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Beetle pollination and fruit predation of *Xanthosoma daguense* (Araceae) in an Andean cloud forest in Colombia

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Abstract: This study describes a pollination system in a species of Araceae that involves three species of beetle, one of which is also a fruit predator. In a tropical cloud forest in Colombia, inflorescences of *Xanthosoma daguense* opened at dusk, releasing a sweet scent and raising their temperature 1–3 °C. Soon after, two species of Scarabaeidae (Dynastinae; *Cyclocephala gregaria* and *C. amblyopsis*) and one species of Nitidulidae (*Macrostola costulata*) arrived with pollen. *Cyclocephala* beetles remained inside the inflorescence for 24 h. The next night, *Cyclocephala* beetles left the inflorescence after picking up the freshly shed pollen, almost always moving to the nearest inflorescence available. The probability of inflorescence abortion and number of fruits set after the visit of one individual was equivalent for both *Cyclocephala* species. However, *C. gregaria* was much more abundant than *C. amblyopsis*, so it was the most important pollinator. There was a positive relationship between the number of dynastine visits and the number of fruits produced. Besides carrying pollen to the inflorescences, nitidulid beetles had a negative effect on female reproductive success through fruit predation. Nitidulid larvae developed inside the infructescence and preyed on up to 64% of the fruits. However, 8% of inflorescences not visited by dynastines were probably pollinated by nitidulids, because hand-pollination experiments showed that self-pollination was unlikely. Inflorescences potentially pollinated by nitidulids comprised 25% of the fruit crop in the year of our study. This interaction with a fruit predator that is also a potential pollinator resembles brood-site pollination systems in which pollinators prey on part of the fruit set (e.g. *Ficus*, senita cacti, *Yucca*), making this system substantially more complex than previously described dynastine-pollinated systems in aroids.

Resumen En este estudio se describe el sistema de polinización de una especie de Araceae que involucra tres especies de coleópteros, una de las cuales es también un depredador de frutos. En un bosque nublado en los Andes de Colombia, las inflorescencias de *Xanthosoma daguense* abren al atardecer, al tiempo que liberan un olor dulce y aumentan su temperatura 1–3 °C. Poco después, escarabajos de dos especies de Scarabaeidae (Dynastinae; *Cyclocephala gregaria* y *C. amblyopsis*) y una de Nitidulidae (*Macrostola costulata*) llegan cargados de polen. Los *Cyclocephala* permanecen en la inflorescencia por 24 h. La noche siguiente, estos escarabajos abandonan la inflorescencia después de haber recogido polen fresco, y casi siempre vuelan a la inflorescencia nueva más cercana. La probabilidad de aborto de la inflorescencia y el número de frutos producidos después de una visita de un individuo, fue equivalente para las dos especies de *Cyclocephala*. Sin embargo, *C. gregaria* era mucho más abundante que *C. amblyiopsis*, por lo que fue el polinizador más importante. Se encontró una relación positiva entre el número de visitas de dinástinos y el número de frutos producidos. Además de llevar polen a las inflorescencias, los nitidúlidos tuvieron un efecto negativo en el éxito reproductivo femenino de la planta por la depredación de frutos. Las larvas de los nitidúlidos se desarrollaron dentro de la inflorescencia y depredaron hasta 64% de los frutos. Sin embargo, el 8% de las inflorescencias no fueron visitadas por dinástinos y probablemente fueron polinizadas por los nitidúlidos, ya que un experimento de polinización manual mostró que la auto-polinización es muy improbable. Las inflorescencias potencialmente polinizadas por nitidúlidos representaron el 25% de la producción de frutos en el año del estudio. Esta interacción con un depredador de frutos que es también un potencial polinizador, asemeja otros sistemas de polinización en los que los polinizadores depredan parte de la fruta producida (e.g. *Ficus*, *Yucca*), lo cual hace a este sistema mucho más complejo que el de otras aráceas polinizadas por escarabajos previamente descritos.

Key Words: Araceae, Colombia, *Cyclocephala*, Dynastinae, *Macrostola costulata*, Nitidulidae, pollination

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INTRODUCTION

Most of the pollination systems in Araceae are characterized by supporting some or all of the pollinator's life stages, offering food, a mating place, shelter against predators, and even a brood site within the inflorescence (Mayo *et al.* 1997). Pollinators of aroids are usually attracted by volatile chemicals produced by the inflorescence. Volatilization of scents is facilitated by the production of heat inside the inflorescence due to an increase in its metabolic rate, a process known as thermogenic respiration (Gibernau & Barabè 2000, Gottsberger & Silberbauer-Gottsberger 1991, Meeuse & Raskin 1988, Pellmyr & Patt 1986, Seymour 1999, 2001). Among the most important pollinators of Araceae in the Neotropics are beetles of the family Scarabaeidae (Dynastinae). Dynastine pollination and thermogenic respiration are broadly documented for *Philodendron* spp. (Barabè *et al.* 2002, Croat 1997, Gibernau & Barabè 2000, 2002; Gibernau *et al.* 1999, 2000; Gottsberger 1990, Gottsberger & Amaral 1984, Gottsberger & Silberbauer-Gottsberger 1991, Seymour 1999, 2001; Whitehill 1993), *Dieffenbachia longispatha* (Beath 1999), *D. nitidipetiolata* (previously referred to as *D. longispatha* in Young 1986, 1988; T. Croat, *pers. comm.*), *D. oerstedii* (Valerio 1983) and *Montrichardia arborescens* (Gibernau *et al.* 2003). Visits by dynastine beetles are also reported in *Caladium bicolor* (Pellmyr 1985), the genera *Homalomena* and *Syngonium* (Mayo *et al.* 1997 and references cited therein) and several species of *Xanthosoma* (Goldwasser 2000, Morón 1997, Valerio 1988). Dynastine beetles are attracted by olfactory and visual signals (Gottsberger & Silberbauer-Gottsberger 1991) and feed on sterile floral structures. They mate within the shelter of the inflorescence, stay in the inflorescence during the day, and fly to a new inflorescence at dusk. However, oviposition and larval development take place elsewhere, as their larvae develop underground (Borror *et al.* 1992).

In fly-pollinated taxa, a more complex relationship has been documented, as some pollinators of Araceae lay eggs within the inflorescence and their larvae feed on structures such as sterile flowers, anthers and ovules. This behaviour is known as brood-site pollination (Patt *et al.* 1995). In *Alocasia* spp., *Colocasia* spp. and *Peltandra virginica*, drosophilid fly pollinators use the staminate area of the inflorescence as a brood site, so no ovules are lost to larval predation (Carson & Okada 1980, Patt *et al.* 1995, Shaw & Cantrelle 1983). However, in other brood-site pollination systems such as *Ficus* (Bronstein 1988), senita cacti (Fleming & Holland 1998), *Trollius* (Pellmyr 1989) and *Yucca* (Marr *et al.* 2000), the larvae destroy part of the fruit set. Brood-site pollination involving ovule destruction in Araceae is known in *Anchomanes difformis* (D. Beath, unpubl. data). In this species the pollinator, a beetle of the family Nitidulidae, lays eggs in the pistillate area of the inflorescence, and the larvae prey on part of the fruit set.

Inflorescences of some dynastine-pollinated Araceae are also visited by nitidulids (Goldwasser 2000, Valerio 1983, Young 1986). These beetles feed on pollen deposited by the dynastine beetles, and mate within the inflorescence (Goldwasser 2000, Mayo *et al.* 1997, Young 1986). In the Central Andes of Colombia, we found that *Xanthosoma daguense* was visited by two dynastine (*Cyclocephala gregaria* Heyne & Taschenberg and *C. amblyopsis* Bates) and one nitidulid (*Macrostola costulata* Reitter) beetle species and that the nitidulid larvae were also fruit predators. Prior to this report, no fruit predation by nitidulid larvae had been reported in infructescences of dynastine-pollinated Araceae. It has been suggested that nitidulids are secondary pollinators in *Xanthosoma* (Mayo *et al.* 1997). So, if these beetles are bringing pollen to *Xanthosoma daguense* inflorescences and damaging infructescences, both dynastine and brood-site pollination are occurring at the same time in this aroid.

In this paper we describe the pollination and fruiting biology of *Xanthosoma daguense* and the roles that dynastine and nitidulid beetles play in these processes. We first describe the floral biology and breeding system, and evaluate the relative importance as pollinators of two dynastine species that visit inflorescences. Finally, at the population level, we evaluate the effect that beetles have as pollinators and predators on female reproductive success in this plant.

METHODS

Study site and species

This study was conducted at the Santuario de Fauna y Flora Otún-Quimbaya, a protected area located on the western drainage of the Central Andes of Colombia (4°39′N, 75°36′W), at an elevation of 1900 m. This premontane humid forest receives an average annual rainfall of 2630 mm which is distributed bimodally, with peaks of rain in April and October. At present, this area is covered with abandoned plantations of ash *Fraxinus chinensis*, oak *Quercus humboldtii*, and naturally regenerated forests (Londoño 1994). The plant studied in this work is *Xanthosoma daguense* (Voucher Croat 84942, MO). It is an abundant, monoecious clonal terrestrial herb (Figure 1a), growing in swampy and relatively open areas in all these habitats. The species flowers throughout the year, with a peak of flowering between May and early July. In the unopened inflorescence, the spathe wraps around the spadix, which has pistillate flowers at the base, an intermediate belt of sterile flowers, and staminate flowers in the upper portion (Figure 1b). The staminate flowers are exposed when the upper whitish

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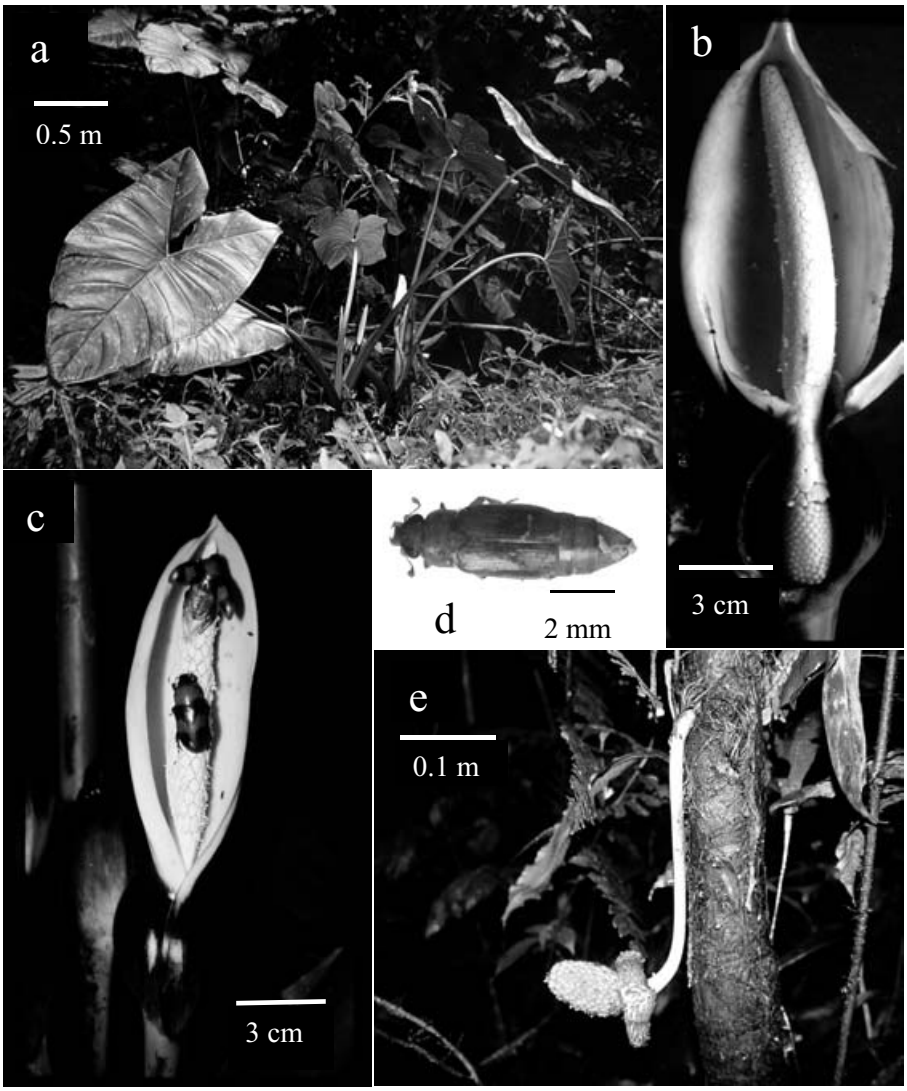

Figure 1. *Xanthosoma daguense* and its pollinators and fruit predators. (a) Habit. (b) Inflorescence with front of spathe tube cut off to show pistillate and sterile flowers on the lower portion, and staminate part of spadix in upper portion in front of spathe blade. (c) *Cyclocephala* beetles leaving an inflorescence. (d) Adult nitidulid beetle *Macrostola costulata*. (e) Mature infructescence (photographs a, d and e by Carlos García, b and c by Gustavo Londoño).

part of the spathe – the spathe blade – opens. The lower part of the spathe remains closed, forming a chamber – the spathe tube – that encloses the pistillate and sterile flowers (Figure 1c).

Floral biology

Data on floral morphology, flowering behaviour, breeding system, and inflorescence visitors were collected between May and early July 2000. We counted the number of staminate, pistillate and sterile flowers in nine inflorescences. We measured the rate of opening of the spathe blade during the first day of opening (n = 8) by painting two small marks on the blade margins, and measuring the distance between these points every hour. Changes in ambient and inflorescence temperature in the air space inside the spathe tube were recorded throughout the first evening after opening (17h00–21h00). Temperature was measured in five inflorescences from different plants, using a fast-response bulb thermometer (accuracy 0.1 °C, Miller & Weber Inc., NY, USA).

Breeding system

To determine if stigmas were receptive on the first night the spathe blade opened, we moistened stigmas in 20 recently opened inflorescences with H_2O_2, and recorded any visible bubbling reaction. Bubbles indicate stigmatic secretion of peroxidase, an enzyme released when stigmas are receptive (peroxidase test, Dafni 1992).

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To determine differences in pollination success (measured as the number of pollen tubes reaching the carpels) between self- and cross-pollinated flowers, we bagged 23 unopened inflorescences in different plants. When the spathe blade started to open, we cut the inflorescences and transferred them to the laboratory. A hand-pollination experiment was performed in two zones of the pistillate spadix area. The first zone was cross-pollinated in the second night of inflorescence opening. Pollination was performed using fresh pollen obtained from different plants at least 200 m away from the recipient flowers, to avoid using pollen from the same clone. The second zone was self-pollinated by hand on the second night, immediately after pollen was shed. To use a similar quantity of pollen in each hand pollination, we saturated each area of the spadix with all of the pollen produced by all of the staminate flowers of inflorescences used as donors. Individual flowers were removed from the spadix 12 h after hand-pollination had been performed, preserved in FAA (9:1:1 of 95% ethanol: formalin: glacial acetic acid), and softened in a solution of NaOH (8 N) for 1 h. Flowers were stained with aniline blue, and gently squashed on microscope slides. Number of pollen tubes arriving at the base of the style was counted under an epifluorescence microscope (Martin 1959). To explore differences between self- and cross-pollinated flowers on the second night of opening we performed a Wilcoxon paired t-test.

Sampling of inflorescence visitors

To identify the insect visitors, we collected inflorescences in the morning after the first (n = 17), second (n = 31) and third (n = 23) night of spathe blade opening. Each inflorescence was covered with a plastic bag and cut off at the base. All arthropods within the spathe tube were collected and fixed in ethanol. For the most abundant visitors, we explored differences in the number of individuals through different nights after opening using a Kruskal–Wallis test.

We collected 15 nitidulid beetles, each arriving at a different recently opened inflorescence, and examined them for presence of pollen under a microscope. When pollen was found, some grains were collected with a dissection needle, observed in a light microscope, and compared with pollen from *Xanthosoma* sp.

Importance of dynastine pollination

Data on dynastine beetle movements between inflorescences and pollination importance of both species were collected during the flowering period of May and early July 2001, and 4 mo later, during the fruiting season of 2001. We established two study plots in secondary forest (area = 10 000 m^2, number of marked inflorescences = 127) and ash plantations (area = 15 000 m^2, number of marked inflorescences = 361). The distance between plots was 200 m. Additional plants were marked in areas surrounding the plots (number of inflorescences = 22). All ramets were mapped to estimate the movements of dynastine beetles between inflorescences. Each morning we recorded all ramets producing inflorescences, and censused the number of beetles within each spathe tube. All dynastines were marked with three small punctures at the tip of each elytron using a unique pattern for each beetle (Unruh & Chauvin 1993, Young 1986).

Pollination importance is the combined result of the effectiveness of the pollinator, and the number of visits per inflorescence (Young 1988). We defined pollination effectiveness as the probability of inflorescences setting fruit, and the number of fruits set after the visit of one dynastine beetle. For the two dynastine species, we contrasted the number of inflorescences that aborted or set fruit after the visit of one individual using a test for comparisons between proportions (Zar 1996). To explore differences in the number of fruits produced between the inflorescences that set fruit after the visit of one individual of each species, we performed a Mann–Whitney U-test. To determine the effect of the number of visits to inflorescences on the number of fruits set, we compared the number of fruits produced by one, two or three or more dynastine visits with a Kruskal–Wallis test. Relative abundance of both dynastine species visiting the inflorescences was estimated using all the captures throughout the 2001 flowering season.

Dynastine movements between inflorescences

We used the movements recorded in successive recaptures to examine differences in one-night flight distances between dynastine species (Mann–Whitney test). To determine if individuals were selectively flying to the nearest inflorescence, we performed a chi-square test comparing the number of individuals flying to inflorescences in different relative spatial positions (i.e. the first, second, third or subsequent nearest inflorescence in the first night of opening, measured from the inflorescence from which the beetle departed).

We also explored the effect of inflorescence density on the selection by a beetle of inflorescences in different relative spatial positions. For this, we performed a Spearman correlation test between the density of flowers available (i.e. the number of recently opened inflorescences within a circular area of 86.5 m radius, the known mean flight distance of a beetle for this flowering season, centred on the departure inflorescence) and the relative spatial position of the inflorescence at which the beetle arrived.

Fruit production and fruit predation

In the study plots, we collected all infructescences produced by the marked inflorescences, and counted the number of fruits produced. Infructescences were collected when fully mature, but before the spathe split, displaying the fruits. We measured the effect of dynastine visits on inflorescence abortion and the number of fruits produced by inflorescences that set fruit, and evaluated the effect of fruit predation and potential pollination by nitidulid beetles on female reproductive success and the net fruit crop (number of infructescences produced through the flowering season) within this population.

Finally, to determine if nitidulid larvae and pupae of *Macrostola costulata* develop within the infructescences of *Xanthosoma daguense*, we collected developing infructescences after 100–110 and 111–121 d of development. We also collected fully mature infructescences just before the spathe tube split and showed fruits (140–151 d of development). The numbers of nitidulid larvae, pupae and adults within infructescences were recorded.

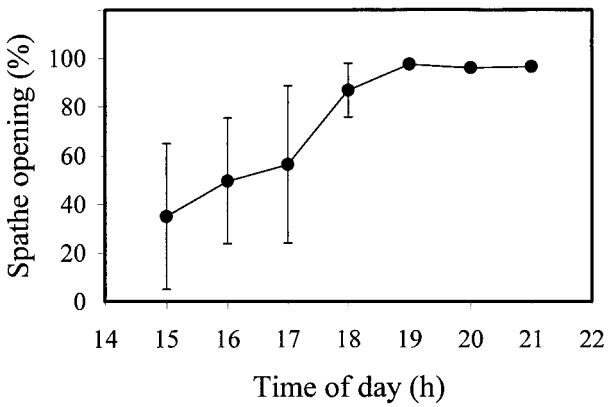

Figure 2. Rate of opening of spathe blades of *Xanthosoma* sp. inflorescences during the first day of anthesis (mean ± SD, n = 8), measured as per cent of distance between blade margins in fully open blade.

RESULTS

Floral biology

Each ramet of *Xanthosoma daguense* opened only one inflorescence at a time, at intervals of between 1 and 27 d (mean = 10.9 ± SD 6.1, n = 67). Inflorescences had a mean of 272 (± 36.3) pistillate, 88 (± 22.3) sterile and 390 (± 41.3) staminate flowers. Inflorescences began to open during the morning, and were completely open at 18h00–19h00 (Figure 2). At the same time, between 18h00–19h00, inflorescence temperature began to rise, peaking at 1–3 °C above environmental temperature (Table 1) and releasing a slightly sweet scent. The second night, between 18h00–19h00, the staminate flowers released pollen. If the inflorescence was pollinated, on the third night the staminate area of the spadix and the spathe blade started to decay and eventually fell, and the fruits started to grow within the protection of the remaining spathe tube. Inflorescences that did not produce fruits aborted about 1 wk after opening.

Breeding system

In all observed inflorescences (n = 20), stigmas of *Xanthosoma daguense* became receptive during the first night of spathe blade opening. In self-pollinated flowers, pollination success was lower than in cross-pollinated flowers ($t = 41$, $n = 23$, $P < 0.01$, Figure 3). Therefore, *Xanthosoma daguense* displays early acting self-incompatibility.

Arthropods visiting inflorescences

Drosophilidae flies arrived at inflorescences when they began to open and were frequently observed on the male spadix area in open inflorescences several nights after opening. We did not record their abundance because few of them were captured within the spathe tube. We also observed *Trigona* bees visiting the staminate

Table 1. Spathe tube (Tube) and ambient (Amb.) temperature (°C) and difference (Diff.) between the two in five *Xanthosoma daguense* inflorescences during the first day of opening.

	Time of day (h)														
	17			18			19			20			21		
Inflorescence	Tube	Amb.	Diff.	Tube	Amb.	Diff.	Tube	Amb.	Diff.	Tube	Amb.	Diff.	Tube	Amb.	Diff.
1	19.0	18.2	0.8	19.1	18.0	1.1	20.0	17.2	2.8	18.2	16.8	1.4	–	–	–
2	18.4	17.8	0.6	20.0	18.2	1.8	19.8	17.8	2.0	18.4	17.8	0.6	–	–	–
3	19.0	19.0	0	19.4	17.8	1.6	19.0	17.6	1.4	17.2	17.0	0.2	–	–	–
4	–	–	–	19.2	18.4	0.8	19.0	17.6	1.4	17.2	16.6	0.6	–	–	–
5	–	–	–	19.2	18.2	1.0	19.4	18.2	1.2	18.0	16.6	1.4	17.1	16.6	0.5

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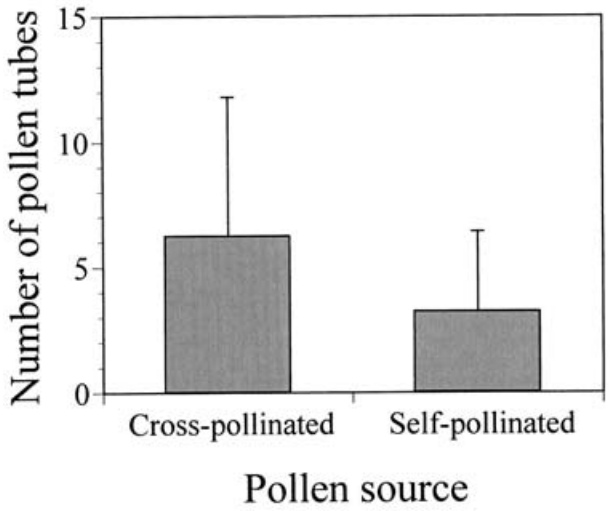

Figure 3. Number of pollen tubes arriving inside carpels in selfed and crossed hand-pollinated flowers on the second night after opening (mean ± SD, n = 23 inflorescences). Selfed and crossed pollinations were performed on different zones of the same inflorescence.

area of the inflorescences in the morning and collecting pollen on their hind leg baskets. Sporadic visitors such as ants, cockroaches, Curculionidae and Staphylinidae (Coleoptera), Miridae (Hemiptera) and undetermined immature stages of Diptera and Coleoptera were found in six or less of the collected inflorescences (n = 71). Excluding dynastines, the most frequent arthropods were Dermaptera, Macrochelidae mites that hitched a ride on dynastine beetles, larvae of Syrphidae (Diptera), and the nitidulid beetle *Macrostola costulata* (vouchers collected by C. García-Robledo, collection numbers: adults: U124, larvae: RN114, Pupae RN64b, are deposited at the Louisiana State Arthropod Museum, and were determined by Andrew R. Cline; Figure 1d). The numbers of dermapterans and mites were similar on the 3 d after spathe opening (Table 2). Syrphid larvae also appeared soon after the inflorescence opened, coming from old inflorescences, and the number of individuals increased as inflorescences aged. Nitidulid beetles also arrived during the first night, and the number of individuals tended to increase on the second night (Table 2). There was no evident damage made on the inflorescence by any of the arthropods visiting the spathe tube. However, in addition to eating pollen deposited by dynastines in the spathe tube, nitidulids also mated and laid eggs. After hatching, nitidulid larvae developed inside the infructescence, preying on the fruits. Nitidulid beetles arriving at recently opened inflorescences carried tetrads of pollen similar in size and shape to those of *Xanthosoma daguense* (7 of 15 beetles examined), suggesting that these beetles could be acting both as predators and vectors of pollen.

Table 2. Number of individuals (mean ± SD) of the most common arthropod visitors found in *Xanthosoma* sp. inflorescences on the first, second and third night after opening.

	Nights after opening					
Arthropod	First	Second	Third	H[1]	df	P
Dermaptera	0.7 ± 0.8	0.7 ± 1.3	0.6 ± 0.7	0.28	2	0.8
Mites	5.1 ± 13.1	1.3 ± 3.2	1.9 ± 4.9	0.80	2	0.6
Nitidulidae	4.1 ± 5.1	9.7 ± 10.4	5.8 ± 6.6	5.30	2	0.06
Syrphidae larvae[2]	1.2 ± 0.6[a]	1.5 ± 1.2[a,b]	2.9 ± 2.9[b]	6.90	2	0.03

[1] Kruskal–Wallis statistic.
[2] Significant differences among nights are indicated by different letters.

Importance of dynastine pollination

Inflorescences of *Xanthosoma daguense* were mainly visited by two species of dynastine beetles, *Cyclocephala gregaria* and *C. amblyopsis* (Figure 1c). Through the flowering seasons of 2000 and 2001 we also recorded outside the study plots two individuals of *Cyclocephala kaszabi* Endrodi visiting inflorescences. This less frequent visitor was not included in the analyses (vouchers of dynastines collected by C. García-Robledo are deposited at the Entomological Museum, University of Nebraska, and were determined by Brett C. Rattcliffe).

Cyclocephala gregaria and *C. amblyopsis* arrived at inflorescences at 18h00–19h00 on the first night the spathes opened; their bodies were covered with pollen (total number of inflorescences examined = 348, total number of *Cyclocephala* arriving on: first night = 160, second night = 4, third night = 0). After landing on the inflorescence, they walked into the spathe tube, where they smeared pollen on the stigmatic surface of the female flowers, mated and ate the sterile flowers. The following night, at 18h00–19h00, the beetles climbed through the staminate spadix area, becoming covered with the copious pollen released by the anthers. They also mated and ate pollen on the staminate area of the spadix before flying to a new inflorescence.

The probability of inflorescence abortion ($\chi^2 = 0.77$, df = 1, P = 0.37, Figure 4a), and the number of fruits produced after a visit by one individual (U = 88, $n_{gregaria} = 24$, $n_{amblyopsis} = 8$, P = 0.7, Figure 4b) were the same for both species of *Cyclocephala*. Therefore, both species were equally effective as pollinators. The number of fruits produced per infructescence was higher when inflorescences were visited by two or more beetles, compared to inflorescences receiving one visit (H = 11, df = 2, $n_{one\ visit} = 32$, $n_{two\ visits} = 16$, $n_{three\ or\ more\ visits} = 8$, P < 0.004, Figure 4c). In inflorescences that were visited, the number of *Cyclocephala* per inflorescence was between 1 and 9 individuals (average number of *Cyclocephala* per inflorescence = 0.5 including inflorescences not visited, 1.6 if counting only inflorescences that were visited). However, most of the inflorescences received no visits

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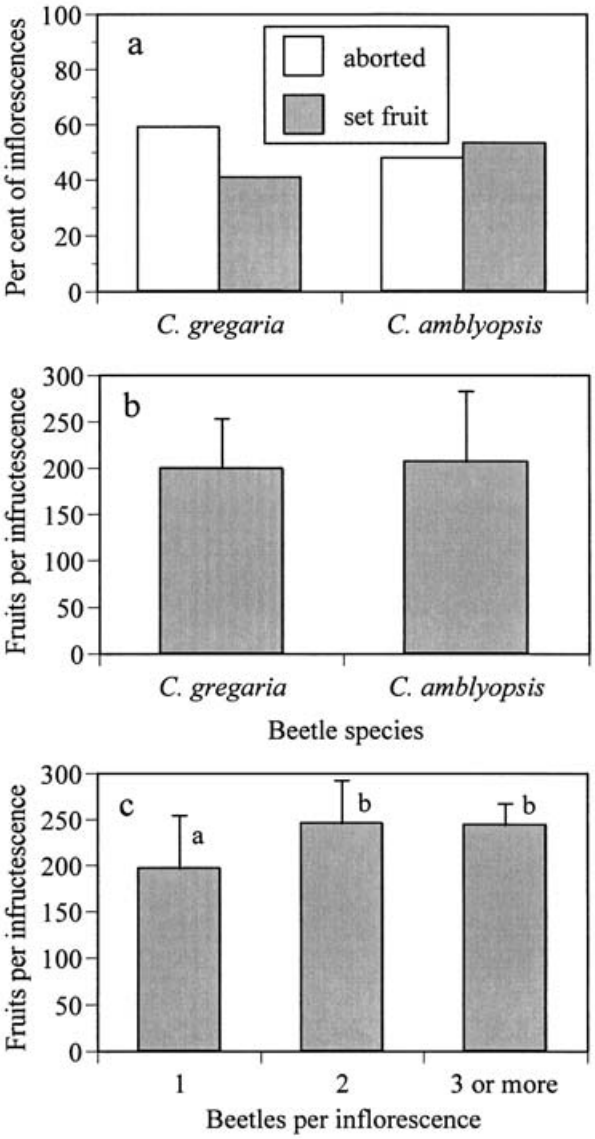

Figure 4. Pollination importance of two species of *Cyclocephala* beetles. (a) Per cent of inflorescences that aborted or set fruit ($n_{gregaria}$ = 24, $n_{amblyopsis}$ = 8). (b) Number of fruits produced per infructescence (mean ± SD) after being visited by one individual ($n_{gregaria}$ = 24, $n_{amblyopsis}$ = 8). (c) Number of fruits produced in inflorescences visited by different numbers of dynastine beetles (mean ± SD; different letters indicate significant differences, $P < 0.02$, $n_1 = 32$, $n_2 = 16$, $n_{\geq 3} = 8$).

($\chi^2 = 885$, df = 6, $P < 0.001$, Figure 5). Only two inflorescences were visited by more than four *Cyclocephala* (Figure 5). Most of the visits were performed by *C. gregaria*, whose abundance was four times higher than that of *C. amblyopsis* ($n_{gregaria} = 181$, $n_{amblyopsis} = 44$).

Dynastine movements between inflorescences

Cyclocephala gregaria and *C. amblyopsis* showed similar flight distances (U = 208, P = 0.42, $n_{gregaria}$ = 35, $n_{amblyopsis}$ = 14). Mean flight distance in one night was 86.5 m (± 128.7, n = 49), ranging from 0 m in beetles that did not leave the inflorescence when pollen was shed, up to 512 m. Most of the beetles flew to the nearest recently opened inflorescence ($\chi^2 = 29.3$, df = 9, $P < 0.001$, Figure 6). However, selection of the nearest inflorescence was dependent upon inflorescence density ($R_s = 0.41$, n = 38, P = 0.01). At low densities, beetles moved to the nearest inflorescence; at higher densities, several inflorescences were available at short distances and beetles did not necessarily move to the nearest one.

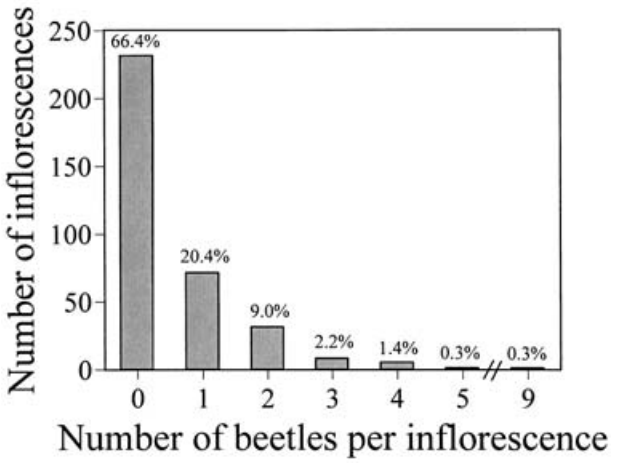

Figure 5. Frequency of numbers of *Cyclocephala* beetles observed per inflorescence. Numbers above the bars represent the percentage of the total number of inflorescences examined, n = 348.

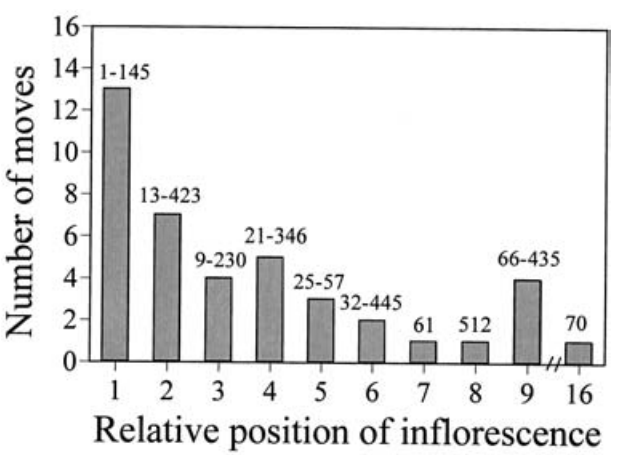

Figure 6. Distribution of number of times that *Cyclocephala* beetles that were recaptured on two consecutive days, moved to inflorescences in different relative spatial positions (nth nearest neighbour). Numbers above the bars represent the range of flight distances (m).

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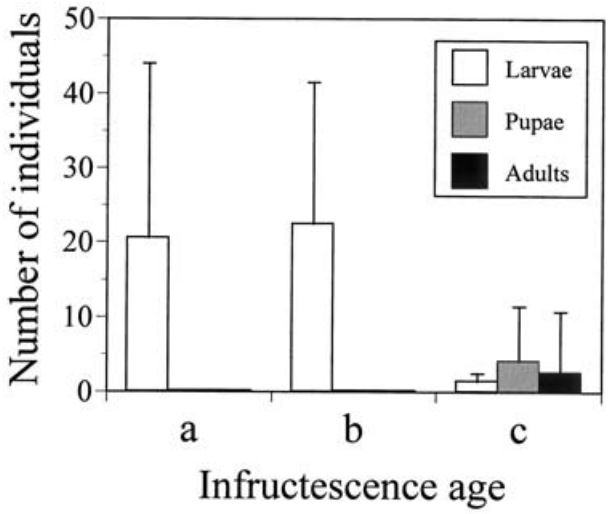

Figure 7. Number of larvae, pupae and adults of *Macrostola costulata* beetles in infructescences at different times of maturation (mean ± SD); a = 100–110 d (n = 13), b = 110–121 d (n = 41), c = 140–151 d (n = 35).

Fruit production and fruit predation

Fruit maturation took 4–5 mo. Fruits started to grow within the shelter of the spathe tube. When the infructescence was mature, it arched back and downward (Figure 1e). Then, the tissue of the spathe tube rolled outwards, exhibiting the bright orange fruits and the velvety pink inner spathe surface. Abortion rate was 78% (n = 349). Infructescences that set fruit produced an average number of 216 fruits (SD ± 49, n = 75). Eight per cent of inflorescences that were not visited by dynastines produced fruit.

It was common to find nitidulid larvae, pupae, or recently emerged adults within the infructescences. Fruit preyed upon by nitidulid larvae were easily recognized by their dull orange to black colour and the presence of a hole at the apex; the seeds were destroyed. Most inflorescences that set fruit showed some fruit damage by nitidulid larvae (93%, n = 75). The percentage of damaged fruits ranged from 0 to 64% (mean = 23.9 ± 18.9, n = 75). We observed immature nitidulid stages in developing infructescences, but adults were found only in nearly mature fruits (Figure 7).

DISCUSSION

The floral biology of *Xanthosoma daguense* reported here is similar to that of *X. robustum* (Goldwasser 2000), *X. pilosum* and *X. helleborifolium* (D. Beath, unpubl. data). In these species, beetles of the genus *Cyclocephala* also arrive on the first night of opening at 18h00–19h00, leave on the second night after pollen is shed, and the upper part of the inflorescence decays and falls if pollination was successful (Goldwasser 2000, D. Beath, unpubl. data). However, pollination is not a 2-d event in all *Xanthosoma* species. In *Xanthosoma wendlandii*, *Cyclocephala* beetles arrive at inflorescences on the first and second nights and pollen is shed in the third night of opening (Valerio 1988).

The temperature increase observed in *Xanthosoma daguense* (1–3 °C) is low compared with *Dieffenbachia longispatha* (3–4 °C), *Xanthosoma robustum* (18 °C) and *Philodendron selloum* (20 °C), which are also dynastine-pollinated (Goldwasser 2000, Young 1986). Differences in measured temperature increase could be a consequence of the method used, i.e. inserting a bulb thermometer in the spathe chamber, as in this study, or piercing the spadix with a thermocouple probe (Seymour 1999, 2001). In any case, heating in *Xanthosoma daguense* was accompanied by a conspicuous release of floral perfume, so this rise in temperature seems to be enough to volatilize the scent substances involved in pollinator attraction.

Our hand-pollination experiment shows early acting self-incompatibility in *Xanthosoma daguense* (*sensu* Seavey & Bawa 1986). Additional lines of evidence indicate that self-pollination is unlikely: (1) pollinators arrive on the first night of opening, loaded with pollen; (2) pollen is shed only on the second night; and (3) when pollen is shed, it remains stuck to the staminate area of the spadix and requires a vector to be introduced into the spathe tube.

All insect visitors that we recorded in *Xanthosoma daguense* have also been recorded in other dynastine-pollinated Araceae (Goldwasser 2000, Young 1986). These authors recorded mites arriving attached to dynastine beetles and feeding on floral exudates; dermapterans fed on detritus accumulated inside the inflorescence. Goldwasser (2000) reported that syrphid larvae moved between adjacent inflorescences in the same plant, and preyed on arthropods within the spathe tube. However, we dissected stomachs of 40 syrphid larvae collected from *Xanthosoma daguense* inflorescences, and found pollen in all of them; we found arthropod exoskeletons in only four larvae.

Our results show that mite numbers were similar on consecutive days after opening, as expected for arthropods that arrive only on the first day, attached to dynastine beetles. The increasing number of syrphid larvae was also expected because arrival of these dipterans and hatching of new eggs occurred on subsequent days after inflorescence opening. The behaviour of these syrphid visitors suggests that inflorescences were not damaged by them and they are unlikely pollinators (Goldwasser 2000). However, they may have some effect on reproductive success if the pollen they consume reduces pollination success. On the other hand, if syrphid larvae are feeding on nitidulid eggs, they may reduce subsequent fruit predation.

Adult nitidulids may also have a negative effect on pollination success through pollen consumption, but the stronger influence on reproductive success of *Xanthosoma daguense* is through larval predation of fruits. Our results suggest that all life stages of the nitidulid *Macrostola costulata* were strongly linked with inflorescences and infructescences of *Xanthosoma daguense*. Adult nitidulids fed and mated inside inflorescences, and the larvae fed and pupated inside the developing infructescences. The presence of pupae and recently emerged adults only in mature infructescences also suggest that the length of the life cycle of this species of nitidulid is similar to the time of infructescence maturation.

We observed a trend to an increase in the number of nitidulids on the second night of opening, and a reduction on the third night. Nitidulids leaving on the third night could carry pollen from the staminate area of the spadix, as well as pollen previously deposited within the spathe tube by dynastine beetles. Viability of pollen after the second and following nights is not known. However, if pollen deposited in the spathe tube is viable on subsequent nights, nitidulids could act also as re-disseminators of pollen among inflorescences.

The behaviour of *Cyclocephala* that we observed in *Xanthosoma daguense* has been reported in other dynastine-pollinated Araceae (Goldwasser 2000, Gottsberger & Silberbauer-Gottsberger 1991, Young 1986). However, the species composition and abundance of dynastine beetles is very variable between aroid species and between localities within their geographic ranges. Beetle species visiting *Dieffenbachia nitidipetiolatum* in tropical rain forest at La Selva Biological Station, Costa Rica, differed from those visiting *D. longispatha* in tropical rain forest on Barro Colorado Island, Panama (Beath 1999). The number of beetle species visiting *Xanthosoma daguense* (this study) and *X. robustum* populations in tropical cloud forests (Goldwasser 2000) were lower than the number visiting *X. violaceum* and *X. robustum* populations in tropical lowland forest in Chiapas, Mexico, and the beetle species were also different (Goldwasser 2000, Morón 1997).

The pollination effectiveness of the two species of *Cyclocephala* that we studied was equivalent. Dynastine pollinators in the genera *Cyclocephala* and *Erioscelis* also display similar effectiveness in single visits to *Dieffenbachia nitidipetiolatum* (Young 1988). However, beetle abundance and the number of visits per inflorescence in our study were low. Sixty-six per cent of *Xanthosoma daguense* inflorescences in our study received no visits, which contrasts with the lower values reported for *D. nitidipetiolatum* in 3 different years (31%, 38% and 3%; Young 1986), for a population of *X. violaceum* in the tropical rain forest of Chiapas, Mexico (41%; Morón 1997) and for *Philodendron solimoesense* in French Guiana (0%, Gibernau *et al.* 1999). Likewise, the mean number of beetles visiting inflorescences (0.5 for all the population, 1.6 for those inflorescences that were visited) in our study was low compared with numbers reported for *Dieffenbachia nitidipetiolatum* in three different years (3.6, 3.6 and 8.7 individuals per inflorescence, respectively; Young 1986), *X. robustum* in the tropical cloud forest of Monteverde, Costa Rica (7 individuals per inflorescence; Goldwasser 2000) and *Philodendron solimoesense* in French Guiana (21 individuals per inflorescence, Gibernau *et al.* 1999).

In *Dieffenbachia nitidipetiolatum*, there is a linear positive effect of the number of visits by dynastines on the number of fruits set when number of visits is low. However, when more than four beetles visit an inflorescence, the number of fruits declines (Young 1988). This decline may be caused by three possible mechanisms: (1) mechanical damage of pistillate flowers; (2) dislodging of ungerminated pollen from the stigmatic surface; and (3) accumulation of beetle waste products that may clog the stigmatic surface (Young 1988). We found an increase in the number of fruits produced when inflorescences were visited by more than one beetle. However, we may not have observed a decline in pollination success because there were very few cases with more than four visitors. The equivalence in effectiveness between the two *Cyclocephala* species, and the positive relation between the number of visits and the number of fruits produced, lead us to conclude that at least for this flowering season, *Cyclocephala gregaria* was the most important pollinator because it was the most frequent visitor.

The mean flight distance of 86.5 m observed in this study for *Cyclocephala amblyopsis* and *C. gregaria* is similar to the value of 83 m reported for the *Cyclocephala* visiting *Dieffenbachia nitidipetiolatum* (Young 1986). Beetle movements to the nearest available inflorescence were also reported for *D. nitidipetiolatum* (Young 1986).

We observed an abortion rate of 78%. This value is higher than that reported for *D. nitidipetiolatum* (52% and 47% in two consecutive years, Young 1986), but similar to the 81% reported for *Dieffenbachia oerstedii* (Valerio 1983). Inflorescences of *Xanthosoma daguense* that did not produce fruits aborted about 1 wk after opening. This suggests that high abortion rates are a consequence of few pollinator visits, not of fruit predation by nitidulids.

We found that the probability of abortion in inflorescences not visited by *Cyclocephala* beetles was five times higher than when visited (García-Robledo, unpubl. data). However, the 8% of inflorescences not visited by *Cyclocephala* that produced fruits comprise 25% of the total number of infructescences produced in the season. These inflorescences either were pollinated by dynastine beetles that entered the spathe tubes and left in the same night, and thus were missed by our daily censuses, or were pollinated by nitidulids. If these inflorescences were pollinated by nitidulids, these beetles

contributed an important part of the fruit crop of this flowering season.

As shown by the contrasting results of different studies on dynastine-pollinated aroids, the effects of pollinators can be very variable at different temporal and spatial scales, and within and between plant populations and species. However, all systems share some basic characteristics related to dynastine pollination. The interaction between *Xanthosoma daguense* and *Cyclocephala* beetles described in this study shows characteristics typical of dynastine-pollinated Araceae. However, the interaction with a nitidulid beetle that is simultaneously a fruit predator and a potential pollinator, adds a complexity that had not been previously described in aroids.

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