

EQUAL AND OPPOSITE EFFECTS OF FLORAL OFFER AND SPATIAL DISTRIBUTION ON FRUIT PRODUCTION AND PRE-DISPERSAL SEED PREDATION IN *XANTHOSOMA DAGUENSE* (ARACEAE)¹

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ABSTRACT

Inflorescences of the terrestrial aroid *Xanthosoma daguense* in the Andes of Colombia are visited by Dynastinae and Nitidulidae beetles. Plants produce one inflorescence at a time, which is pollinated during the first night of opening. Dynastine beetles act as pollinators, whereas the adult Nitidulids lay eggs in the inflorescence, and the larvae damage the seeds. This study explored the effects of floral offer and distance among inflorescences on the number of pollinator visits, fruit production and pre-dispersal seed predation. Number of Dynastine visits per inflorescence tended to increase with increasing distances among inflorescences, but fruit predation increased when inflorescences were more clumped. Both pollinator visitation rates and pre-dispersal seed predation were low at high floral offer. Fruit set increased when inflorescences were visited by two or more Dynastines, but the proportion of fruits damaged by Nitidulid larvae was equivalent to the increase in fruit production due to more Dynastine visits. The net result was a similar number of undamaged fruits in all infructescences produced, independently of the number of Dynastine visits. Our results revealed that in this system, both pollinators and predators responded to the number of available inflorescences and their spatial distribution, but their effects on the infructescences produced were opposite. Thus, our study provides evidence that suggests that the interaction of two ecological processes, pollination and pre-dispersal seed predation, may cancel each other's effects under natural conditions.

RESUMEN

En los Andes colombianos, las plantas de *Xanthosoma daguense* (Araceae) producen sólo una inflorescencia a la vez, que es polinizada en la primera noche de antesis. Las inflorescencias son visitadas por escarabajos Dinastinae y Nitidulidae. Los dinástinos son los principales polinizadores, mientras que los nitidúlidos ovipositan en las inflorescencias y sus larvas depredan parte de las semillas en desarrollo. Este estudio explora los efectos de la oferta floral y la distancia entre inflorescencias sobre el número de visitas por polinizadores, producción de frutos y depredación de semillas. El número de dinástinos por inflorescencia tendió a aumentar cuando se incrementó la distancia entre inflorescencias, pero la depredación de frutos se incrementó cuando las inflorescencias estaban más agrupadas. Tanto las tasas de visitas por polinizadores, como las de depredación de semillas bajaron cuando la oferta floral aumentó. El número de frutos producidos aumentó cuando las inflorescencias fueron visitadas por dos o más dinástinos. La proporción de frutos depredados por larvas de nitidúlidos también aumentó en las infrutescencias que produjeron más frutos. El resultado neto fue un número similar de frutos sin daño en todas las infrutescencias, independiente del número de visitas de dinástinos. En este sistema, tanto los polinizadores como los depredadores de frutos respondieron al número de inflorescencias disponibles y a su distribución espacial, pero sus efectos sobre las infrutescencias producidas fueron opuestos. Este estudio sugiere que los efectos de dos procesos ecológicos, polinización y depredación de frutos en desarrollo, pueden cancelarse mutuamente bajo condiciones naturales.

Keywords: Andes, Araceae, Colombia, *Cyclocephala*, Dynastinae, *Macrostola costulata*, Nitidulidae, pollination, seed predation, *Xanthosoma*.

In animal-pollinated plants, reproduction and fitness are highly influenced by patterns of pollinator visitation. Pollinator visitation rates depend on factors both intrinsic and extrinsic to the plant. The plant's attractiveness to pollinators may be affected by intrinsic attributes such as flower morphology (Totland 2001), quality and quantity of pollinator rewards, and size of floral displays (reviewed by Feinsinger 1987). On the other hand, pollinator visitation rates also are affected by factors extrinsic to the plant, such as climate (Herrera 1995; Totland 2001), species composition and abundance of neighboring flowers (Rathcke 1983; Feinsinger *et al.* 1986; Feinsinger 1987), and pollinator abundance (Young 1986; García-Robledo *et al.* 2004). These external factors, which are known as the pollination context, may have stronger effects on pollination rates and reproductive success than factors intrinsic to the plant (Herrera 1995).

Two potentially important factors in the pollination context are floral offer within the population and distance among plants (Heinrich & Raven 1972; Feinsinger *et al.* 1986, 1991; Fleming 1992). Floral offer is defined as the number of plants available for pollinators within a given area, and the distance among plants is calculated as the average distance among them (Kunin 1997). Floral offer and distance among plants show high temporal and spatial variability (Fleming 1992), and may have variable and contrasting effects on plant-pollinator interactions (Kunin 1997). The effects of floral offer on pollinator visitation rates and fruit production are not necessarily consistent. Some studies have found a reduction in the number of visits and fruit production when floral offer decreases (Sih & Baltus 1987; Menges 1991; Aizen & Feinsinger 1994; Aizen 1997;

Quesada *et al.* 2003; 2004), but others have not found any such effects (Aizen 1997; Kunin 1997; Albert *et al.* 2001; Quesada *et al.* 2004). On the other hand, the general effect of the distance among plants is that visitation rates decrease when plants are sparsely distributed (Feinsinger *et al.* 1986, 1991; Kunin 1993, 1997). However, the effect of the intra-plant distance on reproductive success varies with the breeding system (Schemske 1980; Bosch & Waser 2001).

The pollination context may simultaneously affect not only mutualistic plant-animal interactions such as pollination, but also antagonistic interactions such as pre-dispersal seed predation, if the same display that attracts pollinators is as effective in attracting fruit or seed predators. In some cases the same visitor plays a dual role as pollinator and fruit or seed predator, as occurs in brood-site pollination systems. Examples of these peculiar systems include senita cacti (Fleming & Holland 1998), *Ficus* (Janzen 1979; Bronstein 1992), *Yucca* (Marr *et al.* 2000), and *Trollius* (Pellmyr 1989). More generally, pollinators and predators are different species, and both may respond to the same clues in the pollination context (Brody & Mitchell 1997).

In this study, we explore the consequences of daily variations in the pollination context at a population level for female reproductive success, in a species of plant with a pollination system that involves three beetle species, one of which is also a seed predator. In *Xanthosoma daguense* (Araceae) in the Andes of Colombia, two species of Dinastinae (Scarabaeidae), *Cyclocephala gregaria* Heyne & Taschenberg and *C. amblyopsis* Bates, and one species of Nitidulidae, *Macrostola costulata* Reitter are regular visitors to the

inflorescences (García-Robledo *et al.* 2004). Dynastine beetles are the main pollinators and they do not cause any evident damage to the floral reproductive structures, at least when the number of visits per inflorescence is low (Young 1988; Goldwasser 2000, García-Robledo *et al.* 2004). Although the Nitidulid beetles move pollen among inflorescences, and may be acting as secondary pollinators, they feed on the pollen carried by the Dinastine beetles, lay eggs on the female flowers, and their larvae feed on part of the fruit set, consuming nearly all the seeds within the damaged fruit (García-Robledo *et al.* 2004).

At a population level, *Xanthosoma daguense* displayed marked daily changes in floral offer and distance among inflorescences, suggesting that daily vagaries of the pollination context may have striking consequences on fruit production and fruit predation through the attraction of both pollinators and fruit predators. Although both pollinators and predators are attracted by inflorescences, floral offer and distance among plants do not necessarily have similar effects on Dinastine pollination and Nitidulid predation. In this study, we documented the concurrent effects of daily changes in floral offer and distance among inflorescences on (1) the number of visits by Dinastine beetles, (2) fruit production and (3) Nitidulid fruit predation.

The net effect of simultaneously attracting pollinators and fruit predators on the female reproductive success of *Xanthosoma daguense* could be positive if predation levels are negligible, or negative if a large proportion of fruits is destroyed. Alternatively, the gain obtained by higher pollination rates may be cancelled by the loss caused by attracting more

predators. Therefore, we also explored the effect of the number of visits by *Cyclocephala* beetles and Nitidulid fruit predation on the net fruit production of *Xanthosoma daguense*.

METHODS

STUDY SPECIES.— . The study species, *Xanthosoma daguense* Engl. (Voucher: Croat 84942, MO) is a clonal, terrestrial herb that grows in the understory of humid montane forest in the Central range of the Colombian Andes. Each ramet is about 1.5m tall, and opens only one inflorescence at a time, at intervals between 1 and 27 days (García-Robledo *et al.* 2004).

The inflorescence is composed by a spadix with pistillate flowers at the base, a belt of sterile flowers offered as a reward for pollinators in the middle, and staminate flowers on the upper part. Prior to opening, the inflorescence is enclosed within a leaf-like spathe. When the inflorescences are ready to open, the upper part of the spathe opens and exposes the staminate area of the spadix; the basal area of the spathe remains closed, forming a spacious chamber (i.e. the spathe tube) that encloses the pistillate and sterile flowers (García-Robledo *et al.* 2004).

The inflorescence lasts for two nights and it is protogynous, changing from the pistillate phase that attracts pollinators on the night it opens, to a staminate phase on the second night, when pollen is shed (García-Robledo *et al.* 2004). Therefore the floral offer of the population and the distance among inflorescences change every night.

Dynastine beetles arrive with pollen during the night when the inflorescence opens, and remain in the spathe tube for 24 h., pollinating the pistillate flowers as they feed on the

sterile area of the spadix. On the second night, they come out of the tube and walk over the staminate flowers, getting covered with pollen and then flying to the nearest recently opened inflorescence. Pollination experiments showed that self-pollination is unlikely to occur (García-Robledo *et al.* 2004).

Nitidulids also arrive to newly opened inflorescences covered with pollen and enter the spathe tube. The number of Nitidulids within the spathe tube remains constant in the second day after the inflorescence opened (García-Robledo *et al.* 2004). The effectiveness of Nitidulids as pollinators is unclear. Infructescences were principally produced by inflorescences visited by *Cyclocephala* (García-Robledo *et al.* 2004) and in our analyses we assume that *Cyclocephala* spp. performed all the pollination.

STUDY SITE.—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 area receives an average annual rainfall of 2630 mm which is distributed bimodally, peaking in April and October. A mild dry season occurs during December-January, and a stronger one between July-August (Aguilar & Rangel 1994). This area was originally covered with tropical cloud forest, but exploitation during the first half of the twentieth century left only some patches of forest. Presently, 40 years after a revegetation program was started, the area is a mosaic of abandoned plantations of the exotic Chinese ash *Fraxinus chinensis*, stands of native oak *Quercus humboldtii*, and naturally regenerated forests (Londoño 1994). Plantations were abandoned without further management, and were invaded to different degrees by native

vegetation. In all these habitats, *Xanthosoma daguense* is distributed around creeks and other swampy and sunny areas. The species flowers throughout the year, with a peak between May and early July.

STUDY DESIGN.—Data were collected between May and early July 2001, the months in which flowering of *Xanthosoma daguense* is most abundant. The individuals were naturally divided into two sub-groups, one that occurred in an ash plantation and the other in an adjacent secondary forest, and they were separated by a 200 m-wide old pastures. Thus, we studied these two patches separately. We recorded the spatial position of all ramets that produced inflorescences, totaling 361 ramets in ash plantation and 127 in secondary forest. We expressed the effective area covered by *Xanthosoma daguense* in each plot, as the smallest-area polygon that contained all the inflorescences mapped throughout the period of data collection (polygon in ash plantation = 15,000 m², polygon in natural regeneration = 10,000 m²). We defined the daily floral offer of the population as the number of inflorescences in their first night of opening within the effective area of each plot.

Within each plot, we measured daily the distances among inflorescences available for insect visitors (i.e., in first night of opening), and calculated the daily mean distance among inflorescences. To record the daily number of visits to each inflorescence, each morning we made censuses of the number of *Cyclocephala* within the spathe tube.

When mature, but before the spathe tube split showing the fruits, we collected all infructescences produced by the marked plants, and counted the number of fruits fully developed and undeveloped in each infructescence. Recording the number of adult

Nitidulids visiting inflorescences was not possible because it would have required destroying the spathe tube. However, we measured the effect of predation by Nitidulid larvae on fruit set by counting the number of fruits damaged in all the infructescences. This is a good measure of the effect of Nitidulids on the female reproductive success on *Xanthosoma daguense* because nearly all seeds within infested fruits are damaged by these larvae.

STATISTICAL ANALYSIS—Following the procedures outlined by Adler *et al.* (2001), Schemske & Horvitz (1988), and Sokal & Rohlf (1995), we used path analyses to assess the effect of floral offer and distance among inflorescences on the number of visits by *Cyclocephala*, the number of initiated fruits, and fruit predation by Nitidulids.

The expected path structure is shown in Fig. 1a. In this flowering season, floral offer and distance among inflorescences were not correlated (Table 1), which allowed us to explore the effects of both variables at the same time. Because both species of *Cyclocephala* were equally effective pollinators (García-Robledo *et al.* 2004), we did not discriminate the effect of different species in the path analysis.

We performed a first path analysis to explore the effects of floral offer and distance among inflorescences on the number of visits by *Cyclocephala*, and the effect of each of these three variables on the number of fruits set. To assess the effect of floral offer and distance among inflorescences on the number of damaged fruits, we performed a second path analysis for which we recalculated all the values using only data for days in which we found inflorescences that set fruit. We did not observe fruits damaged by other causes (e.g.

fungi or other pre-dispersal fruit predators), therefore, most of the damage was caused by Nitidulid larvae.

In this second path analysis, the number of *Cyclocephala* per inflorescence, and the mean number of fruits initiated were calculated using the values obtained from the inflorescences that set fruit. We assumed a direct effect of these variables on the number of damaged fruits. A more accurate model would have included an indirect effect of floral offer and distance among inflorescences on the number of damaged fruits through an effect on the number of visits by adult Nitidulids (and a consequent increase in the number of larvae). For each independent variable we calculated the direct effects, indirect effects and path coefficients using standardized partial regression coefficients (for a detailed description of the calculation of direct and indirect effects see Pedhazur and Pedhazur-Schmelkin 1991, Pedhazur 1997, Schemske and Horvitz 1988). The correlation coefficients used to obtain these values are given in Tables 1 and 2. Significance levels for the effect of independent on dependent variables were obtained from the conventional partial regression coefficients. The path diagram proposed does not fully represent all the factors affecting the number of visits, fruits produced, and fruits damaged by Nitidulid larvae. These unknown factors are represented by the residual variables U_1 , U_2 and U_3 (Fig. 1a).

We selected for these analyses daily changes in floral offer and inflorescence spatial distribution because: (1) floral offer and the distance among inflorescences completely change every day, (2) data were recorded when flowering season peaked, and (3) *Cyclocephala* are potentially able to fly in one night to any point inside both plots (mean

flight distance in one night = 86.5 m, min = 0 m, max = 512 m). Therefore, each night beetles were responding to the total offer within our sample area.

Most of the inflorescences were not visited by *Cyclocephala* beetles and among those that were visited, most contained only one or two individuals; finding three or more *Cyclocephala* within an inflorescence was uncommon (García-Robledo *et al.* 2004). Thus, to analyze the effect of the number of visits on fruit production we grouped all cases of three or more visits in one category. To assess the effect of the number of *Cyclocephala* beetles visiting an inflorescence on the proportion of aborted inflorescences, we performed a test for comparisons of proportions (Zar 1996) among inflorescences that aborted or set fruit, and were visited by zero, one, two, or three or more *Cyclocephala*. For this analysis we also included data from sparsely distributed individual plants that flowered in the area between the study plots (N = 22).

To evaluate the effect of the number of visits by *Cyclocephala* (i.e., one, two, or three or more visits per inflorescence) on the number of undeveloped and totally developed fruits, we performed a Kruskal-Wallis test. To evaluate the relationship between the number of visits by *Cyclocephala* and the percent of damaged fruits per inflorescence, we did a one-way ANOVA on the arcsine-transformed data.

The number of undamaged fruits is a good measure of the actual female reproductive success because nearly all seeds in the fruits damaged by Nitidulid larvae are totally destroyed. Therefore we explored the effect of the number of *Cyclocephala* visits on the number of undamaged fruits produced per inflorescence with a Kruskal-Wallis test.

RESULTS

EFFECT OF FLORAL OFFER AND DISTANCE AMONG INFLORESCENCES ON FRUITS PRODUCED—

Mean distance among inflorescences was 51.7 m (SD \pm 34.7, range 8.1-173 m, N for all variables = 56). Floral offer was 6×10^{-4} inflorescences/m² (SD \pm 3.5×10^{-4} , range (1.14-16.8) $\times 10^{-4}$ inflorescences/m²). Floral offer and inter-plant distance were not correlated (Table 1). The mean number of Dinastine beetles per inflorescence per day was 0.5 (SD \pm 0.67, range 0-3.5). The mean number of developed fruits was 58.4 (SD \pm 74.3, range 0-311.). The direction and magnitude of the path coefficients are illustrated in Fig. 1b. The proportion of the variation in number of beetles per inflorescence explained by floral offer and distance among inflorescences was 18 percent (Table 3). There was a marginally significant relationship between distance among inflorescences and number of visits by *Cyclocephala* ($P = 0.06$). The relationship between the number of *Cyclocephala* visits and floral offer was negative and significant (Table 3).

The proportion of the variation in number of initiated fruits collectively explained by floral offer, distance among inflorescences and number of *Cyclocephala* visitors was 32 percent (Table 3). Floral offer and distance among inflorescences did not have a significant direct effect on the number of fruits initiated (Table 3). However, when the number of visits by *Cyclocephala* was high, the number of fruits produced increased (Fig. 1b, Table 3). This suggests that floral offer has an indirect effect on the number of fruits produced through their effect on *Cyclocephala* visitation rates.

EFFECT OF FLORAL OFFER AND DISTANCE AMONG INFLORESCENCES ON THE NUMBER OF FRUITS DAMAGED BY NITIDULID LARVAE.— Mean distance among inflorescences was 61.9 m (SD \pm 37.9, range 8.1-173 m, N for all variables = 37). Floral offer was 6×10^{-4} inflorescences/m² (SD \pm 3.5×10^{-4} , range ((2 – 15) $\times 10^{-4}$ Inflorescences/m²). The mean number of Dinastine beetles per inflorescence per day was 1.1 (SD \pm 0.95, range 0 - 4). The mean number of developed fruits was 216 (SD \pm 50.46, range 98 - 311). The mean number of damaged fruits was 58 (SD \pm 36.4, range 0 - 135). The overall proportion of variation explained by the model in the number of fruits damaged is 39 percent (Table 3). For those inflorescences that set fruit, as distance among inflorescences decreased (i.e., they were more clumped), the number of damaged fruits increased (Fig. 1c, Table 3). In contrast, predation was positively correlated with the number of initiated fruits (Fig. 1c, Table 3).

EFFECTS OF THE NUMBER OF *CYCLOCEPHALA* VISITS ON INFLORESCENCE ABORTION, FRUIT PRODUCTION, AND FRUIT PREDATION BY NITIDULID BEETLES—The number of *Cyclocephala* visits was related to the probability of inflorescence abortion ($\chi^2 = 68.2$, df = 3, $P < 0.0001$). Abortion in unvisited inflorescences was three times higher than in inflorescences visited by at least one *Cyclocephala* (Fig. 2). However, the abortion probability of inflorescences visited by one or more *Cyclocephala* was equivalent (Fig. 2).

When there were two or more *Cyclocephala* per inflorescence, more fruits were produced ($H = 11.8$, df = 3, $P = 0.007$, Fig. 3a). The number of seedless, undeveloped fruits was independent of the number of *Cyclocephala* visits ($H = 6.08$, df = 3, $P = 0.1$, Fig. 3b).

These fruits were commonly found at the bottom of the infructescences, suggesting that due to their position these flowers probably had a low probability of receiving pollen. The proportion of fruits damaged by Nitidulid larvae increased with *Cyclocephala* visitation rates ($F = 3.8$, $df = 3$, $P = 0.01$, Fig. 3c). As a consequence, the positive effect on reproductive success conferred by more *Cyclocephala* visits was cancelled by fruit predation, and the number of fruits without damage was equivalent in all inflorescences irrespective of the number of *Cyclocephala* visits ($F = 0.41$, $df = 3$, $P = 0.7$, Fig. 3d).

DISCUSSION

Our results suggest that floral offer influenced the number of *Cyclocephala* visits and the number of fruits set. Floral offer and the distance among inflorescences also affected fruit predation by nitidulid beetles. When floral offer was low, *Cyclocephala* beetles gathered in the few available inflorescences, resulting in an increase in the number of visits per inflorescence. This seems opposite to the general pattern reported for bat, bee or hummingbird-pollinated plants, in which a reduction of floral resources produces a decrement in the number of pollinator visits (Sih & Baltus 1987; Menges 1991; Aizen & Feinsinger 1994; Aizen 1997; Quesada *et al.* 2003; 2004).

When the number of *Cyclocephala* available for pollination is low, as in the flowering season of our study, the number of pollinator visits and the number of fruits produced show a positive linear correlation (García-Robledo *et al.* 2004; Young 1986). Therefore, inflorescences opening at low floral offer received more visits and produced more fruits. However, in Dinastine pollination, the relationship between the number of

visits and the number of fruits set is not always linear (Young 1988). In other Dynastine pollinated aroids for which high visitation rates have been reported, fruit production shows a peak at an intermediate number of visits, followed by a reduction as the number of visits increases. This reduction in the fruit set may be a consequence of mechanical damage of flowers and/or stigma clogging by Dinastine feces (Young 1986).

For all the inflorescences produced, floral offer and distance among inflorescences were not correlated. However, there was a negative correlation between these variables for the inflorescences that set fruit. This is the result of an increase in the number of inflorescences that set fruit when distance among inflorescences was high, but the number of flowers was low (situation in which inflorescences displayed higher number of visits by *Cyclocephala* and Nitidulid beetles, as suggested by high seed predation), and when distance among flowers was low (situation in which more seed predation by Nitidulid larvae was recorded, and perhaps more pollination by Nitidulid adults occurred).

Floral offer and distance among inflorescences had opposite effects on fruit predation by Nitidulid larvae. When the number of available inflorescences was low, fruit predation was high. This could be a consequence of an increase in the number of adult Nitidulids visiting the few available inflorescences, and therefore an increase in the number of eggs laid and the number of larvae per infructescence. We found that inflorescences opening in a more clumped distribution had more fruits damaged by Nitidulid larvae. The observed increase in pre-dispersal seed predation is likely a consequence of an increase in the number of visits by adult Nitidulids. These beetles may be responding to a stronger

floral scent or visual signal produced by clumped inflorescences. On the other hand, Nitidulids are known to release aggregation pheromones (Harrison 1962; Luckmann 1963), so it is possible that they are responding not only to signals originated in the plant, but also to their own pheromones.

The path analysis suggested that the number of visits by *Cyclocephala* do not have a direct effect on Nitidulid fruit predation. However, the number of *Cyclocephala* visits had an indirect effect on fruit predation because the larvae of Nitidulid beetles require inflorescences that set fruit to survive, and the probability of inflorescence abortion was very high in the absence of *Cyclocephala*. Another indirect effect of the number of visits by *Cyclocephala* on fruit predation was through an increase in fruit production. When more fruits were produced due to an increase in the number of *Cyclocephala* visits, there were more fruits available for the predators, and the path analysis suggested that fruit predation increased in infructescences that set more fruits. In *Ipomopsis aggregata*, flower availability also affects the number of visits by pollinators and fruit predators. In this plant, larger floral displays lead not only to higher visitation rates by hummingbird pollinators, but also to a greater incidence of pre-dispersal seed predators, both in absolute and relative numbers of fruits damaged (Brody & Mitchell 1997).

The probability of abortion in inflorescences not visited by *Cyclocephala* beetles was three times higher than when visited. However, 25 percent of the infructescences were produced without *Cyclocephala* visitation. These inflorescences were either pollinated by Dynastine beetles that entered the spathe tubes and left in the same night, and therefore

were not recorded in our censuses, or were pollinated by Nitidulids (García-Robledo *et al.* 2004).

When exploring the effect of floral offer and distance among inflorescences on fruit predation in the path analysis, results suggest that there is not a significant lineal relationship between the number of *Cyclocephala* visits and the number of initiated fruits. However, in ANOVA analyses, we found a significant increase in the number of fruits set when the number of *Cyclocephala* increased. This suggests there is a positive but non-lineal relationship between these factors. In the ANOVA analyses, we found that the positive effect of increased pollinator visits on fruit production (measured as the proportion of fruits produced) was cancelled by the negative effect of fruit predation. Experimental studies have found that mutualistic (i.e. pollination) and antagonistic (i.e. herbivory) plant-animal interactions may cancel the effects of each other (Brody & Mitchell 1992; Herrera 2000). These studies have suggested that this phenomenon may occur in systems in which fruit predators are preferentially attracted to plants that have larger fruit crops as a result of being favored by pollinators (Herrera 2000). Our results suggest that for inflorescences that set fruit, pollination and fruit predation in *Xanthosoma daguense* cancelled each other due to simultaneous direct and indirect effects of two variables extrinsic to the plant, namely, floral offer and distance among inflorescences. However, to test the causality and magnitude of the patterns described in this paper, further experimental research is required. In addition, contrary to other systems, more fruit production and fruit predation occurred at low floral offer. If the phenomenon of mutualistic and antagonistic plant-animal

interactions canceling each other is frequent and widespread under natural conditions, a more integrative, and not a single-interaction approach is required if we intend to understand the consequences of plant-animal interactions for plant fitness and population dynamics.

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TABLE 1. *Correlation matrix for variables included in the path analysis of the effect of floral offer and density on pollinator visits and fruit production. Inflorescences/m² (OFFER), Mean distance among inflorescences (MEAN), No. Coleoptera/inflorescence (COLE), No. of fruits produced (FRUPROD).*

	MEAN	COLE	FRUIPROD
OFFER	-0.19	-0.29*	-0.29*
MEAN		0.30*	0.13
COLE			0.59**

* $P < 0.05$, ** $P < 0.01$

TABLE 2. Correlation matrix for variables included in the path analysis of the effect of floral offer and density on the number of fruits damaged by Nitidulid larvae. Inflorescences/m² (OFFER), Mean distance among inflorescences (MEAN), No. Coleoptera/inflorescence (COLE), No. of fruits produced (FRUPROD), No. of fruits damaged by Nitidulid (DAMAGED).

	MEAN	COLE	FRUIPROD	DAMAGED
OFFER	-0.34*	-0.55**	-0.21	-0.45**
MEAN		0.35*	0.1	-0.18
COLE			0.21	0.24
FRUPROD				0.47**

* $P < 0.05$, ** $P < 0.01$

TABLE 3. Decomposition into direct and indirect effects of the correlations of distance among inflorescences and floral offer with number of *Cyclocephala* per inflorescence, number of developed fruits and number of damaged fruits. r^2 represents the variation explained by all the standardized variables.

Dependent variable	Independent variable	Direct effect	Indirect effect	Path coefficient	r^2
No. <i>Cyclocephala</i> /inflorescence					0.18
	Distance among inflorescences (m)	0.23	0	0.23	
	Floral offer (inflorescences/m ²)	-0.36	0	-0.36**	
No. of fruits initiated					0.32
	Distance among inflorescences (m)	0	0.13	0.13	
	Floral offer (inflorescences/m ²)	0	-0.20	-0.20	
	No. <i>Cyclocephala</i> /inflorescence	0.58	0	0.58***	
No. of damaged fruits					0.39
	Distance among inflorescences (m)	-0.35	-0.18	-0.53***	
	Floral offer (inflorescences/m ²)	-0.48	-0.36	-0.84***	
	No. <i>Cyclocephala</i> /inflorescence	0	-0.05	-0.05	
	No. of fruits initiated	0.37	0	0.37**	

** $P < 0.01$, *** $P < 0.001$

FIGURE LEGENDS

FIGURE 1. a. Diagram of the expected causal paths of interactions among floral offer, distance among inflorescences, number of *Cyclocephala* visits, fruits initiated and fruit predation by Nitidulid beetles. b. Path diagram for the number of visits by *Cyclocephala* per inflorescence and the number of fruits produced ($N = 56$). c. Path diagram for the number of fruits damaged by Nitidulid larvae ($N = 37$), a significant correlation between floral offer and distance among inflorescences is depicted in the model as a double-headed arrow, see appendix for correlation values. Positive effects are indicated by solid lines and negative effects by dashed lines. Legend gives the approximate magnitude of the direct effect coefficients indicated by line widths. See Table 3 for the exact values and significance levels of the variables. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

FIGURE 2. Number of inflorescences aborted after visits by different numbers of *Cyclocephala*. Letters group categories with similar abortion proportions ($P < 0.05$).

FIGURE 3. a. Number of fruits developed. b. Number of fruits undeveloped. c. Percent of fruits damaged by Nitidulid larvae. d. Number of fruits undamaged in inflorescences visited by different number of *Cyclocephala*. Letters group similar categories ($P < 0.05$). $N_{zero\ visits} = 19$, $N_{one\ visit} = 32$, $N_{two\ visits} = 16$, $N_{three\ or\ more\ visits} = 8$

Fig2

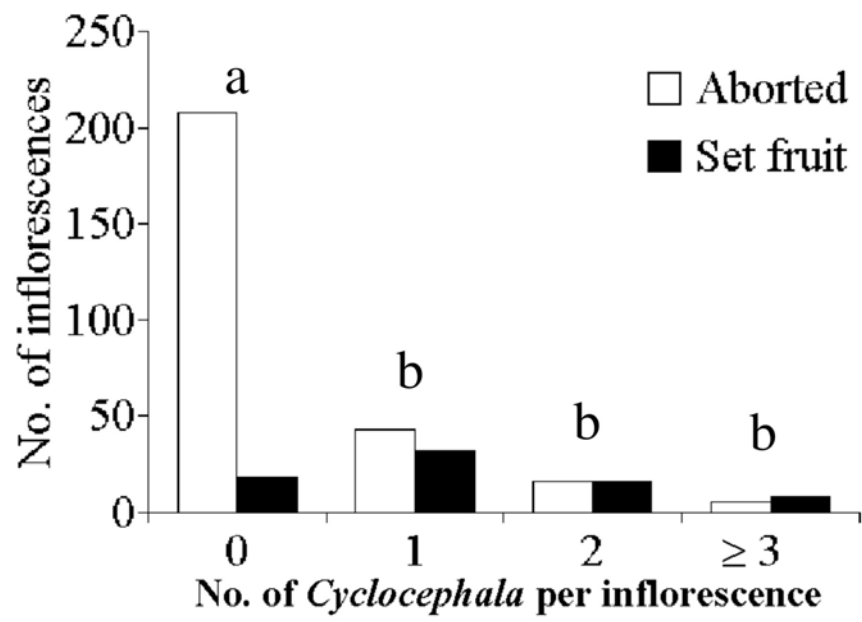


Fig3

