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SEED PREDATION IN *PHILODENDRON SOLIMOESENSE* (ARACEAE) BY CHALCID WASPS (HYMENOPTERA)

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The relationships between *Philodendron solimoesense* and the larvae of two chalcid wasp species, inhabiting up to 88% of the infructescences, were studied in French Guiana. *Exurus* sp. (Chalcidoidea, Eulophidae, Tetrastichinae), is a gall maker and its larvae develop at the expense of seeds which are transformed into galls. We estimate that two seeds are necessary for the development of one eulophid. Their impact on plant reproductive success appears to be important, since parasitized fruits produce 60% fewer seeds than nonparasitized fruits and could explain the reduced seed set observed (53%). The larvae of a *Sycophila* sp. (Chalcidoidea, Eurytomidae, Eurytominae) are also present in the fruits of *P. solimoesense* occupied by eulophid larvae. The eurytomid larvae apparently develop at the expense of about one eulophid and are responsible for the death of 39% of them by direct predation or indirectly by consuming the gall tissues. Eulophids are far more abundant than eurytomids, since parasitized fruits contain an average of 11 eulophids but only one eurytomid. As chalcid wasp emergence takes place in a closed cavity and sex ratios are strongly biased in a given gall, local mate competition may occur as observed for fig wasps within figs.

Keywords: Chalcidoidea, Eulophidae, Eurytomidae, parasitism, reproductive success, seed predation.

Introduction

Plant tissues represent a resource for numerous phytophagous organisms, not only as food but also as egg-laying sites. Larval development can take place on or within vegetal tissue. In the latter case, abnormal growth and differentiation usually affect the infected tissue, galls or *cecidia* (Meyer 1987). Cecidogenous parasites are very diverse and include viruses, bacteria, fungi, and animals, mainly insects, representing ca. 13,000 species from 20 families (Jolivet 1998). Insect galls may be induced by a larval auxin-like secretion on vegetative parts as well as on reproductive organs (Jolivet 1998). Ovaries are often chosen as oviposition sites by insects because ovules/seeds are among the most energy-rich parts of the plant (Grant 1950; Baker 1983; Crepet 1983). For example, *Aylax papaveris* (Hymenoptera, Cynipidae) parasitizes the ovaries of *Papaver dubium* (Papaveraceae); *Miarus campanulae* (Coleoptera, Curculionidae), the fruits of *Campanula rapunculoides* (Campanulaceae); and *Asphondylia scrophulariae* (Diptera, Cecidomyiidae), the flowers of *Scrophularia canina* (Scrophulariaceae; Meyer 1987).

Gall makers affect plant fitness when they develop at the expense of seeds, thus decreasing the reproductive success of their host. Parasite encapsulation in a gall can be a defense strategy of the parasite against its own natural enemies, but it might also be an induced plant defense strategy, since it protects the plant organ against more damage (Meyer 1987). Other plant defensive strategies that limit herbivore damage include the production of chemicals (e.g., alkaloids, insect-like phytohormones, terpenoids) with toxic or repellent actions or morphological structures such as thick cuticles and hooked hairs (Hodkinson and Hugues 1982; Harborne 1987).

Cecidogenous insects on inflorescences of Araceae are known from a few studies, especially on *Philodendron* spp. (Chodat and Vischer 1920; Mayo 1991). In *Philodendron* fruits, two species of gall-making wasps have been described: *Exurus* (*Trichaporus*) *gallicola* (Eulophidae, Tetrastichinae), a phytophagous seed predator, and *Prodecatoma philodendri* (Eurytomidae), an inquiline wasp that eats ovarian tissues and, accidentally, eulophid larvae (Chodat and Vischer 1920; Ferrière 1924).

Eulophids constitute a large family, ca. 4000 species, that is composed mainly of insect parasites or predators, a few phytophagous (inquilines in host galls) and very few gall makers (*Epichrysocharis*, *Oncastichus*, and *Quadrastichodella* in Australia; *Paragaleopsomyia* and *Trichaporus* in the Neotropics) or seed parasites (*Lisseurytomella* in the Neotropics) (Noyes 1998; J. LaSalle, unpublished manuscript). The Eurytomidae, ca. 1400 species, whose classification appears to be complicated (Burks 1971, 1979; Stage and Snelling 1986; Zerova 1989), also has a wide host range, even within the same genus (Noyes 1998). For example, some species of the genus *Sycophila* (Eurytomidae, Eurytominae) are parasitic on insect larvae (Diptera: Cecidomyiidae; Hymenoptera: Cynipidae), whereas other species are phytophagous, seed feeders, borers, gall makers, or inquilines of galls made by other insects (Zerova 1989; Compton 1993).

Although eulophid and eurytomid wasps are often collected, the biology of phytophagous species has rarely been studied

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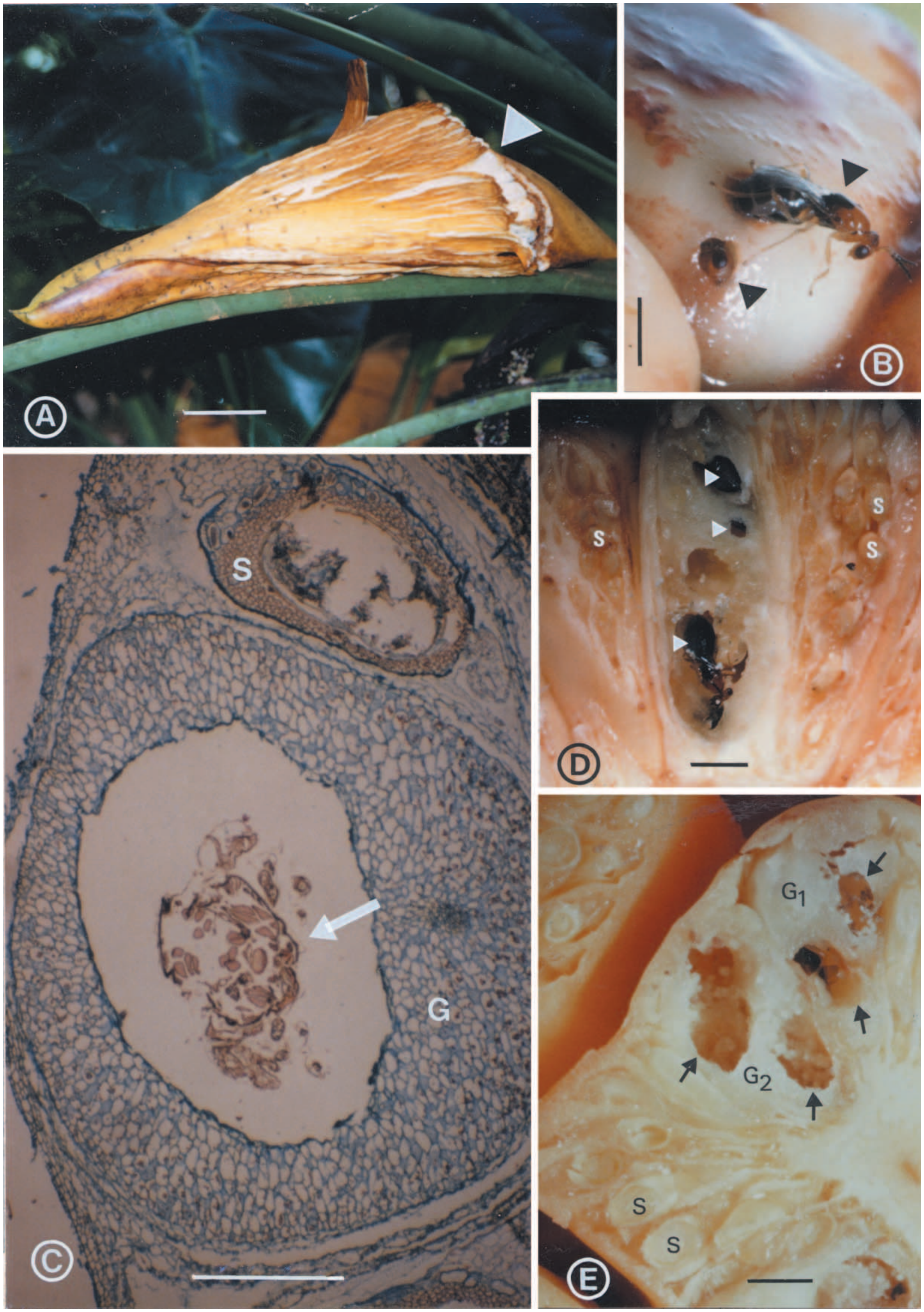
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(Uematsu and Yamashita 2000). For species developing in inflorescences, their impact on seed production has never been quantified, except for eurytomid species associated with *Ficus* (Compton et al. 1994; Kerdelhué et al. 2000). In this study, we provide data on seed predation in *Philodendron solimoesense* A. C. Smith by two chalcid wasps. First, we quantified the impact of seed predation on the reproduction of *P. solimoesense*. Second, we documented the life cycle of the two wasp species associated with the inflorescences of *P. solimoesense*.

Material and Methods

This study was conducted in July 2000 in French Guiana. Three populations of *Philodendron solimoesense* were studied and collected along National Road 1 (kilometer points 92, 94.5, and 96.5). The plants used were originally hemiepiphytic individuals growing on trees that were cut down during the construction of the road in 1989 (Gibernau et al. 1999).

Philodendron solimoesense is a hemiepiphyte of terra firma or flooded (riverine) forests that can also be terrestrial on sandy soils in tropical and southern subtropical America. The large inflorescences (22–32 cm in length) develop sequentially from the base of each petiole during the reproductive phase. One mature individual can bear from one to 10 inflorescences during the flowering season. The inflorescence is constituted by a spike, the spadix, bearing small flowers enclosed in a fleshy bract, the spathe. The pistillate flowers occupy the lower portion of the spadix, whereas the male flowers are located on the upper portion. In the median portion of the spadix, there is a zone consisting of sterile male flowers. The inflorescence is closed during its entire development except for the 2 d of anthesis, when pollination is achieved by the scarab beetle *Cyclocephala colasi* (for further details, see Gibernau et al. 1999).

Two different chalcid wasps belonging to two families were found laying their eggs in *P. solimoesense* fruits: *Exurus* (*Tetrastichus*) aff. *gallicola* (Eulophidae: Tetrastichinae; J. LaSalle, personal communication) and *Sycophila* (*Prodecatoma*) sp. (Eurytomidae: Eurytominae; J.-Y. Rasplus, personal communication). The *Exurus* sp. may be moved to a new genus composed exclusively of phytophagous species (taxonomy in revision; J. LaSalle, personal communication). Eulophid female wasps laid their eggs during the 2 d of anthesis, when the inflorescence is receptive and open. They were frequently found dead, trapped in closed pollinated inflorescences, as the spathe closes up around the spadix after pollination. Specimens used for the preparation of microscopic slides and the photographs in figure 1 were collected in 1997 (voucher specimen: *Barabé 42* [MT]), along the National Road (kilometer point 96.5).

The frequency of chalcid wasps was estimated by counting the proportion of infructescences parasitized among all the maturing infructescences ($n = 52$) in the three populations. We observed oviposition by female wasps on seven receptive inflorescences in the field and wasp emergence from galls on six infructescences in the laboratory. The number of female flowers was counted on 48 receptive inflorescences, as were the number of berries on 40 mature infructescences. The fruits can be normal, aborted, or parasitized. Aborted fruits start their development but decay rapidly, whereas parasitized fruits develop normally except that they have gall(s) containing wasp larvae (M. Gibernau, J. Albre, A. Dejean, and D. Barabé, personal observation). Nine mature parasitized infructescences collected on three different plants in each studied population were fixed in alcohol before wasp emergence. From these infructescences, a total of 480 fruits without emergence holes were dissected under a stereomicroscope to determine the number of seeds, galls, eulophids, and eurytomids per fruit (see table 1 for sample sizes). Eulophids and eurytomids were counted within each gall of, respectively, 447 and 117 fruits. Fruits containing larvae were excluded from the analyses because identification was not always easy. Finally, we cut 28 fruits into transverse sections and 18 into longitudinal sections in order to determine the spatial distribution of seeds and galls.

For the anatomical observations of galls, parasitized fruits were dehydrated in a tertiary butanol series, embedded in paraffin at 56°C (paraplast tissue-embedding medium manufactured by Monoject Scientific, St. Louis). Sections 10 mm thick were cut on a rotary microtome (American Optical, model 820) and stained with safranin and astra blue.

Statistical analyses were performed using SYSTAT 8.0 software (SYSTAT 1998) except when mentioned otherwise. When necessary, data were log transformed. The relationships between the number of locules, seeds, galls, eulophids, and eurytomids were studied at different levels (fruit, locule, and gall) with linear regressions. The number of seeds in parasitized and nonparasitized fruits were also compared using a two-sample *t*-test.

On transverse sections, the observed distribution of galls and seeds, expressed by the number of locules between two successive galls or seeds, was compared to a theoretical random distribution (mean expected distance = number of locules/number of galls or seeds) using a χ^2 test. On longitudinal sections, gall and seed positions (bottom, middle, or top of the fruit) were analyzed using a generalized linear model (GLIM 1986) with presence/absence data (binomial error) for the three considered positions.

Results

During seed and fruit development, both the spathe and the base of the spadix grow for at least 3 mo (D. Barabé, personal

Fig. 1 *A*, Infructescence of *Philodendron solimoesence*. When the infructescence is fully mature, a circular zone of dehiscence appears at the base of the spathe (arrowhead). Bar = 5 cm. *B*, Detail of a mature fruit (e.g., berry) showing the emergence of two eulophids (arrowheads). Bar = 1 mm. *C*, Transversal section of a locule enclosing a gall (*G*) and a seed (*S*). A section of a eulophid is visible inside the gall cavity (arrow). Bar = 0.5 mm. *D*, Longitudinal section of a fruit showing a locule occupied by a gall containing several eulophids (arrowheads) and, on its right, a locule enclosing seeds (*S*). Bar = 1 mm. *E*, Transversal section of a portion of fruit seeds (*S*) and galls enclosed in different locules. Note the presence of two adjacent galls (*G1*, *G2*), each of them containing two cavities (arrows). Bar = 1 mm.

Table 1

Mean (Numbers ± SD) of Locules, Seeds, Galls, Eulophids, and Eurytomids per Fruit (e.g., Berries)

	Locules		Seeds		Galls		Eulophids		Eurytomids	
	n	Mean	*n*	Mean	*n*	Mean	*n*	Mean	*n*	Mean
Nonparasitized	4	30.25 ± 3.10	46	133.5 ± 50.63	46	…	46	…	46	…
Parasitized	31	29.48 ± 3.80	157	52.60 ± 55.30	434	3.27 ± 2.12	99	11.03 ± 9.17	99	0.97 ± 1.39
All	35	29.57 ± 3.70	203	70.93 ± 63.92	480	2.96 ± 2.24	145	7.53 ± 9.15	145	0.66 ± 1.23

Note. n = number of fruits taken from nine parasitized infructescences for each category count. The number of seeds was significantly higher in nonparasitized than in parasitized fruits ($t = 9.42$, $\mathrm{df} = 78,6$, $P = 1.5 \times 10^{-14}$).

observation). When the fruits mature, the spathe color changes from green to orange, and finally the base of the spathe swells around the female flowers, forming a cavity. When the fruits are completely mature, the spathe splits at its base (fig. 1*A*), falling to the ground with the rotten male flowers and exposing the mature fruits to seed dispersers. The wasp larvae develop within galls formed by modified seeds present in the locules of the fruits (fig. 1*C*–1*E*). They complete their development before the fruit completes its maturation. The chalcid wasps emerge from their galls, in the spathe cavity, chewing an exit hole through the fruit wall (fig. 1*B*). As soon as the spathe base dehisces, the chalcid wasps fly away from the infructescence.

We observed two eurytomid females trying to oviposit from outside through the spathe wall into a recently closed pollinated inflorescence. We do not know whether they also lay their eggs when the spathe is receptive and open. In the laboratory, emerging wasps walked directly or flew toward the light source, exhibiting strong light attraction and ignoring other individuals. Wasp copulations were not observed, but they could take place after their emergence from the galls, within the closed and dark inflorescence cavity, before the splitting of the spathe.

The observed distributions of galls and seeds among the locules were not significantly different from a random distribution ($\chi^2 = 5.7$, $\mathrm{df} = 2$, $P = 0.057$). Thus, there was no particular organization (i.e., aggregation, dispersion) between seeds and galls; 27.5% of the locules contained only gall(s), 30% only seeds, and 42.5% both gall(s) and seeds. Locules occupied entirely by galls and seeds are shown on transverse or longitudinal views in figure 1*D*, 1*E*. Moreover, the galls ($\chi^2 = 0.24$, $\mathrm{df} = 2$, $P = 0.88$) and the seeds ($\chi^2 = 3.21$, $\mathrm{df} = 2$, $P = 0.20$) were equally frequent along the locule (top, middle, bottom). However, the position within the locule had a significant effect on the number of seeds present ($F = 5.53$, $\mathrm{df} = 2,105$, $P = 5 \times 10^{-3}$). Seeds were on the average about twice as numerous at the top of the locule as in the middle or at the bottom (0.54 vs. 0.29 and 0.17, respectively).

The number of female wasps laying their eggs in one inflorescence varied greatly from a few up to 120. Thus, the rate of ovule/seed parasitism varied highly from one inflorescence to another. We noted that 88% of the infructescences ($n = 46$) were parasitized by wasps. A high number of fruits (209 ± 31) began to mature per infructescence, representing 88% of the receptive female flowers initially present (238 ± 38), but 27.6% (±30.6) of these developing fruits aborted during infructescence maturation.

The parasitism rate per infructescence varied greatly among samples, from zero to totally parasitized fruits, with a mean rate of 31% ± 25% (55% ± 33% when excluding nonparasitized infructescences). On average, a nonaborted fruit contained 30 locules, in which 71 seeds and three galls developed (table 1). The number of locules had no significant effect on the number of mature seeds per fruit ($P = 0.32$), whereas it was negatively correlated with the number of galls ($r^2 = 0.19$, $F = 8.44$, $\mathrm{df} = 1,36$, $P = 0.006$) and eulophids ($r^2 = 0.18$, $F = 6.46$, $\mathrm{df} = 1,30$, $P = 0.016$). The number of seeds was significantly higher in nonparasitized than in parasitized fruits (133.5 ± 50.6 vs. 52.0 ± 55.2; table 1). Moreover, there was a negative linear regression between the number of seeds and the number of galls per fruit (fig. 2) and also per locule (fig. 3). These results indicate that galls, and thus eulophids, developed at the expense of the seeds.

Eulophids were far more abundant than eurytomids. A parasitized fruit contained an average of 11 eulophids and one eurytomid (table 1), and only 42% of the fruits parasitized by eulophids contained eurytomid(s). Galls also contained more eulophids (2.2 ± 2.1) than eurytomids (0.22 ± 0.43). The number of eulophids significantly decreased with an increasing number of eurytomids within each gall (fig. 4). These results indicate that eurytomids develop at the expense of eulophids, by direct parasitism (i.e., they are parasitoids) or indirect competition for plant tissue (i.e., they are inquilines). In addition, eulophid remains, e.g., heads or pieces of cuticle, were regu-

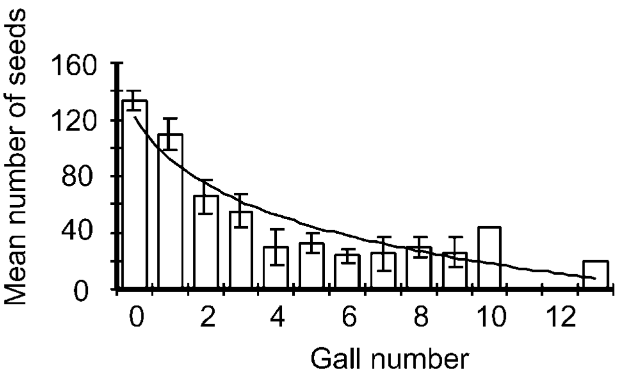

Fig. 2 Relationship between the number of seeds per fruit (mean ± SE) according to the number of galls present in the fruit; $n = 205$ fruits from nine infructescences ($r^2 = 0.85$, $F = 80.6$, $\mathrm{df} = 1,203$, $P = 2.3 \times 10^{-11}$).

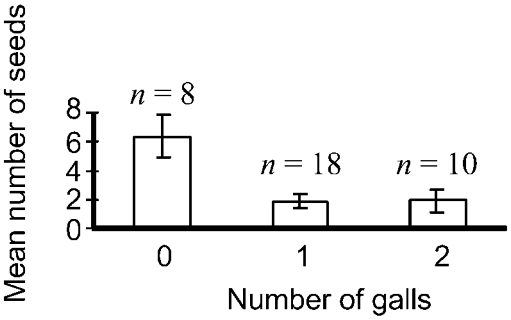

Fig. 3 Negative relationship between the number of seeds (mean ± SE) and the number of galls per locule ($r^2 = 0.31$, $F = 15.9$, df = 1,35, $P = 3.2 \times 10^{-4}$); n = number of fruits collected from nine infructescences in each category.

larly found in galls ($n = 26$). Some of these remains (19%) were observed in galls containing no eurytomid; however, a eurytomid larva occupied an adjacent gall of the same fruit. Finally, the mean sex ratios per fruit appeared to be close to 0.5 for eulophids (0.55 ± 0.28) as well as for eurytomids (0.47 ± 0.45), but sex ratios were not normally distributed for both species (one-sample Kolmogorov-Smirnov test: $P = 3 \times 10^{-5}$ and $P = 0.023$, respectively) with one sex being predominant in a given gall.

Discussion

The seeds of *Philodendron solimoesense* appear to have been heavily damaged by the seed parasite wasp, *Exurus* sp. A fruit of *P. solimoesense* can potentially produce ca. 150 seeds, five in each of the 30 locules (Mayo 1991); in accordance with this estimation, an average of 133 seeds was found in nonparasitized fruits. Phytophagous larvae strongly reduced seed sets as parasitized fruits produced 60% fewer seeds than nonparasitized fruits (table 1). We estimated that one eulophid develops on the average at the expense of about two seeds. Parasitized fruits mature thus on the average only one-third of their potential seed production (Mayo 1991). Hence, chalcid wasp larvae have a highly negative impact on the reproduction of *P. solimoesense* and may be the first responsible for the low seed set observed (39%–53%). This seed destruction occurs through the direct consumption of the seeds by wasp larvae of the eulophid. But spatial competition among galls and seeds may also occur, as a gall is on average 17 times larger than a seed. Galls may thus prevent seed development and enlargement.

Eulophids develop at the expense of seeds; however, eurytomid development depends on eulophid presence. First, eurytomids are always found in fruits containing eulophids. Second, there is a negative linear regression between the number of eurytomids and the number of eulophids per gall. We estimated that 39% of the eulophid larvae are eaten by the larvae of an inquiline eurytomid. Moreover, eurytomid larvae are able to move to neighboring galls by chewing holes in order to attack eulophids in other galls (J. Albre, personal observation). This behavior may explain the presence of eulophid remains found in empty galls, e.g., without eurytomids. Thus, *Sycophila* sp. may be either a eulophid predator, as are most eurytomid species, or an inquiline parasite, as proposed by Chodat and Vischer (1920). In fact, in several other *Philodendron* species, eurytomid wasps were found to share galls with eulophids, and this system appears to be comparable (Chodat and Vischer 1920). Even if the species may differ, the genera of both the plant parasite and the wasp parasite are the same.

As in all the Hymenoptera, eulophid and eurytomid females are able to control the sex of their progeny and thus the sex ratio of their clutches (Werren 1987; Uematsu and Yamashita 2000). Even if the mean sex ratio per fruit is close to 0.5 for both species, the sex ratio of a given gall is strongly biased toward one sex. Moreover, the emergence of the chalcid wasps takes place in a closed cavity formed at the base of the spathe of *P. solimoesense*. This situation may be comparable to figs and fig wasps. The emergence and mating of fig pollinators take place in the fig cavity before dispersion. In this enclosed system, local mate competition (LMC) between males can occur (Greeff 1996; Kathuria et al. 1999). Thus, if chalcid wasps also mate in the spathe cavity, LMC could also occur. Further studies are necessary to assess whether copulations really occur within the spathe cavity.

Insects ovipositing on inflorescences of Araceae have already been documented for pollinating and nonpollinating flies (Drosophilidae, Chloropidae, Phoridae, and Neurochaetidae). This is particularly the case in *Alocasia macrorrhiza* (Shaw et al. 1982), *Alocasia odora* (Yafuso 1993, 1994), *Colocasia esculenta* (Carson and Okada 1982), *Dieffenbachia oerstedii* (Valerio 1984), *Peltandra virginica* (Patt et al. 1995), and *Xanthosoma robusta* (Tsacas and Chassagnard 1992). A *Tyloderma* sp. (Coleoptera, Curculionidae) has also been observed laying its eggs in small holes on the outer surface of the spathe of *P. solimoesense*, but the consequences for fruit and seed maturation were not assessed (Gibernau et al. 1999). It appears from these studies that the fly larvae develop in the decaying tissue of the male portion of the spadix, apparently without affecting seed production, even if in some cases adults emerge by making holes in the spathe. Thus, none of them appear to be seed predators, contrary to the chalcid wasps found on *Philodendron* (Chodat and Vischer 1920; this study).

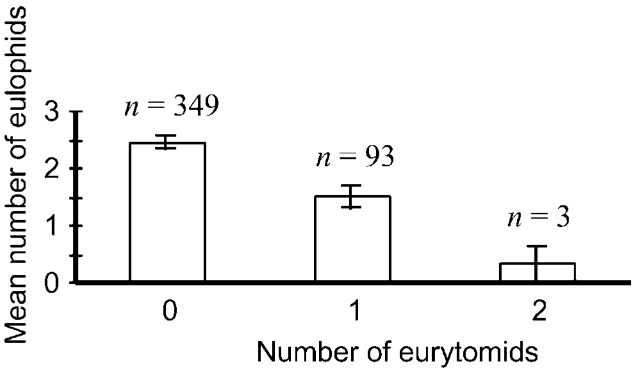

Fig. 4 Negative relationship between the number of eulophids (mean ± SE) and the number of eurytomids present within each gall ($r^2 = 0.05$, $F = 22.05$, df = 1,445, $P < 10^{-5}$); n = number of fruits collected from nine infructescences in each category.

In some inflorescences of *A. macrorrhiza*, holes near the base of berries with damage to the enclosed seed were observed, but the agent was not determined (Shaw et al. 1982).

Araceae seeds may frequently be attacked by insects even if this phenomenon is poorly documented. Defensive mechanisms such as calcium oxalate raphides, needle-like trichosclereids, persistent perianth, sclerified pericarp, and wrapped spathes appear to be diversified and widespread within the Araceae family (Madison 1979). They may have evolved in order to protect the developing seeds. In *Philodendron,* the protection of developing fruits appears to be mainly ensured by the persistent leathery spathe wrapped around the spadix and the production of a liquid that fills the spathe cavity (Madison 1979). Another defensive mechanism may be the number of locules. Species of the subgenus *Meconostigma* have eight to 30 locules, whereas species of the subgenus *Philodendron* have only four to 12 locules per fruit (Mayo 1989). Such a high number of locules in the subgenus *Meconostigma* may have evolved in response to seed parasitism (Mayo 1991). Our data are consistent with this hypothesis because the number of locules per fruit in *P. solimoesense* (fig. 1*E*), which belongs to the subgenus *Meconostigma*, is high (22–38; average of 30). Moreover, we found a negative relationship between the number of locules and the number of eulophids or galls per fruit.

Further studies are needed to assess how frequent and diverse seed parasites are in Araceae. How efficient are the defensive mechanisms and which one has evolved against a given parasite? Araceae appears to be potentially a good model for studying the coevolution between seed parasites and seed plant protection. At least in *P. solimoesense*, eulophids appear to exert a selective pressure on seed protection because they have a major negative effect on seed production, and thus on plant reproduction, leading to a strongly reduced seed set.

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Literature Cited

Baker HG 1983 An outline of the history of anthecology, or pollination biology. Pages 7–28 *in* L Real, ed. Pollination biology. Academic Press, Orlando, Fla.

Burks BD 1971 A synopsis of the genera of the family Eurytomidae (Hymenoptera: Chalcidoidea). Trans Am Entomol Soc 97:1–89.

——— 1979 Families Eurytomidae and Eulophidae. Pages 835–860 and 967–1022 *in* KV Krombein, PD Hurd, Jr, DR Smith, BD Burks, eds. Catalog of Hymenoptera in America north of Mexico. Vol 1. Smithsonian Institution Press, Washington, D.C.

Carson HL, T Okada 1982 Ecology and evolution of flower-breeding pomace flies of New Guinea (Diptera: Drosophilidae). Entomol Gen 8:13–16.

Chodat R, W Vischer 1920 La végétation du Paraguay. Imprimerie Jent, Geneva.

Compton SG 1993 One way to be a fig. Afr Entomol 1:151–158.

Compton SG, JY Rasplus, AB Ware 1994 African fig wasp parasitoid communities. Pages 343–368 *in* BA Hawkins, W Sheehan, eds. Parasitoid community ecology. Oxford University Press, Oxford.

Crepet WL 1983 The role of insect pollination in the evolution of the angiosperms. Pages 29–50 *in* L Real, ed. Pollination biology. Academic Press, Orlando, Fla.

Ferrière C 1924 Chalcidiens du Paraguay. Ann Soc Entomol Fr 93: 1–21.

Gibernau M, D Barabé, P Cerdan, A Dejean 1999 Beetle pollination of *Philodendron solimoesense* (Araceae) in French Guiana. Int J Plant Sci 160:1135–1143.

GLIM 1986 GLIM: generalised linear interactive modelling 3.77. Royal Statistical Society, London.

Grant V 1950 The protection of the ovules in flowering plants. Evolution 4:179–201.

Greeff JM 1996 Alternative mating strategies, partial sibmating and split sex ratios in haplodiploid species. J Evol Biol 9:855–869.

Harborne JB 1987 Chemical signals in the ecosystem. Ann Bot 60: 39–57.

Hodkinson ID, MK Hugues 1982 Insect herbivory. Chapman & Hall, London.

Jolivet P 1998 Interrelationship between insects and plants. CRC, Boca Raton, Fla.

Kathuria P, JM Greeff, SG Compton, KN Ganeshaiah 1999 What fig wasp sex ratios may not tell us about sex allocation strategies. Oikos 87:520–530.

Kerdelhué C, JP Rossi, JY Rasplus 2000 Comparative community ecology studies on old world figs and fig wasps. Ecology 81: 2832–2849.

Madison M 1979 Protection of developing seeds in Neotropical Araceae. Aroideana 2:52–61.

Mayo SJ 1989 Observations of gynoecial structure in *Philodendron* (Araceae). Bot J Linn Soc 100:139–172.

——— 1991 A revision of *Philodendron* subgenus *Meconostigma* (Araceae). Kew Bull 46:601–681.

Meyer J 1987 Plant galls and gall inducers. Borntraeger, Berlin.

Noyes JS 1998 Catalogue of the Chalcidoidea of the world. CD-ROM. Expert Center for Taxonomic Information, Amsterdam.

Patt JM, JC French, C Schal, J Lech, TG Hartman 1995 The pollination biology of Tuckahoe, *Peltandra virginica* (Araceae). Am J Bot 82:1230–1240.

Shaw DE, BK Cantrell, KJ Houston 1982 *Neurochaeta inversa* McAlpine (Diptera: Neurochaetidae) and seed set in *Alocasia macrorrhiza* (L.) G. Don (Araceae) in southeast Queensland. Proc Linn Soc NSW 106:67–82.

Stage GI, RR Snelling 1986 The subfamilies of Eurytomidae and systematics of the subfamily Heimbrinae (Hymenoptera: Chalcidoidea). Nat Hist Mus Los Angel Cty Contrib Sci 375:1–17.

SYSTAT 1998 Systat for Windows Statistics, version 8.0 ed. SPSS, Chicago.

Tsacas L, MT Chassagnard 1992 Les relations *Araceae-Drosophilidae*: *Drosophila aracea* une espèce anthophile associée à l'aracée

Xanthosoma robustum au Mexique (Diptera: Drosophilidae). Ann Soc Entomol Fr 28:421–439.

Uematsu H, T Yamashita 2000 Number and sex ratio of adult wasps, *Oomyzus sokolowskii* (Hymenoptera: Eulophidae), emerging from diamondback moth pupae collected in cabbage fields. Jpn J Appl Entomol Zool 44:197–200.

Valerio CE 1984 Insect visitors to the inflorescence of the aroid *Dieffenbachia oerstedii* (Araceae) in Costa Rica. Brenesia 22:139–148.

Werren JH 1987 Labile sex ratio in wasps and bees. BioScience 37: 498–506.

Yafuso M 1993 Thermogenesis of *Alocasia odora* (Araceae) and the role of *Colocasiomyia* flies (Diptera: Drosophilidae) as cross-pollinators. Environ Entomol 22:601–606.

——— 1994 Life history traits related to resource partitioning between synhospitalic species of *Colocasiomyia* (Diptera, Drosophilidae) breeding in inflorescences of *Alocasia odora* (Araceae). Ecol Entomol 19:35–73.

Zerova MD 1989 The main trends of evolution and the system of chalcids of the family Eurytomidae (Hymenoptera: Chalcidoidea). Entomol Rev 68:102–128.