Trophic relationships between palms and bruchids (Coleoptera: Bruchidae: Pachymerini) in Peruvian Amazonia

by

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Abstract

Qualitative and quantitative host plant data are provided for palm bruchids in a part of Amazonia from where previously few or no data were available. The host range and geographical distribution of several species are extended. The role of fruit structure on susceptibility to bruchid infestation and fruit maturity on oviposition site selection is discussed. The importance of mesologic conditions, particularly in areas subjected to flooding, on population dynamics of palm seed beetles is stressed. A specialist parasitoid of *Caryoborus serripes*, which is a specific predator of *Astrocaryum* nuts, is recorded for the first time; a trichogrammatid parasitic on the eggs of the same bruchid is also identified.

Keywords: Bruchidae, Astrocaryum, seed beetles, palms, floodplains, Amazon.

Resumo

São apresentados dados qualitativos e quantitativos sobre os bruquídeos das palmeiras da Amazônia peruana, os quais pouco se conhecia. O número de plantas hospedeiras e a distribuição geográfica de várias espécies se encontram ampliados. Discute-se o papel da estrutura dos frutos sobre sua sensibilidade aos bruquídeos. Dá-se novos dados sobre o papel da maturação dos frutos na seleção do local de postura, e sobre a importância das condições do meio, particularmente em solos inundados, à dinâmica de população de bruquídeos nas palmeiras. Apresenta-se, pela primeira vez, um parasito de *Caryoborus serripes*, que é consumidor das sementes de *Astrocaryum*; um Trichogrammatidae parasito de ovos da mesma espécie do bruquídeo está igualmente identificado.

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Introduction

Members of the tribe Pachymerini (Bruchidae: Pachymerinae) of New World origin almost exclusively use palms as host plants and are therefore commonly called palm bruchids. These specialists are presently distributed in four genera: *Caryoborus* (3 species), *Caryobruchus* (6 species), *Pachymerus* (7 species) and *Speciobruchus* (4 species). Almost all species are South and Central American, only one species, *Caryoborus gleditsiae* (JOHANSSON & L.), reaches the southern part of the United States (NILSSON & JOHNSON 1993). *Pachymerus cardo* (FÅHRAEUS) and *Pachymerus lacerdae* Chevrolat have been introduced in tropical Africa (PREVETT 1966).

Bruchids have a negative impact on palms by consuming seeds which are suited for human consumption, and also by reducing the reproductive potential of palms. This last point is documented in a few instances (JANZEN 1971b; SIST 1989; WRIGHT 1990). However, the state of both palm and bruchid taxonomy has not yet permitted a precise assessment of relationships between host species and their associated bruchids. New data on 33 palm and 5 seed beetle species in Peru are reported.

Study area, materials and methods

Study area

Fallen palm fruits were collected between October 1990 and June 1992, and in August 1993, in five locations in Peru: Iquitos, Department of Loreto, Province of Maynas, (3°55'S, 73°45'W), 125 m above sea level; Santa Cecilia in the Maniti River valley, Department of Loreto, Province of Maynas (3°24'S, 72°45'W), 125 m above sea level; Jenaro Herrera, Department of Loreto, Province of Requena (4°55'S, 73°40'W), 125 m above sea level; Moyobamba, Department of San Martin, Province of Moyobamba (6°02'S, 76°58'W), 832 m above sea level; Puerto Maldonado, Department of Madre de Dios, Province of Tambopata (12°38'S, 69°12'W), 265 m above sea level.

Palms of the studied areas

According to KAHN & GRANVILLE (1992), 33 of the 39 Amazonian genera occur in Peru. MOUSSA et al. (1992) present the distribution of palm species in the main river valleys of Peruvian Amazonia. Their distribution per Departments and Provinces is found in KAHN & MOUSSA (1994a). A total of 33 species in 20 genera were sampled. Most of them belong to the subfamily Arecoideae which is particularly diversified in Amazonia with 28 genera (KAHN & GRANVILLE 1992). The others belong to the Calamoideae and Phytelephantoideae (Tab. 1). *Chelyocarpus* and *Itaya*, the two Amazonian Coryphoideae, like *Chamaedorea* and *Wendlandiella*, the Amazonian Ceroxyloideae, occur in Peruvian Amazonia but were not sampled. Monotypic Nypoideae do not occur naturally in the Americas (UHL & DRANS-FIELD 1987). Latin names follow the list presented by KAHN & MOUSSA (1994a, b) for Peru.

Sampling techniques

Sample size varied according to fruit availability and size. Fruits were assigned to three age classes according to apparent maturity: class 1 - fresh fruits, with epicarp and mesocarp (pulp) intact; class 2 - fruits with epicarp and mesocarp partly destroyed; class 3 - fruits with epicarp and mesocarp removed and with endocarp completely cleaned. Fruits in the first category were assumed to have fallen less than a few weeks before sampling took place, whereas the age of fruits without mesocarp was assumed to be more than two months. Fruits were usually incubated in the laboratory until all beetle adults had emerged. In some cases, they were opened, and larvae and pupae were counted. Larval identification used mouthparts and spiracle morphology and last abdominal segment chaetotaxy (DELOBEL unpubl.). Bruchid eggs were examined and trichogrammatid emergence holes were recorded for evaluation of parasitism. When

unhatched eggs were observed, they were removed and kept in aerated plastic vials until emergence of bruchid larvae or parasitoids.

Voucher specimens of all mentioned palm seeds are deposited in the Orstom collection of seeds (Entomology Laboratory, Paris), under references PALMAE 0016 to 0050. Bruchid and Scolytid voucher specimens are deposited in the Orstom collection of palm insects.

Results

Palms infested

Members of the Calamoideae and of the Phytelephantoideae, as well as of the tribe Iriarteeae in the Arecoideae did not yield any seed beetle. Other tribes of the Arecoideae were diversely associated with Bruchidae (Tab. 1 & 2). In the Areceae, *Oenocarpus bataua* was infested by *Caryoborus gracilis* NILSSON. In the Geonomeae, *Pholidostachys synanthera* was infested by the same species. And all members of the Cocoeae except *Bactris* were the host of one or more bruchid species.

Infestation rates

Infestation rates by bruchids (Tab. 1) were highly variable, both between palm species and between trees within a species. Up to 90 % (*Attalea tessmannii*) and even 97 % of the fruits (*Scheelea phalerata*) were infested, with corresponding infestation rates of the seeds reaching 75 and 84 %, respectively. On the other hand, low levels of infestation often indicated that fruits had not reached a susceptible stage of maturation at the time of sampling.

Bruchid specificity (Tab. 2)

Pachymerus cardo (FÅHRAEUS), developed alone or together with Speciomerus giganteus and Caryoborus serripes in fruits of Scheelea butyracea (in Jenaro Herrera), Scheelea phalerata (in Puerto Maldonado), Attalea tessmannii BURRET, Scheelea butyracea, Maximiliana maripa and Elaeis guineensis (in Iquitos). Its large eggs (2.1 to 2.6 mm long) were laid singly, either glued to the ligneous fibers surrounding the nut or to the endocarp itself. Penetration tunnels were drilled by newly emerged larvae perpendicularly to the surface and were often more than 15 mm long. Some larvae died in the process. One larva usually totally consumed the seed it reached. When several larvae developed in the same seed, only one reached maturity. Adults emerged through a circular hole measuring 4.5 to 6 mm.

On fruits of *Oenocarpus bataua*, *Caryoborus gracilis* NILSSON, usually laid isolated, 1.0 to 1.1 mm long eggs on the ligneous fibres which constitute the endocarp. Fruits having lost their endocarp after several months on the soil were however still suitable for oviposition. Up to 5 larvae could develop in a single fruit. Adult exit hole was 3.2 to 4.2 mm in diameter.

Caryoborus serripes STURM, was found in the fruits of all Astrocaryum species except Astrocaryum jauari. It was already known from Jenaro Herrera on Astrocaryum chonta (COUTURIER & KAHN 1992). In addition, two specimens were bred from 100 fruits of Scheelea phalerata in Puerto Maldonado, and one specimen from 15 nuts of *E.* guineensis left under Astrocaryum chambira palms in Iquitos, among A. chambira fruits heavily infested by C. serripes. Eggs were laid in batches of 3 to 6 1.1 to 1.3 mm long eggs. As Astrocaryum fruits usually contain only one seed, the number of larvae which could complete their development in a nut depended on fruit size: up to five larvae in Astrocaryum javarense and A. macrocalyx, up to 7 larvae in A. chonta, up to ten larvae in A. huicungo, and up to 15 larvae in A. chambira. The adult emergence hole was 4.0 to 5.2 mm in diameter, and all emerging adults often used the same exit hole.

Speciomerus giganteus was found either alone or in combination with *P. cardo* in seeds of *Attalea racemosa*, *Scheelea butyracea* and *S. phalerata* in the Iquitos area, and of *S. phalerata* in Jenaro Herera. Only one larva developed in a seed, and the number of larvae in a single fruit ranged from one (in *S. butyracea*) to three (in *A. racemosa*). Eggs were laid singly. Adult exit hole was 6 to 7 mm in diameter.

Fruits of *Elaeis guineensis* collected in an abandoned palm-grove in Santa Cecilia belonged to selected varieties with high oil content. A sample of 462 nuts did not yield any bruchid, and casual observation of numerous fallen nuts failed to reveal any sign (emergence holes) of seed beetle infestation. The mean endocarp diameter of a sample of 35 of these nuts was 14.0 ± 1.7 mm. A sample of 30 palm nuts collected in Iquitos was heavily infested by *P. cardo* (94 %). These nuts were larger (mean diameter: 22.8 ± 3.6 mm) than the former, as shown by a Student-test (t = 11.4; difference significant at the 0.001 % level).

Effect of nut age

The effect of *Oenocarpus bataua* and *Astrocaryum* spp. fruit maturation on seed beetle infestation was studied. Out of 152 freshly fallen (class 1) *O. bataua* nuts, 8 were infested by *C. gracilis*; out of 762 older (classes 2 and 3) fruits, 59 were infested (χ^2 : 1.11, difference not significant). On the other hand, 15.8 % of 177 freshly fallen *Astrocaryum* nuts were infested by *C. serripes*, as compared with 24.9 % of 1032 up to two months old (class 2) nuts, and 25.9 % of 420 older (class 3) nuts (χ^2 : 7.76, difference significant at the 2.0 % level).

Hymenopterous parasitoids

Two species of Hymenopterous parasitoids were obtained from bruchid-infested palm nuts: a braconid parasitic on larvae and a trichogrammatid parasitic on eggs. C. serripes larvae and pupae breeding in Astrocaryum chonta, A. javarense and A. macrocalyx nuts were affected by the braconid, and parasitism rates ranging from 5 to 20 % were recorded (QUICKE & DELOBEL unpubl.). The trichogrammatid, apparently referable to Uscana caryedoni VIGGIANI, heavily parasitized eggs of C. serripes on Astrocaryum huicungo. A sample of 33 egg batches (245 eggs) showed a 60 % infestation level by the trichogrammatid, and in some batches only the innermost egg was not parasitized. Eggs of C. serripes laid on Astrocaryum macrocalyx, A. javarense and A. chonta were also infested by U. caryedoni. Signs of parasitization (adult emergence holes) by an unidentified trichogrammatid were recorded on P. cardo eggs infesting fruits of Attalea tessmannii and Scheelea butyracea (in Tarapoto Isla near Iquitos). Parasitism rates were sometimes very high (up to 92 % on Scheelea butyracea).

Bruchid diversity

The present survey extends our knowledge of the host range and/or geographical distribution of several palm bruchids: C. serripes, which was previously known from Astrocaryum spp. only (there is a doubtful record from a Maximiliana nut: BRIDWELL 1929), is recorded from Scheelea phalerata and Elaeis guineensis. C. gracilis is recorded for the first time on *Pholidostachys synanthera*; this constitutes the first record of a bruchid from a palm in the Geonomeae. We record for the first time Pachymerus sveni NILSSON in Peru; it was hitherto known only from Brazil, Venezuela (NILSSON & JOHNSON 1993) and French Guiana (SIST 1989). On the other hand, four palm genera with known bruchid hosts failed to yield any seed beetle: Euterpe oleracea is the host of P. sveni in Brazil; there are records of Pachymerus bactris, P. cardo and P. sveni on Bactris spp. seeds in different parts of South America; and there is one record of C. gracilis on Mauritia flexuosa in Venezuela. We did not obtain Caryoborus chiriquensis SHARP from *Phytelephas macrocarpa*; C. chiriquensis is recorded from Ecuador on Phytelephas sp. and Phytelephas aequatorialis (NILSSON & JOHNSON 1993). Members of the tribe Iriarteeae are recorded as hosts of Pachymerinae (JOHNSON in litt.), whereas Mauritiella and Lepidocaryum in the Calamoideae have no known bruchid predator (NILSSON & JOHNSON 1993).

JANZEN (1971b) found that 1.8 % only of the fruits collected below an adult Scheelea rostrata in Costa Rica had at least one viable seed, predation by Caryobruchus buscki BRIDWELL (= Speciomerus giganteus) and an unidentified species of Pachymerus (probably P. cardo) being by far the most important mortality factor. In the study area, bruchids are the major factor of seed mortality for some, but not all, of the palms sampled (Tab. 1). Other factors were identified in the course of this study, particularly scolytids and moulds. The scolytid Coccotrypes carpophagus (HORNUNG) was found in seeds of Socratea exorhiza, Mauritia carana, Astrocaryum spp., Desmoncus polyacanthos, Lepidocaryum gracile, Elaeis guineensis; Coccotrypes cyperi (BEESON) was found on E. oleracea, J. bataua and Scheelea bassleriana; Coccotrypes dactyliperda (F.) on Astrocaryum macrocalyx; Hypothenemus obscurus (F.) on Euterpe oleracea and Araptus laevigatus (EGGERS) on Jessenia bataua.

Factors affecting bruchid population levels

Seed eaters with a narrow host range are known to have highly variable population levels; this is due in part to alternate bearing, as shown in Barro Colorado Island, Panama (WRIGHT 1990). Speciomerus giganteus has discrete generations in this area on a single palm host, Scheelea zonensis; in years of high seed production, "satiation" occurs in the predator; early maturing seeds become heavily infested, whereas late maturing fruits escape oviposition by the seed beetle. The situation is quite different in the Peruvian forest, where Speciomerus giganteus has at least three different hosts, with probably highly asynchronous fruiting seasons. The same is true for *P. cardo* (5 host species), *C. serripes* (8 host species) and *C. gracilis* (2 host species). Continuous breeding of the seed beetles, with at times intense inter- and intraspecific competition is plausible, provided their mobility and searching capacity are high enough. Mesologic conditions may drastically affect infestation levels by seed beetles. For example, Astrocaryum jauari and Elaeis oleifera grow in areas subjected to flooding, and their

seeds usually fall in the water, where infestation by bruchids cannot take place. Astrocaryum jauari fruits are predated upon by several fish species (Piaractus brachypomus, Brycon sp., Colossoma macropomum) during high waters (GOTTSBERGER 1978; GOULDING 1980), and by rodents during low waters. In the 1993 dry season, 81 % of Astrocaryum jauari nuts collected in the Maniti river valley had been predated upon by rodents. On the other hand, variable climatic conditions could explain the difference observed between 1992 and 1993 in the infestation levels of Oenocarpus bataua by C. gracilis: 17 % of the fruits collected in Jenaro Herrera in 1992 were infested by the bruchid, a rate which fell to 0.4 % in 1993 in the same area.

JANZEN (1971b) found that *Scheelea rostrata* nuts become infested by *C. buscki* only after the mesocarp has been removed by external agents. Similar observations have been made since (BRADFORD & SMITH 1977; WRIGHT 1990) for the same species breeding in *Scheelea zonensis* seeds. Observations reported here indicate that, in the case of *C. serripes*, egg-laying on various *Astrocaryum* species is also significantly affected by fruit maturity. The same could not be demonstrated in the case of *Caryoborus gracilis* and *Oenocarpus bataua*.

Factors affecting host range

Seed coat hardness and thickness may appear as a barrier to predators, and indeed JANZEN (1971a) mentions the thickness of the endocarp as an evidence of coevolution between palms and Pachymerini. However, extremely hard and thick (up to 25 mm in *Attalea racemosa*) nuts are penetrated by first instar larvae of both *P. cardo* and *S. giganteus*, with a mortality which is probably not significantly higher than observed in nuts with a much thinner endocarp. The subfamily Coryphoideae, numerous members of which are hosts of Pachymerinae, is characterized by a thin endocarp and seeds with an homogeneous or ruminate endosperm. Among other subfamilies of Palmae, fruits with a thin endocarp seem however to be less prone to seed beetle infestation: fruits of the Calamoideae (Lepidocaryeae), with a scaly epicarp but practically no endocarp, have no known seed beetle predator. The same is true for Iriarteeae. Euterpeinae are intermediate for this character (*Oenocarpus bataua* has a ruminate endocarp). *Elaeis guineensis* gives an interesting example where selection on agronomic traits (oil content of the fruit) has apparently led to an increased resistance to *P. cardo*, through a decrease in seed size.

Predation and parasitism are commonly assumed to be among the driving forces leading to host specialization and, ultimately, to speciation (BERNAYS & GRAHAM 1988). It was hypothesized (JANZEN 1971a) that specialists are unlikely to be found among parasitoids of seed predators. RASPLUS (1988) showed in the case of parasitoids of Coleopterous (mainly bruchids) predators of leguminous seeds in Ivory Coast that a range of specificities existed, from specialists to generalists. The only information available on palm bruchid parasitoids is the mention of exit holes on the dorsal surface of *S. giganteus* or *P. cardo* eggs on *Scheelea* nuts (WILSON & JANZEN 1972). The host range of *Uscana caryedoni* as well as its geographical distribution is very wide: it has been recorded from *Caryedon serratus* (OLIVIER) in Ivory Coast (GAGNEPAIN & RASPLUS 1989), also from *Caryedon congense* DECELLE and *Callosobruchus rhodesianus* (PIC) in Central Africa (DELOBEL 1989) and is also present in India (VIGGIANI in litt.). By drastically reducing at times the pressure of bruchid predation on palm reproduction or increasing the optimal number of bruchid eggs per seed

(SIEMENS & JOHNSON 1992), it undoubtedly plays an important role in population dynamics of the bruchids and of their palm hosts, the precise mechanism of which are far from being fully understood. Parasitism by the braconid seems restricted to *Caryoborus serripes*, which itself is a specific predator of the genus *Astrocaryum*: a high specificity of the parasitoid is associated in this case with a high specificity of the host. We failed to identify any generalist predator of bruchids.

Little is known of the evolutionary sequence and historical interactions which led to the extant distribution of Pachymerini over palm genera, subfamilies and tribes. As mentioned by NILSSON & JOHNSON (1993), palm taxonomy has long been obscure, and numerous older host plant records need be confirmed. Also, groups with small fruits, such as Geonomeae, have yet to be investigated. A preliminary assessment of the number of host taxa used by some Pachymerini shows contrasting situations: the hosts of *P. cardo*, which has the broadest diet, belong to at least 13 genera in two subfamilies (Arecoideae and Coryphoideae); *S. giganteus* is restricted to one tribe of the Cocoeae, Attaleinae, which includes very close genera, and *C. serripes* is almost restricted to *Astrocaryum*. The existence of a pachymerine species restricted to a single host species seems unlikely.

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Palm species	Location	Sample size	Seed number per fruit	Min.	Instation rate of fruits (per cent) Mean) Max.	Min.	Infestation rate of seeds (per cent) Mean	Max.	Insects per 100 fruits	
ARECOIDAE					-						
Euterpe oleracea MARTIUS	Нſ	06	-		0			0		0	
Euterpe precatoria MARTIUS	НГ	122	-		0			0		0	
Oenocarpus balickii KAHN Oenocarpus bataua MARTIUS	JH I JH Ma	40 904	1 1.02.	0	0	32	0	0	32	0 2	
Cocoeae Bactridinae											
Astrocaryum chambira BURRET	-	161	I	0	22	46	0	22	46	41	
A. chonta MARTIUS	НГ	228	-	4	59	84	4	59	84	63	
A. gratum KAHN & MILLÁN	PM	160	-		17			17		23	
A. huicungo BURRET	Mo	192	1	30	35	41	30	35	41	133	
A. jauari MARTIUS	Ma	68	-		0			c		0	
A. javarense TRAIL cx DRUDE	Ma	182	-	0	19	38	0	61	38	23	
A. macrocalyx BURRET	I	638	-	0	16	45	0	16	45	23	
Bactris gasipaes KUNTH	HL 1	182	1		0			0		0	
Desmoneus polyacanthos MARTIUS	Hr Si	122	_		7			7		7	
Cocoeae Attaleinae											
Attalea racemosa SPRUCE	I	14	2.21		50			35		50	
Attalea tessmannii BURRET	-	20	2.07		06			75		150	
Maximiliana maripa (AURLET) DRUDE	I Ma	204	1 22	c	41	20	C	44	67	47	
Scheelea burvacea (MUTIS ex				,		2	5				
L.f.) KARSTEN ex WENDLAND	I QN	123	1.04	45	58	68	42	52	58	55	
Scheelea phalerata (MARTIUS ex											
SPRENGEL) BURRET	JH Ma PM	500	2.98	c	48	67	C	42	84	125	
Cocoeae Elacidinae											
Elaeis guineensis JACQUIN	I Ma	603	10.1	0	2	94	0	8	78	2	
Elaeis oleifera (KUNTH) WENDLAND	НГ	160	-		0			0		0	

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			Seed		Instation rate			Infestation rate		Insects	
Palm species	Location	Sample size	number per fruits	Min.	of fruits (per cent) Mean	Max.	Min.	of seeds (per cent) Mean	Max.	per 100 fruits	
Iriarteeae Iriarteinae							¢ .				
Iriartea deltoidea RUIZ & PAVÓN	Ι	365	-		0			0		0	
Iriartella stenocarpa BURRET	Ma	8	-		0			0		0	
Socratea exorrhiza (MARTIUS) CORTÈS	I JH	331	-		0			0		0	
Iriarteeae Wettiniinae											
Catoblastus drudei COOK & DOYLE Ma	Ma	S	_		0			0		0	
Geonomeae											
Pholidostachys synanthera											
(MARTIUS) MOORE	JH	32	1		7			7		7	
Geonoma sp.	Ma	24	-		0			0		0	
CALAMOIDEAE Lepidocaryeae											
Lepidocaryum gracile MARTIUS	JH	69	-		0			0		0	
Mauritia carana WALLACE	Ι	104	1		0.			0		0	
Mauritia flexuosa L.f. Mauritiella aculeata (KUNTH)	I Ma	89	1.30		0			0		0	
BURRET	Ι	8	-		0		ų.	0		0	
PHYTELEPHANTOIDEAE											
Phytelephas macrocarpa		8									
								c		c	

Table 1: Continuation

Table 2: Trophic relationships between palms and bruchids: infestation rates by the different species. Thelast column shows the number of insects (adults and larvae) on which rates are based. Rates aredevoid of statistical significance.

Palm species (C. gracilis	C. serripes	P. cardo	P. sveni	S. giganteus	Nber insects
		100				
Astrocaryum chambi	ra -	100	-	-		56
A. chonta	-	100	-		-	137
A. gratum	-	100	-	-	-	37
A. huicongo	-	100	-	-	-	255
A. javarense	-	100	-	-	-	33
A. macrocalyx	-	100	-	-	-	121
Attalea racemosa	-	-	-	-	100	6
A. tessmannii	-	-	100	-	-	30
Desmoncus						
polyacanthos	-	-7	-	100	-	4
Elaeis guineensis	-	3	97	-	-	36
Maximiliana maripa	-	-	100	-	-	107
Oenocarpus bataua	100	-	-	-	-	64
Pholidostachys						
synanthera	100	-	-	-	-	1
Scheelea butyracea	-	-	10	-	90	68
S. phalerata		6	81	-	19	626

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