. Ambrosia fungi when cultured on laboratory media yield mycelial growth and micro and macroconidia.

X. compactus is one of the few species of ambrosia beetles that attacks live twigs and branches, while most other species primarily attack newly felled or dead trees. Apparently, the pathogenic action of the ambrosia fungus, *F. solani* to the host plants enables *X. compactus* to attack live plants. The pathogenic action of *F. solani* to woody host plants of *X. compactus* has been proven by pure culture isolates of *F. solani* from discolored vascular tissues of a large number of host species (Dr. E. Trujillo, personal communication).

Infestation in host plants

The typical symptom of the host plant that characterized black twig borer infestation was the necrosis of leaves and stem extending from the entry hole distally to the terminal of the branch (Fig. 6). Flagging of branches was noted 5 to 7 days after initial tunneling and gallery formation. Woody dicotyledonous stems larger than 10 to 15 mm in diameter, depending on the species of host plant, were observed with entry holes, but rarely with successful gallery formation. Brader (1964) related this behavior to the adult dependency on the ambrosia fungus as the only source of food. During construction of the gallery, females appeared to live entirely on food reserves accumulated in the mother gallery, and, to survive, were soon obliged to find a suitable place (the pith) for growth of the ambrosia fungus. To do this they first had to pass through the bark and wood tissues, and, as a consequence, only succeeded in establishing galleries in branches of smaller diameter (2.5 to 15.0 mm).

With herbaceous monocotyledons, such as red ginger, *Alpinia purpurata* (Viell.) K. Schum., successful gallery formation was seen in stems as large as 25 to 30 mm in diameter. These stems, with scattered vascular system and no woody tissues, were relatively easily penetrated by *X. compactus,* with gallery formation occurring 2 to 8 mm beneath the epidermis.

Entry holes with exuding sap on branches, 2.5 to 15 mm in diameter, were observed on *Croton reflexifolius* HBK. and *Acacia koa* Gray. Of these, none were found with galleries, nor were adult females present. In successful borings in these hosts, there were no signs of exuding sap in entry tunnels leading to brood galleries containing adult females and broods. The sap exudation is considered to be a factor repellent to *X. compactus* infestation. The primary attack of stressed host plants by *X. compactus* seems to be due to the presence of such repellent factors in healthy plants. Evidently, the production of sap in shrubs and trees is less when they are in stress, and thus, *X. compactus* is best able to form galleries and produce progeny in stressed hosts.

Summary

The life history of *Xylosandrus compactus* (Eichhoff) was studied by rearing the beetles on *Coffea arabica* L. stems in the laboratory and by collecting infested host plants.

The eggs of *X. compactus,* which were laid in clusters on the ambrosia fungus, had an incubation period of 3 to 5 days. There were 2 instars identified in field collected larval samples in various stages of development. The larval period ranged from 8 to 13 days and the pupal stage, 6 to 7 days.

The teneral adult is light brown and turns black in 3 to 4 days. The male is reddish brown, smaller than the female and is incapable of flying.

Adult females of the new generation left parental galleries after an average of 29.0 ± 1.1 days following initial boring by mother beetles. A male to female sex ratio of 1:9.0 ± 2.1 was determined from samples of field population, while laboratory population had a sex ratio of 1:6.0 ± 1.9. Unmated females produced all male progeny, showing that the type of parthenogenesis involved was arrhenotoky. A preoviposition period of 12 to 14 days was observed, with young females remaining within the gallery during the first 7 to 9 days after pupal ecdysis, where mating occurred. Thereafter, the females emerged from the gallery, bored into a new host twig, introduced the ambrosia fungus, and constructed a gallery. Eggs were laid in the gallery on the ambrosia fungus lining from the 4th to the 14th day after initial boring. Total longevity for females ranged from 38.6 to 41.6 days. Most females that had already reared one brood failed to excavate new galleries.

The ambrosia was identified by Dr. E. Trujillo as *Fusarium solani* (Mart.) Synd. & Hans. The ambrosia fungus appeared to constitute the only food for *X. compactus* throughout the life cycle. Trujillo (personal communication) confirmed the pathogenicity of *F. solani* to woody host plants of *X. compactus*.

The typical symptom in host plants that characterized black twig borer infestation was a necrosis of leaves and stem, extending from the entry hole distally to the terminal of the branch.

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